

Effect of water deficit on photosynthesis and yield in pea plants (*Pisum sativum* L.): A systematic review

Efecto del déficit hídrico en la fotosíntesis y el rendimiento de arveja (*Pisum sativum* L.): una revisión sistemática

Óscar Alvarado-Sanabria^{1*}, Diana Marcela Arias-Aguirre¹, Javier Álvarez-Herrera¹, and Luz Marina Melgarejo²

ABSTRACT

Water deficit caused by drought is common and extreme because of climate change. Pea (*Pisum sativum* L.) crops undergo water deficits depending on the sowing season and location. Some mechanisms of these plants in response to drought include stomatal closure and a reduction in photosynthetic capacity. However, as a consequence, such mechanisms disrupt reproductive processes such as flowering and pod filling, which diminishes the yield of plants. Although these mechanisms have been studied, there is no systematic review of the effect of water deficit on photosynthesis and yield in *P. sativum*. This review aimed to combine, summarize, and interpret the current knowledge on the impact of water deficiency on photosynthesis and yield in *P. sativum*. We carried out a systematic review using the databases Scopus, Web of Science, and ScienceDirect. Water deficit diminishes CO₂ assimilation by as much as 25%. This reduction is apparently due to stomatal closure (reduced by 28%) and, to a lesser degree, to variables such as the real efficiency of photosystem II (reduced by 15%). Water deficit reduces pea yield by 30% compared to control treatments (watered plants). The yield components most affected are the number of pods per plant, grains per plant, and pods per square meter. Few studies have assessed the relationship among yield, photosynthesis, and water status in *P. sativum* under water deficit conditions. Furthermore, significant knowledge gaps remain with respect to the combined effects of water deficit and interacting environmental factors (such as light intensity, temperature, and vapour pressure deficit) on the responses of field pea photosynthesis and yield. Additionally, there is a need to standardise methodologies for assessing water deficit status in both plant tissue and soil.

Keywords: drought, water stress, legumes, water potential, water use efficiency.

RESUMEN

El déficit hídrico causado por sequías es común y extremo debido al cambio climático. Los cultivos de arveja (*Pisum sativum* L.) sufren déficit hídrico, dependiendo de la época de siembra y la ubicación. Algunos mecanismos de estas plantas en respuesta a la sequía son el cierre de estomas y la reducción de la capacidad fotosintética. Sin embargo, como consecuencia, se alteran procesos reproductivos como la floración y el llenado de vainas, lo que disminuye el rendimiento de las plantas. Aunque estos mecanismos han sido estudiados, no existe una revisión sistemática del efecto del déficit hídrico en la fotosíntesis y el rendimiento en *P. sativum*. Esta revisión tuvo como objetivo combinar, resumir e interpretar el conocimiento actual sobre los efectos del déficit hídrico en la fotosíntesis y el rendimiento en *P. sativum*. Se realizó una revisión sistemática utilizando las bases de datos Scopus, Web of Science y ScienceDirect. El déficit hídrico disminuye la asimilación de CO₂ en 25%. Esta reducción se debe aparentemente al cierre estomático (reducido en un 28%) y, en menor medida, a variables como la eficiencia real del fotosistema II (reducida en un 15%). El déficit hídrico reduce el rendimiento de arveja en un 30% en comparación con los tratamientos de control (plantas regadas). Los componentes del rendimiento más afectados son número de vainas por planta, granos por planta y vainas por metro cuadrado. Pocos estudios han evaluado la relación entre el rendimiento, la fotosíntesis y el estado hídrico en *P. sativum* en condiciones de déficit hídrico. Adicionalmente, prevalecen varios vacíos del conocimiento acerca de los efectos combinados del déficit hídrico con otros factores ambientales (como intensidad lumínica, temperatura y déficit de presión de vapor) en la respuesta del rendimiento y la fotosíntesis de la arveja. También existe la necesidad de estandarizar metodologías para evaluar el déficit hídrico tanto en plantas como en el suelo.

Palabras clave: sequía, estrés hídrico, leguminosas, potencial hídrico, uso eficiente del agua.

Received for publication: February 11, 2025. Accepted for publication: August 9, 2025.

Doi: 10.15446/agron.colomb.v43n2.118788

¹ Grupo de Investigaciones Agrícolas GIA, Universidad Pedagógica y Tecnológica de Colombia, Tunja, Boyacá (Colombia).

² Universidad Nacional de Colombia, Facultad de Ciencias, Departamento de Biología, Laboratorio de Fisiología y Bioquímica Vegetal, Bogotá (Colombia).

* Corresponding author: ohalvarados@unal.edu.co



Introduction

Because of their nutritional attributes and capacity for nitrogen-fixing, legumes (such as *Pisum sativum* L.) have great potential to deal with the challenge of sustainably alimenting an increasing population (Soñta & Rekiel, 2020). The pea grain is rich in protein (200 g kg⁻¹) (Foyer *et al.*, 2016) and has health benefits that include antihypertensive, antioxidant, and anti-inflammatory properties. For humans, peas reduce cholesterol levels and regulate intestinal bacterial activity (Ge *et al.*, 2020). Additionally, pea crops have lower environmental impact because of lower nitrogen-fertilizer dependency (Soñta & Rekiel, 2020), reducing the carbon footprint. Despite health and environmental benefits, research on legumes such as peas has been less than on cereals (Soñta & Rekiel, 2020).

As a result of the increase in climate variability, the yield and quality of pea grains are affected by extreme climatic conditions (drought, flooding, and heat waves). Climate change in the tropics will affect agriculture more severely in developing countries (Lee *et al.*, 2023), particularly the yield of legumes (Foyer *et al.*, 2016; Soba *et al.*, 2022). Extreme conditions include water stress caused by drought, which affects the physiology and yield of peas (Nadeem *et al.*, 2019). This stress reduces photosynthetic rate, chlorophyll (chl) content, stomatal conductance, number of grains per pod, number of pods, and yield by up to 50% (Nadeem *et al.*, 2019; Ney *et al.*, 1994). These impacts are more severe when plants undergo water stress in the reproductive stage (Fougereux *et al.*, 1997; Henriët *et al.*, 2019).

Water stress effects on photosynthesis are well-studied in plants. These stress effects mainly are affected by stomatal closure that prevents CO₂ entry into the substomatal cavity and, thus, the entrance of CO₂ into mesophyll cells (Flexas *et al.*, 2012). Depending on the intensity, water stress also affects the activity and synthesis of photosynthetic enzymes and chlorophyll (Analín *et al.*, 2023; Chaves *et al.*, 2009). Couchoud *et al.* (2020) demonstrate that photosynthesis in peas mainly decreases from stomatal closure, and the decrease is less severe in the Afila cultivar.

Water stress diminishes yield not only because of its effects on leaves but also because of its effects on the reproductive organs. Water stress triggers flower fall, stigma dehydration, and pollen infertility (Soba *et al.*, 2022; Suzuki *et al.*, 2014). Moreover, water stress decreases the number of reproductive nodes of the pea plants, the average grain weight, and the number of pods per plant, and increases the number of aborted seeds (Henriët *et al.*, 2019).

Gas exchange variables such as CO₂ assimilation and stomatal conductance could be used to predict yield and, directly or indirectly, to evaluate the water status of plants and crops (Furbank *et al.*, 2019). Although the relationship between yield and leaf photosynthesis is not straightforward due to factors such as canopy, genotype, transpiration, and environmental conditions, under specific circumstances, leaf photosynthesis has been used to predict mass accumulation in crops (Wu *et al.*, 2019). Knowing the photosynthesis-yield relationship with a water deficit would help select management alternatives, detect deficits earlier, and predict pea yields.

This study aimed to summarize and interpret current knowledge about water deficit effects on yield and photosynthesis in *Pisum sativum*. Specifically, we addressed the following questions: Which factors have been evaluated in water deficits? Which methodological approaches have been used? Which yield component or photosynthesis-related process is most affected by water deficits? And what is the effect of water deficits on yield and photosynthesis in pea plants? We hypothesize the following: Enough information exists addressing the impact of drought stress on photosynthesis and yield. Furthermore, we expect that canopy CO₂ assimilation is positively correlated with yield but not with leaf CO₂ assimilation. Finally, yield components such as grains per area or pods per area are positively related to yield.

Materials and methods

Web of Science, Scopus, and ScienceDirect databases were searched to identify original studies on drought, irrigation, or water stress effects on yield and photosynthesis in peas (*Pisum sativum* L.). The search terms were as follows: drought, water stress, aridity, and irrigation. For yield and photosynthesis, the terms were these: yield, productivity, photosynthesis, and gas exchange (Tab. 1). The search was broad in order to obtain a significant number of articles related to the subject.

Literature such as reviews, abstracts, theses, or meta-analyses was excluded. During screening, studies on drought, irrigation, or water stress in *P. sativum* organs, plants, or crops were selected. Studies whose experimental unit was organelles or studies that were carried out on different species were omitted. Finally, studies where drought, irrigation, or water stress treatment were not clearly defined were excluded (Fig. 1).

TABLE 1. Databases, searching terms, search date, and number of publications.

Database	Search string	Search terms	N°	Search date
Scopus	Title-Abstract-Key words	(<i>Pisum sativum</i> OR pea OR <i>P. sativum</i>) AND (drought OR water stress OR aridity OR water scarcity OR irrigation) AND (yield OR productivity OR photosynthesis OR chlorophyll OR gas exchange OR stomata OR carbon dioxide fixation OR photosystem OR photochemistry OR radiation use efficiency)	805	09/01/2024
Web of Science	Topic (TS)	(<i>Pisum sativum</i> OR pea OR <i>P. sativum</i>) AND TS= (drought OR water stress OR aridity OR water scarcity OR irrigation) AND TS= (yield OR productivity OR photosynthesis OR chlorophyll OR gas exchange OR stomata OR carbon dioxide fixation OR photosystem OR photochemistry OR radiation use efficiency)	880	09/01/2024
ScienceDirect	Title, Abstract, or Author-specified keywords	(<i>Pisum sativum</i>) AND (drought OR water stress OR irrigation) AND (yield OR photosynthesis OR chlorophyll OR radiation use efficiency)	50	09/01/2024
Total			1735	

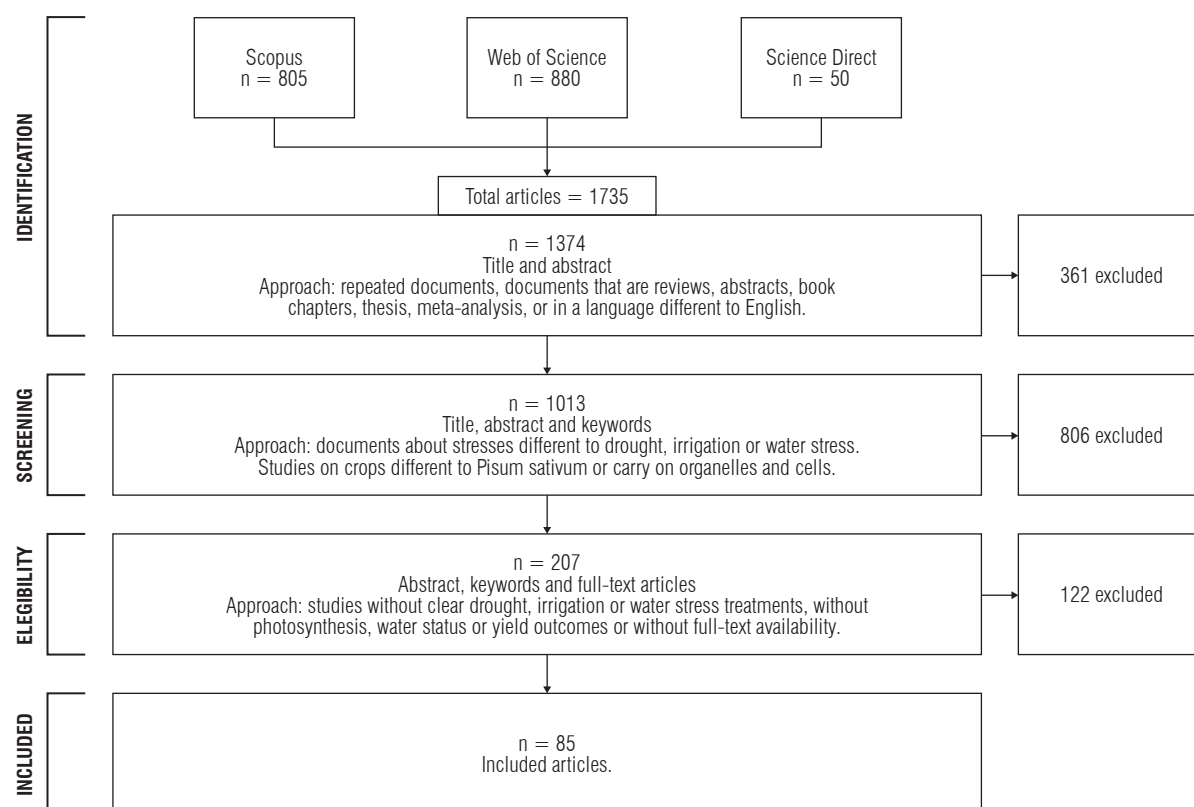


FIGURE 1. Flow diagram of the identification, screening, and selection of studies related to water stress on the yield and photosynthesis of *Pisum sativum* L.

Variables related to yield, yield components, growth, water status, and gas exchange were extracted from the selected studies. From each selected article, both the response variables and other treatment variables (e.g., genotype, temperature, phenological stage, etc.) were entered into an Excel file. The absolute values of each variable reported in the literature were extracted. Finally, the relative increase or decrease from water or irrigation deficit treatments compared to the control treatments (in which the plants were well irrigated) were calculated. When the authors reported the results on bar or point plots, the plugin

figure calibration of ImageJ was used (available at http://www.astro.physik.uni-goettingen.de/~hessman/ImageJ/Figure_Calibration/) to obtain numeric data.

To summarize, the effect of water or irrigation deficit on photosynthesis and yield, boxplots of each treatment combination were plotted. The boxplots represented the relative change of the treatments in comparison to the control treatment. In each boxplot, minimally the data from two studies were plotted. Plots were made using the ggplot2 and ComplexHeatmap packages in R software V. 4.0.5.

Results and discussion

Common factors and variables

Most of the studies assessed the interaction between water deficit and sowing date, followed by water deficit versus genotype, water deficit versus duration, and water deficit versus phenology (Fig. 2). The remaining factors were evaluated by fewer than five studies. They were related to environmental conditions (temperature, light, CO₂), chemical substances, fertilizers (organic matter, phosphorus, potassium, nitrogen, and sulfur), timing of the measurements, nanoparticles, and osmolytes (such as proline and glycine betaine).

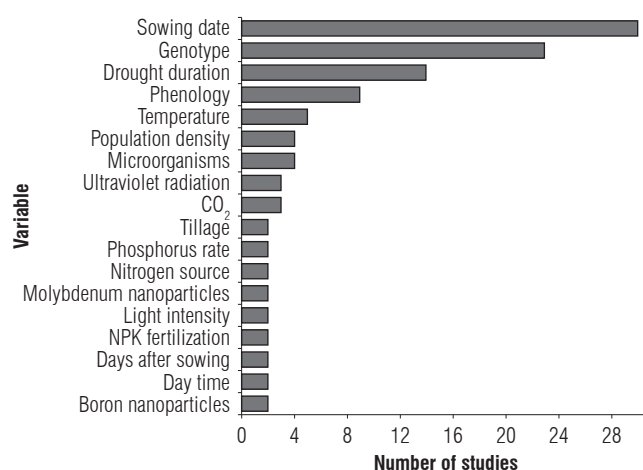


FIGURE 2. Frequency of evaluated factors (more than one study). Evaluated factors were evaluated along with water deficit in studies of water or irrigation deficit on *Pisum sativum*.

The interaction of water deficit with other environmental variables, represented by sowing dates and water-deficit duration, is typical in the field and significantly impacts pea crop yield. For instance, Bueckert *et al.* (2015) find that the sowing date substantially affects the yield and duration of the reproductive phase of pea plants. They also show a positive correlation between yield and precipitation and a negative correlation between the duration of the reproductive phase and the mean daily maximum temperature.

Breeding to obtain genotypes tolerant to water stress is a common strategy, but it demands time and resources. However, this strategy has remarkable benefits: Rodríguez-Maribona *et al.* (1992) report that, for the ‘Desso’ cultivar undergoing a water deficit, yield decreases around 40%, while, for the ‘Fride’ cultivar, the decrease is only 10%. ‘Fride’ cultivar presents a mechanism of greater efficiency in water use or its conservation in the face of drought events. Another example is reported by Nemeskéri *et al.*

(2015), who demonstrate that mild and early-ripening cultivars are less susceptible to water deficit than late-ripening cultivars.

The duration of water withholding determines the intensity of water stress in plants. Still, without soil and plant measurements, it is difficult to know the intensity of the water stress. Some authors (Embiale *et al.*, 2016) only report the withholding duration but not the water potential of plants or soils. However, others report the water potential of both plants and soil, while some report it only for soil (Al-Quraan *et al.*, 2021; Frechilla *et al.*, 2000; Lepore *et al.*, 1998).

Some factors are rarely measured yet are essential due to their practicality or their interaction with water stress. For example, fertilizers are practical and frequently used. Still, only one study evaluates both phosphorus and potassium fertilization on pea plants undergoing irrigation deficit (Carter & Stoker, 1988), yielding no benefit. However, Jin *et al.* (2015) find that fertilization with phosphorus increases the WUE (water use efficiency) and growth of pea plants under drought conditions, and Abd El-Mageed *et al.* (2017) observe the same pattern with potassium fertilization in soybeans.

Other factors such as temperature, light or UV radiation, and water deficit might coincide and be more severe and common under a climate change scenario (Lee *et al.*, 2023; Zandalinas *et al.*, 2021). For instance, Zandalinas *et al.* (2021) show that the response of *Arabidopsis thaliana* to high light, heat stress, osmotic stress, and oxidative stress is different when plants are subjected to each stress individually compared to when such stresses are combined. The same authors find that the combination of stresses reduces the survival and growth of plants than do each stress individually. This underscores the necessity of researching the effect of stress combinations on the physiology and yield of pea crops.

Having selected the most common variables related to yield, photosynthesis, and water status, the majority of the studies evaluated yield (41) and total dry mass (24) (Fig. 3). On the other hand, 24 studies evaluated stomatal conductance, 21 looked at CO₂ assimilation and only 23 measured relative water content (RWC) or leaf water potential (Fig. 3).

It is difficult to establish the relationship between yield, water status, and photosynthesis in pea plants undergoing drought because few studies have simultaneously assessed these processes. Only five of the selected studies evaluated yield and stomatal conductance simultaneously, and only

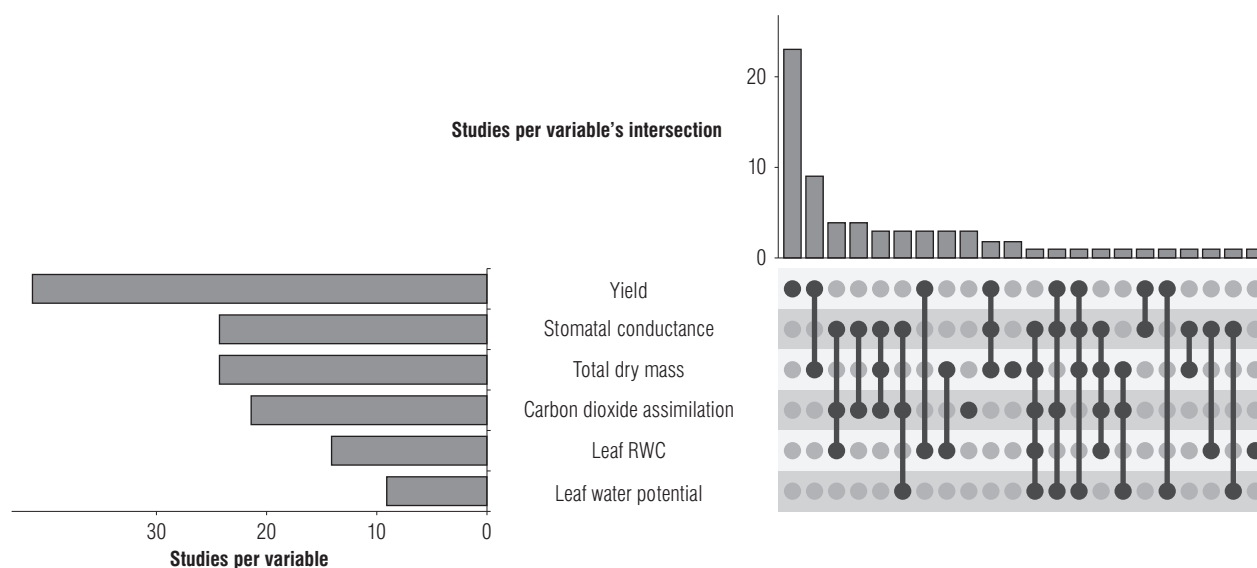


FIGURE 3. UpSet plot of the most common variables related to yield, photosynthesis, and water status of pea plants undergoing water deficit. Studies per variable indicate the number of articles in which the variables were measured. Each point indicates in which studies the variable was measured; when two variables (two points) are linked by a line, both variables were measured in the same study. RWC – relative water content.

one assessed yield and CO₂ assimilation (Fig. 3). Additionally, few studies evaluated both yield and water status (only six measured leaf water potential or RWC and yield) (Fig. 3). Currently, the diagnosis of water stress is based on the spectral response of plants and crops, which is related to their photosynthetic response and water status (Beebe *et al.*, 2013; Furbank *et al.*, 2019). The limited knowledge of the relationship between yield, photosynthesis, and water status makes it difficult to use technologies to recognize water stress earlier.

Because photosynthesis is the primary source of dry mass and yield of crops, determining the relationship between yield and photosynthesis would benefit the prediction of yields beforehand (Honda *et al.*, 2021; Wu *et al.*, 2019). The relationship between leaf photosynthesis and crop yield is not straightforward because other factors, such as canopy architecture, nitrogen dynamics, phenology, and crop management, also play a role (Wu *et al.*, 2019). However, considering these factors allows us to find the best match between leaf photosynthesis and yield. For example, Honda *et al.* (2021) reveal a strong relationship between the photosynthesis of the flag leaf and the yield of rice plants during the heading stage.

Effect of water deficit on water status

All studies assessed irrigation or water deficit in pea plants. Still, only 23 of the 85 studies measured a variable related to water status in plants (Fig. 3). The most common variables were leaf RWC (13 studies) and leaf water potential

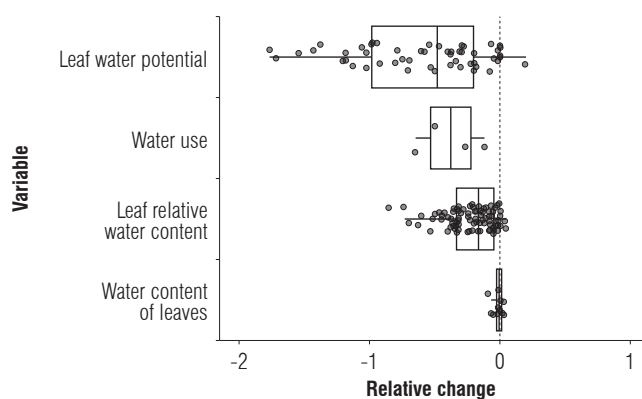


FIGURE 4. Relative changes from water deficit on water status variables in *P. sativum* L. Each boxplot represents the relative change of 34 cases (represented by each point) in 27 studies. Boxes represent 50% of the observations (relative change of each treatment different from control), and whiskers represent the minimum and maximum value or 1.5 times the interquartile range.

(7 studies) (Fig. 3). Meanwhile, other water status variables were measured in five articles each. In general, leaf water potential was more affected (50%) by water deficit than other variables (Fig. 4).

The main variables used as indicators of water stress were leaf water potential and leaf RWC. Generally, leaf water potential is more variable and sensitive to water deficit than leaf RWC (Fig. 4). Both variables indicate the water status of plants. Higher RWC in plants undergoing water deficit is related to the osmotic adjustment mechanism, where the accumulation of solutes maintains the water content.

The fact that leaf water potential has been more sensitive than leaf RWC probably indicates an osmotic adjustment in pea plants (Turner *et al.*, 2007; Turner, 2018). However, only Nogués *et al.* (1998) measure both variables. They did not discuss whether there was an osmotic adjustment, indicating a gap in knowledge on osmotic adjustment in peas.

Water deficit effect on photosynthesis

Although stomatal limitation is a mechanism to conserve water in plants, it is also the leading cause of a reduction in CO₂ assimilation in plants undergoing drought or irrigation deficit. Only three studies report simultaneously the internal CO₂ concentration and stomatal limitation. This stomatal limitation should have been reported by the authors because devices used to measure CO₂ assimilation and stomatal conductance (measured in 19 and 17 studies, respectively) also measure ambient and internal CO₂ concentration.

In our study, chlorophyll showed contrasting behavior: despite the minor changes in the total chlorophyll of plants undergoing drought, chlorophyll a and b decreased by approximately 30% when plants suffered a water deficit (Fig. 5). CO₂ assimilation was reduced by 25% due to the water deficit. Gas diffusion variables such as stomatal conductance, internal CO₂, and transpiration were similarly affected (~28%), while some photochemistry variables such as *Fv/Fm* (Maximum quantum efficiency of PSII photochemistry), Φ PSII (PSII operating efficiency), qP (Photochemical quenching), and NPQ (Non-photochemical quenching) were affected to a lesser extent (15%) (Fig. 5). Generally, water deficits slightly increased the water use efficiency (WUE) when measured at the leaf level ($\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$) but not at the crop level (Fig. 5).

Gas exchange and chlorophyll content variables are more frequently measured than variables related to photochemistry (e.g. Φ PSII, Jmax, OJIP analysis variables). Regarding the variability of photosynthetic variables between studies, *Fv/Fm* was much less variable than CO₂ assimilation, transpiration, and stomatal conductance (Fig. 5). The low variability of *Fv/Fm* indicated that the plant uses biochemical mechanisms to protect the photosynthetic apparatus. Depending on the intensity of the stress, if it is moderate, dynamic photoinhibition occurs, and PSII recovery happens through the turnover of the D1 protein (Pandey *et al.*, 2023). However, if the stress is severe, there would be damage at the PSII level, leading to a decrease in the maximum potential photochemical efficiency of photosystem II and consequently a decrease in the operational performance of the photosystem (Pandey *et al.*, 2023).

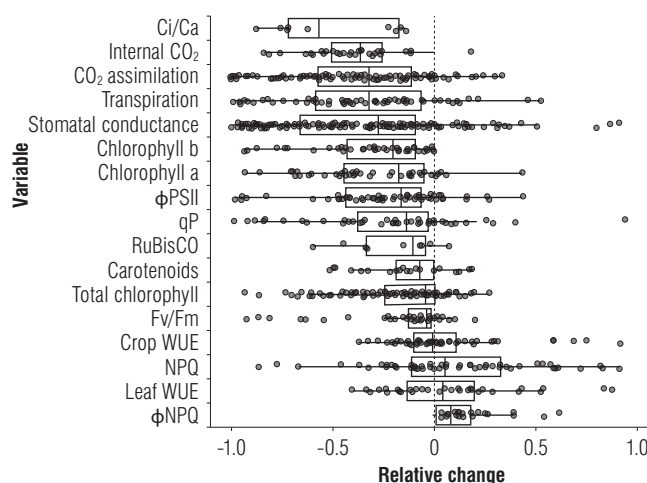


FIGURE 5. Relative changes from water deficits in photosynthesis-related variables in *P. sativum* L. Each boxplot represented the relative change of 173 cases (represented by each point) from 35 studies. Boxes represent 50% of the observations (relative change of each treatment different from the control), and whiskers represent the minimum and maximum value or 1.5 times the interquartile range. Ci – internal CO₂ concentration, Ca – ambient CO₂ concentration, Φ PSII – actual quantum efficiency of PSII, qP – photochemical quenching, *Fv/Fm* – maximum quantum efficiency of PSII, NPQ – non-photochemical quenching, WUE – water use efficiency.

The photosynthetic response of pea plants follows a similar pattern to other crops: Initially, there is stomatal limitation caused by a considerable reduction in stomatal conductance, followed by a decrease in internal CO₂ concentration and CO₂ assimilation, and finally a slight reduction in Φ PSII, *Fv/Fm* and chlorophyll content (Fig. 5) (Flexas *et al.*, 2012; Sun *et al.*, 2020). According to Flexas *et al.* (2012), the first response of plants to water deficits is stomatal closure, which occurs under mild and moderate water deficits. On the other hand, under severe water stress, variables such as chlorophyll content or integrity of photosynthetic enzymes are disturbed (non-stomatal or biochemical limitation). Most studies have assessed the effect of mild or moderate stress on pea plants, but few have assessed severe stress.

Although the first response of plants to water stress is closing their stomata, when the stress is severe or long-lasting, biochemical damage occurs (Flexas *et al.*, 2012; Sun *et al.*, 2020). During water stress, reactive oxygen species are accumulated, leading to oxidative damage that causes membrane damage and turnover of the D1 protein (Wang *et al.*, 2018). This protein is part of PSII; thus, its turnover decreases the activity of PSII (Wang *et al.*, 2018). Additionally, chlorophyll biosynthesis declines because of the decrease of enzymes responsible for the synthesis of chlorophyll intermediates such as protoporphyrinogen IX oxidase, Mg-chelatase, and protochlorophyllide oxidoreductase (Dalal & Tripathy, 2012).

Despite the reduction of the contents of chlorophyll a and b, there was no such reduction for total chlorophyll content (Fig. 5). The reason might be the scale used to measure each parameter: the contents of chlorophyll a and b were measured in the laboratory, in most cases per unit mass; whereas, total chlorophyll content was calculated per unit area and, in half of the cases, with a SPAD chlorophyll meter. Although the chlorophyll meter is a non-destructive method and is helpful in the field, it is less sensitive to fluctuations in chlorophyll content than destructive measurements (Parry *et al.*, 2014).

Water deficit effect on yield

In general, yield was reduced by 30% under water deficit compared to the control treatments. However, the yield ranged from 20% to 80% less than the control treatment. The yield components most affected by water deficit were pods and grains per plant; meanwhile, variables such as pod dry mass, harvest index, 1,000 seed weight, and the average mass of one grain were slightly affected by water deficit (Fig. 6).

Variables such as seed yield, grains per plant, pods per plant, and grains per pod were frequently measured. In contrast, others, such as aborted grains per pod, flowers per plant, and grains per square meter, were rarely measured. The variability of the more common variables, seed yield, and grains per plant was higher among studies than grains per pod, harvest index, and 1,000-seed mass (Fig. 6).

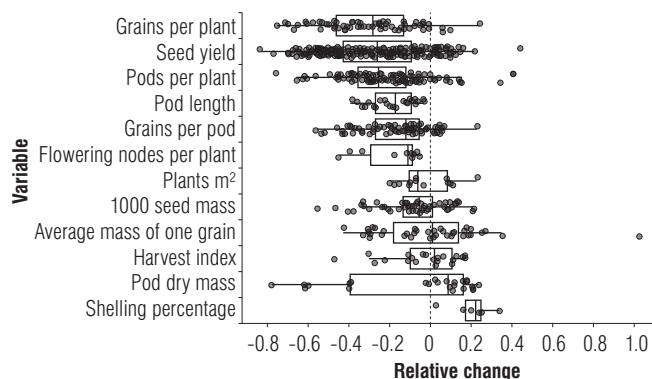


FIGURE 6. Relative changes of yield-related variables in *P. sativum* L. from water deficit. Each boxplot represents the relative change of 758 cases (represented by each point) from 82 studies. Boxes represent 50% of the observations (relative change of each treatment different from control), and whiskers represent the minimum and maximum value or 1.5 times the interquartile range.

Yield, represented as the grain mass produced per unit area or per plant, was reduced by water stress, with a reduction of 30% compared to control treatments (Fig. 6). Grains per plant showed the most similar pattern to yield,

with comparable reductions and variability. Several studies report the relationship between water deficit and the reduction of reproductive structures such as flowers and pods, mainly when the water deficit occurs during flowering or pod-filling stages (Fougereux *et al.*, 1997; Martin & Jamieson, 1996). This explanation aligns with the fact that most studies measuring yield assessed plants undergoing water deficit during their entire cycle or critical stages such as flowering and pod filling.

Variables related to the number of grains per plant or area were more affected by water deficits than variables related to grain size. Variables related to grain size, such as the mass of 1,000 seeds or the average mass of one grain, are conservative compared to variables associated with the number of grains, such as grains per pod or pods per plant (Fougereux *et al.*, 1997; Jeuffroy *et al.*, 2010). Grain size is usually affected if the water stress occurs only during the pod-filling stage (Jeuffroy *et al.*, 2010; Munier-Jolain, 2010).

Although they were rarely measured, variables such as flowers per plant, reproductive nodes per plant, or number of nodes with pods can indicate if the water deficit occurred during flowering (Farooq *et al.*, 2017). This is because the number of flowers, pollen viability, and pistil function are severely affected by terminal droughts, which reduce the number of pods (Fang *et al.*, 2010). If the drought event occurred between flowering and the final stage of seed abortion, the primary affected variable would be the number of grains per pod. Therefore, if a study aims to elucidate the timing of the stress and the process concerned, it is essential to consider variables related to both reproductive structures and yield, such as the number of grains (Farooq *et al.*, 2017; Lecoer, 2010).

In some studies, seed yield was not measured, but biomass yield was. Water deficit sharply decreased total and shoot dry mass, while leaf area and root dry mass were less affected. Even the relative growth rate (RGR) of roots was higher in some plants that suffered a water deficit compared to the control treatments (Fig. 7).

Growth is the first to be affected and one of the most susceptible processes to water deficit (Fig. 7). The shoot growth rate was more affected than root growth because roots can grow at a lower water potential than leaves. Their osmotic adjustment occurs faster than in leaves (Hsiao & Xu, 2000). In both cases, the cell expansion process involves the absorption of water and the weakening of the cell wall, and both methods are reduced by water deficits (Farooq *et al.*, 2009). Additionally, the dry mass of a plant

depends mainly on photosynthesis; thus, any decline in the photosynthetic process diminishes CO₂ assimilation and carbohydrate synthesis.

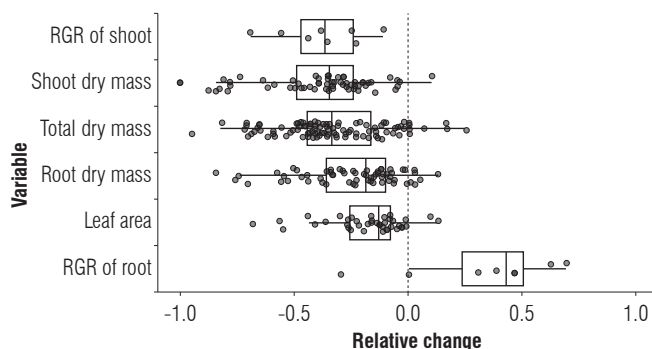


FIGURE 7. Relative changes from water or irrigation deficit on growth-related variables in *P. sativum* L. Each boxplot represents the relative change of 94 cases (represented by each point) from 33 studies. Boxes represent 50% of the observations (relative change of each treatment different from control), and whiskers represent the minimum and maximum value or 1.5 times the interquartile range. RGR – relative growth rate.

The reduction of growth points and sinks (such as young shoots and pods as in Figures 6 and 7) diminishes the sink strength of the plants. This decrease may induce feedback inhibition, thereby reducing the photosynthetic rate. In other grain crops, such as barley, for instance, the reduction of grain number through spike trimming results in sugar accumulation in stems and leaves, which in turn suppresses leaf photosynthesis (Serrago *et al.*, 2013). These findings highlight the importance of assessing source–sink dynamics and photosynthetic performance under drought stress conditions.

Limits and challenges

Some methodological problems prevent the standardization or complete analysis of some variables. Several authors did not report the stage or moisture content at which grains were harvested; this could affect the estimation of water deficit effects on yield. Many authors reported the days on which the measurements were taken, but not the phenological stage of the plants, which hinders the relationship between phenology and water deficit.

Variables used as indicators of drought or deficit irrigation should be unified to facilitate comparisons between studies. Some studies used only the days of withholding water as a drought indicator. In contrast, other studies used the soil and leaf water potential. Authors should at least indicate water stress with a measure of soil moisture, but ideally with

a measure of soil and plant water potential, as well as the depth at which the soil potential or moisture was measured.

Because this study evaluated articles whose drought and control treatments were well established, articles whose objective was to assess sowing dates with different weather conditions were not considered. Additionally, due to differences in levels of water deficits and units, the difference between water deficit levels was not established. Still, they were categorized between extremes: with or without a water deficit.

During the article screening, several studies examining the salt effect on pea plants or crops were identified. These studies were not considered in this review. Still, a future review of this topic could expand knowledge on osmotic stress in peas. Osmotic stress affects plants undergoing both a water deficit and salinity because both stresses reduce the water potential of the soil solution (Zhao *et al.*, 2020). Salinity reduces the water potential due to the accumulation of salts. In contrast, water deficits decrease the water available in the soil, thus lowering the water potential of the soil solution. Additionally, both stresses share several genetic and enzymatic responses (Forni *et al.*, 2017).

There is a lack of information on the relationship between yield, water status, and photosynthesis in pea plants. Although the interaction between water deficits and other factors has been evaluated, other essential factors such as light, fertilization, soil type, chemical primers, microorganisms, and population density have rarely been assessed. Environmental variables such as soil type, vapor pressure deficit, or light commonly interact with water deficits under field conditions. At the same time, fertilization, microorganisms, and chemical primers might alleviate water deficits.

Conclusions

Water deficit significantly reduces CO₂ assimilation of pea plants due to substantial stomatal closure and slight photochemical impairment. Contrarily, non-photochemical quenching, and water use efficiency rise moderately as strategies to quench energy excess and avoid water loss (Fig. 8). Pea yield appears to diminish because of reductions in grains per square meter, resulting from a lower number of pods per plant, grains per pod, or flowers per plant during the reproductive stage. Similarly, most growth processes decrease, except for the relative growth of the root.

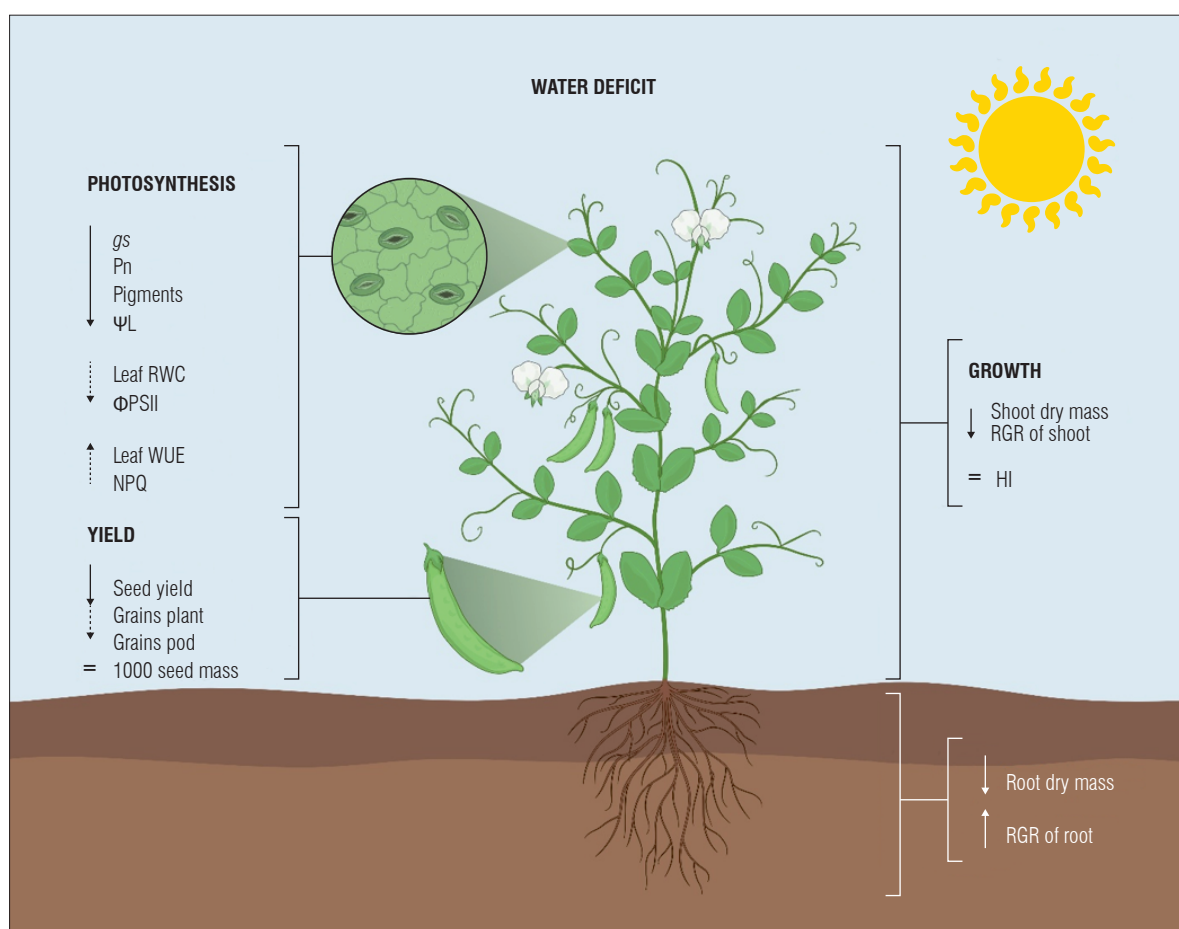


FIGURE 8. The main photosynthetic and yield processes are affected by water deficit. *gs* –Stomatal conductance; *Pn* – CO_2 assimilation; Ψ_L – leaf water potential; RWC –relative water content; ΦPSII –photosystem II maximum real efficiency; WUE –water use efficiency; HI –harvest index; RGR –relative growth rate. Solid and dashed arrows mean a strong and a moderate impact on each process. Created in BioRender. <https://BioRender.com/x1ioacv>.

Acknowledgments

The authors would like to thank the Universidad Nacional de Colombia for funding this study within the framework of the doctoral thesis project “Uso del *cis*-priming por déficit hídrico como estrategia para aliviar el efecto del déficit hídrico en la fotosíntesis y el rendimiento de arveja (*Pisum sativum* L.)”. Additionally we would like to thank the Universidad Pedagógica y Tecnológica de Colombia and Ministerio de Ciencia, Tecnología e Innovación-MIN-CIENCIAS for funding the project “Determinar el efecto interactivo del estrés hídrico y la etapa fenológica sobre el crecimiento, rendimiento y la fotosíntesis de la planta de arveja” CD 890-82276 – CT ICETEX 2023-0787.

Conflict of interest statement

The authors declare that there is no conflict of interests regarding the publication of this article.

Author’s contributions

OHAS, DMAA, JAH, and LMM contributed to the study’s conceptualization and design. Data curation, formal analysis, research, and writing of the original draft were performed by OHAS. DMAA, JAH, and LMM carried out the critical review, commentary, and revision of the manuscript. All authors have read and approved the final version of the manuscript.

Literature cited

- Abd El-Mageed, T. A., El-Sherif, A. M. A., Ali, M. M., & Abd El-Wahed, M. H. (2017). Combined effect of deficit irrigation and potassium fertilizer on physiological response, plant water status, and yield of soybean in calcareous soil. *Archives of Agronomy and Soil Science*, 63(6), 827–840. <https://doi.org/10.1080/03650340.2016.1240363>
- Al-Quraan, N. A., Al-Ajlouni, Z. I., & Qawasma, N. F. (2021). Physiological and biochemical characterization of the GABA shunt

- pathway in pea (*Pisum sativum* L.) seedlings under drought stress. *Horticulturae*, 7(6), Article 125. <https://doi.org/10.3390/horticulturae7060125>
- Analín, B., Bakka, K., & Challabathula, D. (2023). Exacerbation of drought-induced physiological and biochemical changes in leaves of *Pisum sativum* upon restriction of COX and AOX pathways of mitochondrial oxidative electron transport. *Journal of Biosciences*, 49(1), Article 5. <https://doi.org/10.1007/s12038-023-00380-0>
- Beebe, S. E., Rao, I. M., Blair, M. W., & Acosta-Gallegos, J. A. (2013). Phenotyping common beans for adaptation to drought. *Frontiers in Physiology*, 4, Article 35. <https://doi.org/10.3389/fphys.2013.00035>
- Bueckert, R. A., Wagenhoffer, S., Hnatowich, G., & Warkentin, T. D. (2015). Effect of heat and precipitation on pea yield and reproductive performance in the field. *Canadian Journal of Plant Science*, 95(4), 629–639. <https://doi.org/10.4141/cjps-2014-342>
- Carter, K. E., & Stoker, R. (1988). Responses of non-irrigated and irrigated garden peas to phosphorus and potassium on Lismore stony silt loam. *New Zealand Journal of Experimental Agriculture*, 16(1), 11–15. <https://doi.org/10.1080/03015521.1988.10425608>
- Chaves, M. M., Flexas, J., & Pinheiro, C. (2009). Photosynthesis under drought and salt stress: Regulation mechanisms from whole plant to cell. *Annals of Botany*, 103(4), 551–560. <https://doi.org/10.1093/aob/mcn125>
- Couchoud, M., Salon, C., Girodet, S., Jeudy, C., Vernoud, V., & Prudent, M. (2020). Pea efficiency of post-drought recovery relies on the strategy to fine-tune nitrogen nutrition. *Frontiers in Plant Science*, 11, Article 204. <https://doi.org/10.3389/fpls.2020.00204>
- Dalal, V. K., & Tripathy, B. C. (2012). Modulation of chlorophyll biosynthesis by water stress in rice seedlings during chloroplast biogenesis. *Plant, Cell and Environment*, 35(9), 1685–1703. <https://doi.org/10.1111/j.1365-3040.2012.02520.x>
- Embale, A., Hussein, M., Husen, A., Sahile, S., & Mohammed, K. (2016). Differential sensitivity of *Pisum sativum* L. cultivars to water-deficit stress: Changes in growth, water status, chlorophyll fluorescence, and gas exchange attributes. *Journal of Agronomy*, 15(2), 45–57. <https://doi.org/10.3923/ja.2016.45.57>
- Fang, X., Turner, N. C., Yan, G., Li, F., & Siddique, K. H. M. (2010). Flower numbers, pod production, pollen viability, and pistil function are reduced, and flower and pod abortion increased in chickpea (*Cicer arietinum* L.) under terminal drought. *Journal of Experimental Botany*, 61(2), 335–345. <https://doi.org/10.1093/jxb/erp307>
- Farooq, M., Gogoi, N., Barthakur, S., Baroowa, B., Bharadwaj, N., Alghamdi, S. S., & Siddique, K. H. M. (2017). Drought stress in grain legumes during reproduction and grain filling. *Journal of Agronomy and Crop Science*, 203(2), 81–102. <https://doi.org/10.1111/jac.12169>
- Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., & Basra, S. M. A. (2009). Plant drought stress: effects, mechanisms and management. *Agronomy for Sustainable Development*, 29(1), 185–212. <https://doi.org/10.1051/agro:2008021>
- Flexas, J., Galle, A., Galmés, J., Ribas-Carbo, M., & Medrano, H. (2012). The response of photosynthesis to soil water stress. In R. Aroca (Ed.), *Plant responses to drought stress: From morphological to molecular features* (pp. 129–144). Springer Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-32653-0_5
- Fougereux, J.-A., Doré, T., Ladonne, F., & Fleury, A. (1997). Water stress during reproductive stages affects seed quality and yield of pea (*Pisum sativum* L.). *Crop Science*, 37(4), 1247–1252. <https://doi.org/10.2135/cropsci1997.0011183X003700040036x>
- Foyer, C. H., Lam, H. M., Nguyen, H. T., Siddique, K. H. M., Varshney, R. K., Colmer, T. D., Cowling, W., Bramley, H., Mori, T. A., Hodgson, J. M., Cooper, J. W., Miller, A. J., Kunert, K., Vorster, J., Cullis, C., Ozga, J. A., Wahlqvist, M. L., Liang, Y., Shou, H., ..., & Considine, M. J. (2016). Neglecting legumes has compromised human health and sustainable food production. *Nature Plants*, 2(8), Article 16112. <https://doi.org/10.1038/NPLANTS.2016.112>
- Frechilla, S., González, E. M., Royuela, M., Minchin, F. R., Aparicio-Tejo, P. M., & Arrese-Igor, C. (2000). Source of nitrogen nutrition (nitrogen fixation or nitrate assimilation) is a major factor involved in pea response to moderate water stress. *Journal of Plant Physiology*, 157(6), 609–617. [https://doi.org/10.1016/S0176-1617\(00\)80003-6](https://doi.org/10.1016/S0176-1617(00)80003-6)
- Furbank, R. T., Jimenez-Berni, J. A., George-Jaeggli, B., Potgieter, A. B., & Deery, D. M. (2019). Field crop phenomics: enabling breeding for radiation use efficiency and biomass in cereal crops. *New Phytologist*, 223(4), 1714–1727. <https://doi.org/10.1111/nph.15817>
- Ge, J., Sun, C. X., Corke, H., Gul, K., Gan, R. Y., & Fang, Y. (2020). The health benefits, functional properties, modifications, and applications of pea (*Pisum sativum* L.) protein: Current status, challenges, and perspectives. *Comprehensive Reviews in Food Science and Food Safety*, 19(4), 1835–1876. <https://doi.org/10.1111/1541-4337.12573>
- Henriet, C., Aimé, D., Térézol, M., Kilandamoko, A., Rossin, N., Combes-Soia, L., Labas, V., Serre, R.-F., Prudent, M., Kreplak, J., Vernoud, V., & Gallardo, K. (2019). Water stress combined with sulfur deficiency in pea affects yield components but mitigates the effect of deficiency on seed globulin composition. *Journal of Experimental Botany*, 70(16), 4287–4303. <https://doi.org/10.1093/jxb/erz114>
- Honda, S., Ohkubo, S., San, N. S., Nakkasame, A., Tomisawa, K., Katsura, K., Ookawa, T., Nagano, A. J., & Adachi, S. (2021). Maintaining higher leaf photosynthesis after the heading stage could promote biomass accumulation in rice. *Scientific Reports*, 11(1), Article 7579. <https://doi.org/10.1038/s41598-021-86983-9>
- Hsiao, T. C., & Xu, L. K. (2000). Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport. *Journal of Experimental Botany*, 51(350), 1595–1616. <https://doi.org/10.1093/jexbot/51.350.1595>
- Jeuffroy, M.-H., Lecoœur, J., & Roche, R. (2010). The seed number. In N. Munier-Jolain, V. Biarnes, I. Chaillat, J. Lecoœur, & M.-H. Jeuffroy (Eds.), *Physiology of the pea crop* (pp. 104–109). CRC Press. <https://www.taylorfrancis.com/chapters/edit/10.1201/b10504-6/seed-number-marie-h%C3%A9lie-jeuffroy-j%C3%A9lie-lecoeur-romain-roche?context=ubx&refId=932a093a-1c4e-463d-b6c0-1d22111fad9f>

- Jin, J., Lauricella, D., Armstrong, R., Sale, P., & Tang, C. (2015). Phosphorus application and elevated CO₂ enhance drought tolerance in field pea grown in a phosphorus-deficient vertisol. *Annals of Botany*, 116(6), 975–985. <https://doi.org/10.1093/aob/mcu209>
- Lecoeur, J. (2010). Vegetative development: The morphogenesis of plant organs. In N. Munier-Jolain, V. Biarnès, I. Chaillet, J. Lecoeur, & M.-H. Jeuffroy (Eds.), *Physiology of the pea crop* (pp. 3–43). CRC Press. <https://www.taylorfrancis.com/chapters/edit/10.1201/b10504-2/vegetative-development-morphogenesis-plant-organs-lecoeur?context=ubx&refId=fb9bfba7-40ad-414a-9c9c-e2cc4ed6286f>
- Lee, H., Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P., Trisos, C., Romero, J., Aldunce, P., & Barret, K. (2023). IPCC, 2023: Climate Change 2023: Synthesis Report, Summary for Policymakers. Contribution of Working Groups I, II, and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (Eds.)]. IPCC, Geneva, Switzerland. https://www.ipcc.ch/report/ar6/syr/downloads/report/IPCC_AR6_SYR_LongerReport.pdf
- Leport, L., Turner, N. C., French, R. J., Tennant, D., Thomson, B. D., & Siddique, K. H. M. (1998). Water relations, gas exchange, and growth of cool-season grain legumes in a Mediterranean-type environment. *European Journal of Agronomy*, 9(4), 295–303. [https://doi.org/10.1016/S1161-0301\(98\)00042-2](https://doi.org/10.1016/S1161-0301(98)00042-2)
- Martin, R. J., & Jamieson, P. D. (1996). Effect of timing and intensity of drought on the growth and yield of field peas (*Pisum sativum* L.). *New Zealand Journal of Crop and Horticultural Science*, 24(2), 167–174. <https://doi.org/10.1080/01140671.1996.9513949>
- Munier-Jolain, N. (2010). Individual seed weight. In N. Munier-Jolain, V. Biarnès, I. Chaillet, J. Lecoeur, & M.-H. Jeuffroy (Eds.), *Physiology of the pea crop* (pp. 109–117). CRC Press.
- Nadeem, M., Li, J., Yahya, M., Sher, A., Ma, C., Wang, X., & Qiu, L. (2019). Research progress and perspective on drought stress in legumes: a review. *International Journal of Molecular Sciences*, 20(10), Article 2541. <https://doi.org/10.3390/ijms20102541>
- Nemeskéri, E., Molnár, K., Vígh, R., Nagy, J. J., & Dobos, A. (2015). Relationships between stomatal behaviour, spectral traits, and water use and productivity of green peas (*Pisum sativum* L.) in dry seasons. *Acta Physiologiae Plantarum*, 37(2), Article 34. <https://doi.org/10.1007/s11738-015-1776-0>
- Ney, B., Duthion, C., & Turc, O. (1994). Phenological response of pea to water stress during reproductive development. *Crop Science*, 34(1), 141–146. <https://doi.org/10.2135/cropsci1994.001183x003400010025x>
- Nogués, S., Allen, D. J., Morison, J. I. L., & Baker, N. R. (1998). Ultraviolet-B radiation effects on water relations, leaf development, and photosynthesis in droughted pea plants. *Plant Physiology*, 117(1), 173–181. <https://doi.org/10.1104/pp.117.1.173>
- Pandey, J., Devadasu, E., Saini, D., Dhokne, K., Marriboina, S., Raghavendra, A. S. S., & Subramanyam, R. (2023). Reversible changes in the structure and function of the photosynthetic apparatus of pea (*Pisum sativum*) leaves under drought stress. *Plant Journal*, 113(1), 60–74. <https://doi.org/10.1111/tpj.16034>
- Parry, C., Blonquist Jr., J. M., & Bugbee, B. (2014). *In situ* measurement of leaf chlorophyll concentration: Analysis of the optical/absolute relationship. *Plant, Cell and Environment*, 37(11), 2508–2520. <https://doi.org/10.1111/pce.12324>
- Rodríguez-Maribona, B., Tenorio, J. L., Conde, J. R., & Ayerbe, L. (1992). Correlation between yield and osmotic adjustment of peas (*Pisum sativum* L.) under drought stress. *Field Crops Research*, 29(1), 15–22. [https://doi.org/10.1016/0378-4290\(92\)90072-H](https://doi.org/10.1016/0378-4290(92)90072-H)
- Serrago, R. A., Alzueta, I. I., Savin, R., & Slafer, G. A. (2013). Understanding grain yield responses to source-sink ratios during grain filling in wheat and barley under contrasting environments. *Field Crops Research*, 150, 42–51. <https://doi.org/10.1016/j.fcr.2013.05.016>
- Soba, D., Arrese-Igor, C., & Aranjuelo, I. (2022). Additive effects of heatwave and water stresses on soybean seed yield is caused by impaired carbon assimilation at pod formation but not at flowering. *Plant Science*, 321, Article 111320. <https://doi.org/10.1016/j.plantsci.2022.111320>
- Soñta, M., & Rekiel, A. (2020). Legumes – use for nutritional and feeding purposes. *Journal of Elementology*, 25(3), 835–849. <https://doi.org/10.5601/jelem.2020.25.1.1953>
- Sun, Y., Wang, C., Chen, H. Y. H., & Ruan, H. (2020). Response of plants to water stress: a meta-analysis. *Frontiers in Plant Science*, 11, Article 978. <https://doi.org/10.3389/fpls.2020.00978>
- Suzuki, N., Rivero, R. M., Shulaev, V., Blumwald, E., & Mittler, R. (2014). Abiotic and biotic stress combinations. *New Phytologist*, 203(1), 32–43. <https://doi.org/10.1111/nph.12797>
- Turner, N. C. (2018). Turgor maintenance by osmotic adjustment: 40 years of progress. *Journal of Experimental Botany*, 69(13), 3223–3233. <https://doi.org/10.1093/jxb/ery181>
- Turner, N. C., Abbo, S., Berger, J. D., Chaturvedi, S. K., French, R. J., Ludwig, C., Mannur, D. M., Singh, S. J., & Yadava, H. S. (2007). Osmotic adjustment in chickpea (*Cicer arietinum* L.) results in no yield benefit under terminal drought. *Journal of Experimental Botany*, 58(2), 187–194. <https://doi.org/10.1093/jxb/erl192>
- Wang, Z., Li, G., Sun, H., Ma, L., Guo, Y., Zhao, Z., Gao, H., & Mei, L. (2018). Effects of drought stress on photosynthesis and photosynthetic electron transport chain in young apple tree leaves. *Biology Open*, 7(11), Article 035279. <https://doi.org/10.1242/bio.035279>
- Wu, A., Hammer, G. L., Doherty, A., von Caemmerer, S., & Farquhar, G. D. (2019). Quantifying impacts of enhancing photosynthesis on crop yield. *Nature Plants*, 5(4), 380–388. <https://doi.org/10.1038/s41477-019-0398-8>
- Zandalinas, S. I., Fritsch, F. B., & Mittler, R. (2021). Global warming, climate change, and environmental pollution: recipe for a multifactorial stress combination disaster. *Trends in Plant Science*, 26(6), 588–599. <https://doi.org/10.1016/j.tplants.2021.02.011>