

Postprint: Response of Flax Physiological and Biochemical Metabolic Indicators to Drought Stress and Its Simulation Model

Authors: Konka

Date: 2022-06-08T00:00:00+00:00

Abstract

To further investigate the impact of flax physiological and biochemical metabolic indicators responding to drought stress on flax yield, a pot water control method was employed to simulate drought stress in flax. Based on experimental data from Xigongyi Town, Dingxi City, Gansu Province during 2013-2014, a flax drought stress model was developed and validated to simulate the effects of drought stress on flax physiological and biochemical indicators and yield. Root mean square error (RMSE) and coefficient of determination (R^2) were utilized to describe model goodness of fit. The results demonstrated: (1) The RMSE of simulated yield values ranged from 41.3159 to 155.6685 kg · hm⁻², with an average of 80.1837 kg · hm⁻²; R^2 ranged from 0.8929 to 0.9894, with an average of 0.9387, indicating the model possessed satisfactory goodness of fit and strong feasibility. (2) Under severe drought stress, among antioxidant metabolic indicators—superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT)—CAT activity exhibited a declining trend, while POD activity at the final flowering stage demonstrated the greatest increase (26.09%~28.00%); the contents of three osmotic adjustment substances increased significantly, with proline showing the maximum increase of 236.22%. (3) Three groups of indicators exhibited extremely significant correlations: proline with chlorophyll, malondialdehyde, and CAT activity; soluble protein with malondialdehyde and CAT activity; and POD activity with SOD activity. Flax physiological and biochemical indicators responding to varying degrees of drought stress are strongly correlated with flax yield. The establishment of this model serves as a scientific supplement to studies on the response of flax physiological and biochemical indicators to drought stress, and further offers theoretical basis and support for efficient flax production management and agricultural production systems.

Full Text

Response of Physiological and Biochemical Metabolic Indices of Flax to Drought Stress and Its Simulation Model

KANG Jia, LI Yue, KANG Lianghe

College of Information Science and Technology, Gansu Agricultural University, Lanzhou 730070, Gansu, China

Abstract

Drought constitutes a critical stress factor affecting plant growth and development, causing significant damage to agricultural production in northwestern China. Plants employ photosynthetic, osmotic, and antioxidant metabolic indicators to cope with water deficit conditions. To investigate how physiological and biochemical metabolic indices of flax influence yield under drought stress, we conducted pot experiments using controlled water regimes to simulate drought conditions. Based on measured flax yield data from Xigongyi Town, Dingxi City, Gansu Province, collected during 2013–2014, we constructed, calibrated, and evaluated a drought stress response model for flax physiological and biochemical indices. Model performance was assessed using root mean square error (RMSE) and coefficient of determination (R^2). The results demonstrated that: (1) The RMSE of simulated yield ranged from 41.3159 to 155.6685 $\text{kg} \cdot \text{hm}^{-2}$, with an average of 80.1837 $\text{kg} \cdot \text{hm}^{-2}$; R^2 values ranged from 0.8929 to 0.9894, averaging 0.9387, indicating good model fit and strong feasibility. (2) Under severe drought stress, among the antioxidant metabolic indices (superoxide dismutase, peroxidase, and catalase), peroxidase (POD) activity showed the largest increase (26.09%–28.00% at the final flowering stage), while catalase (CAT) activity decreased. All osmoregulation substances increased significantly, with proline showing the greatest increase at 236.22%. (3) Proline content exhibited extremely significant positive correlations with chlorophyll content, malondialdehyde content, and CAT activity; soluble protein content showed extremely significant positive correlations with malondialdehyde and CAT; and POD activity displayed significant positive correlation with superoxide dismutase (SOD). The physiological and biochemical indices of flax respond strongly to drought stress, and this stress response is closely associated with yield. This model provides a scientific supplement to understanding flax physiological and biochemical responses to drought stress and offers theoretical support for efficient flax production management within agricultural systems.

Keywords: flax; Agricultural Production Systems Simulator (APSIM); drought stress; physiology and biochemistry; simulation model

Introduction

Flax (*Linum usitatissimum* L.), also known as oilseed flax, is a crop with strong resistance to cold, drought, and poor soil conditions. In China, Gansu Province

has the largest flax cultivation area. Previous studies have investigated the effects of drought on physiological characteristics of different flax varieties and the changes in physiological and biochemical indices of various drought-resistant flax types under water stress during the seedling stage. Water scarcity remains a primary environmental and resource issue affecting crop growth and limiting agricultural production. Extensive research has been conducted internationally on the response mechanisms of physiological and biochemical metabolic indices to drought stress in various crops including soybean, peanut, wheat, and olive. These studies indicate that due to diverse crop types and genetic backgrounds, crops exhibit distinct physiological differences in their adaptive responses to drought stress. Under varying degrees of drought stress, the primary response characteristics include reduced plant height, decreased leaf number, lower leaf area index, and reduced crop yield.

The Agricultural Production Systems Simulator (APSIM) is an agricultural system modeling framework developed by Australian scientists that simulates various components of agricultural production systems through integrated modules for soil, crops, fertilizer, water, and pasture. In China, APSIM research has primarily focused on: (1) effects of precipitation and temperature on spring wheat yield in dryland areas; (2) quantitative analysis of spring maize sensitivity to drought disaster during the growth period; and (3) studies on alfalfa-wheat rotation systems in the Loess Plateau dryland region. However, research combining flax crop yield with simulation models remains scarce domestically and requires further investigation. Therefore, this study focuses on flax as the research object, establishing a flax drought stress model based on APSIM and using field experimental data to validate the model, thereby revealing the response mechanisms of flax physiological and biochemical metabolic indices to drought stress and providing a theoretical basis for applying models to analyze flax drought stress.

Materials and Methods

1.1 Study Area

The long-term experiment was conducted in Xigongyi Town (35°34'48" N, 104°37'12" E), located in the Loess Plateau region of Dingxi City, Gansu Province. The experimental site is dryland at an altitude of 1793 m, with annual sunshine duration of 2500 h, average annual precipitation of 400 mm, and average annual temperature of 6.4°C. The experimental soil (black loam) was collected from local farmland.

1.2 Experimental Design

The experimental materials included flax varieties Longya 10, Longya 11, and Longyaza 1. Flax seeds were sown in plastic pots (23 cm diameter × 30 cm height) containing a 2:1 mixture of field soil (black loam) and fine soil that had been sterilized. Basal fertilizer (N 0.15 g/kg, P₂O₅ 0.10 g/kg) was mixed

uniformly into the substrate. The experiment included four drought periods: seedling stage, rosette stage, budding stage, and final flowering stage. Three water treatments were established: (1) control group with soil relative water content at 70%–75% of field capacity; (2) moderate stress group at 50%–55% of field capacity; and (3) severe stress group at 35%–40% of field capacity. Water content was controlled using the weighing method. A randomized block arrangement was employed to prevent systematic errors, with each pot labeled.

1.3 Measurement Methods

1.3.1 Gas Exchange Measurements

Stomatal conductance and transpiration rate were measured using a portable photosynthesis system (Li-6400).

1.3.2 Osmotic and Antioxidant Metabolite Measurements

Proline content was determined using the ninhydrin method. Malondialdehyde content was measured by the thiobarbituric acid method. Soluble protein content was assayed using the Coomassie brilliant blue G-250 staining method. Superoxide dismutase (SOD) activity was determined by the nitroblue tetrazolium method, peroxidase (POD) activity by the guaiacol method, and catalase (CAT) activity by ultraviolet spectrophotometry.

1.4 Model Construction

The model was constructed based on flax growth characteristics, comprehensively considering radiation use efficiency and the effects of radiation interception on photosynthetic rate. The model incorporates CO₂ concentration factors, photosynthetic water stress factors, and transpiration efficiency coefficients. All correlation coefficients in the parameters are biologically relevant and meaningful for describing the response mechanisms of flax physiological and biochemical indices to drought stress, enhancing model accuracy and universality.

The Agricultural Production Systems Simulator (APSIM) is a modeling framework for agricultural systems. Crops in arid regions are affected by soil, precipitation, light, and seasonal conditions, among which light intensity, diurnal temperature variation, and seasonal changes critically influence actual photosynthesis. The emergence of SUCROS and MACROS models, with their strong mechanistic basis, greatly advanced photosynthetic production modeling. Subsequent models such as CERES, GOSSYM, and others followed. Existing oil crop models, such as the rapeseed model, simulate photosynthesis and radiation relatively maturely, with biomass accumulation calculated through radiation use efficiency. The required meteorological data for the model were provided by the Gansu Provincial Meteorological Bureau.

Photosynthesis is particularly sensitive to drought stress among all physiological processes. The drought stress factor for photosynthesis and biomass accumulation is calculated as follows:

The water stress response function is given by:

$$W_{photo} = \frac{W_{supply}}{W_{demand}}$$

where W_{supply} is soil water supply and W_{demand} is soil water demand.

Soil water demand is calculated as:

$$W_{demand} = \min(W_{demand,pot}, R)$$

where $W_{demand,pot}$ is potential water demand and R is root water uptake.

Potential biomass accumulation is determined by:

$$B_{pot} = RUE \times I_{PAR}$$

where RUE is radiation use efficiency and I_{PAR} is intercepted photosynthetically active radiation.

Root water uptake is calculated as:

$$R = KL \times (SW - LL)$$

where KL is root length density, SW is soil water content, and LL is lower limit of plant available water.

The vapor pressure deficit (VPD) is calculated as:

$$VPD = 6.1078 \times \exp\left(\frac{17.269 \times T_{max}}{237.3 + T_{max}}\right) - 6.1078 \times \exp\left(\frac{17.269 \times T_{min}}{237.3 + T_{min}}\right)$$

The relationship between water supply/demand and water stress factors in the APSIM model is illustrated in [Figure 1: see original paper].

1.5 Model Parameter Calibration

The APSIM model demonstrates good simulation capability for crop growth influencing factors and physiological-ecological mechanisms, with wide application and high precision. However, as the model was originally developed based on southern hemisphere geographical environments, localization is required for northern hemisphere study areas. This involves scientific calibration, adjustment, and optimization of simulation parameters. This study employed localized APSIM model parameters to simulate flax photosynthesis and drought stress. Required water data were derived from the research group's technical specification "Regulation Techniques for Target Flax Yield." Model parameters were divided into two categories: (1) flax species parameters from previous studies, and (2) adjustable genetic parameters (Table 1). The model was run using

meteorological data from the Dingxi region for 2013–2014, soil data for black loam, and local crop management data. Parameters were adjusted to minimize differences between simulated and measured data, achieving model calibration and adjustment. Data from an additional year were used for model validation.

Table 1 Model parameters for response of flax physiological and biochemical metabolic indices to drought stress

Parameter	Description
RUE	Radiation use efficiency ($\text{g} \cdot \text{MJ}^{-1}$)
fCO ₂	CO ₂ concentration factor affecting photosynthesis rate
fVPD	Vapor pressure deficit factor limiting photosynthesis
fW _{,photo}	Photosynthetic water stress factor
TE_{coeff}	Transpiration efficiency coefficient representing plant water use efficiency

1.6 Model Evaluation Methods

Model localization was performed using 2013–2014 meteorological data from the Dingxi experimental station, soil profile data for black loam, and local variety management data. Parameters were adjusted to align simulated data with measured data. Model validation compared simulated yields with actual field measurements using two statistical indices: root mean square error (RMSE) and coefficient of determination (R^2). Generally, smaller RMSE values indicate higher precision, while R^2 values approaching 1.0 indicate more ideal simulation effects.

The RMSE is calculated as:

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (M_i - S_i)^2}{n}}$$

where M_i is the measured value, S_i is the simulated value, and n is the number of observations.

The R^2 is calculated as:

$$R^2 = 1 - \frac{\sum_{i=1}^n (M_i - S_i)^2}{\sum_{i=1}^n (M_i - \bar{M})^2}$$

where \bar{M} is the mean of measured values and \bar{S} is the mean of simulated values.

1.7 Statistical Analysis

All data were analyzed using SPSS 26.0 software. Model programming was implemented in Python.

Results

2.1 Model Validation

Using actual yield data from the Xigongyi Town research area in Dingxi City, the model's effectiveness in simulating the impact of photosynthetic indices on yield under drought stress was validated. The results (Figure 2) showed that simulated yield values had RMSE ranging from 41.3159 to 155.6685 $\text{kg} \cdot \text{hm}^{-2}$, with an average of 80.1837 $\text{kg} \cdot \text{hm}^{-2}$. The R^2 between measured and simulated yield values ranged from 0.8929 to 0.9894, with an average of 0.9387. These results demonstrate that the model can effectively simulate flax yield responses to drought stress through physiological and biochemical indices.

Figure 2 [Figure 2: see original paper] Measured versus simulated values of flax yield

2.2 Physiological and Biochemical Responses to Drought Stress

2.2.1 Changes in Gas Exchange Under Drought Stress Transpiration rate (T_r) is a key physiological indicator that regulates various crop mechanisms and responds to environmental changes. As shown in Figure 3, greater drought stress led to more pronounced decreases in T_r across all three flax varieties. The inhibition was particularly evident under severe stress, where average reductions reached 86.67% compared to the control group. Under moderate stress, Longya 11 showed the smallest average reduction (25.00%), while Longyaza 1 exhibited the greatest sensitivity to drought stress. These results indicate that intensifying drought stress has detrimental effects on flax gas exchange.

Stomatal conductance (G_s) reflects the degree of damage crops suffer from external adverse effects. Figure 3 demonstrates that more severe drought stress caused more significant differences in G_s among the three flax varieties, with all showing declining trends. Under moderate and severe stress treatments, average reductions were 70.97% and 87.10%, respectively. These findings confirm that reduced stomatal conductance is a primary response mechanism to drought stress.

Figure 3 [Figure 3: see original paper] Effects of drought stress on gas exchange

2.2.2 Osmotic Regulation Metabolic Indices Response to Drought Stress Under drought stress, osmotic regulation substances (proline, soluble protein, and malondialdehyde) accumulate in leaves. Proline accumulation helps protect plant cell structure and function while maintaining osmotic potential. As shown in Figure 4, flax leaf proline content increased substantially under drought stress, with the most significant increases occurring under severe stress treatment. At the budding stage, proline content increased by 116.85%-236.22% compared to the control group, demonstrating that increased proline content enhances flax's drought adaptation capacity.

Soluble protein content also increased significantly across different growth stages under drought stress, with the magnitude of increase following the order: budding stage > rosette stage > final flowering stage > seedling stage. Under severe stress, the largest increases occurred at the budding stage (107.17%–154.33%), while the smallest increases were observed at the seedling stage (9.31%–12.78%). These results indicate that flax employs different osmotic regulation strategies across growth stages to adapt to varying drought conditions.

Malondialdehyde (MDA), a product of membrane lipid peroxidation, increased in flax leaves across all growth stages under drought stress (Figure 4). Under severe stress, MDA content increased dramatically by 80.00%–84.00%. While MDA content remained relatively low under mild stress, exceeding physiological limits resulted in substantial MDA production, indicating membrane damage.

Figure 4 [Figure 4: see original paper] Variation characteristics of osmotic adjustable substance content under drought stress

2.2.3 Antioxidant Metabolic Indices Response to Drought Stress Superoxide dismutase (SOD) converts reactive oxygen species into less active substances, protecting membranes from peroxidation. As shown in Figure 5, SOD activity decreased under drought stress across flax growth stages. Under severe stress, the smallest reductions occurred at the seedling stage (20.44%–28.09%), while the largest decreases were observed at the final flowering stage (27.00%). Generally, smaller reductions in SOD activity indicate stronger antioxidant capacity.

Catalase (CAT) works synergistically with SOD to scavenge reactive oxygen species and maintain metabolic balance. CAT activity increased significantly under severe stress, with the largest increases at the budding stage (19.46%–24.61%). Peroxidase (POD) activity also increased substantially, with the greatest 增幅 at the final flowering stage (26.09%–28.00%). As protective enzymes sensitive to environmental changes, increased SOD and POD activities reflect enhanced drought resistance mechanisms.

Figure 5 [Figure 5: see original paper] Variation characteristics of antioxidant metabolite content under drought stress

2.2.4 Correlation Analysis of Physiological Indices Under Drought Stress When subjected to drought stress, various crop physiological indices exhibit complex interactions and correlations (Table 2). Under different drought stress levels and growth stages, proline content showed extremely significant positive correlations with chlorophyll content, malondialdehyde content, and CAT activity. Soluble protein content was extremely significantly positively correlated with malondialdehyde and CAT. POD activity displayed significant positive correlation with SOD activity. These correlations demonstrate the integrated physiological response network through flax adapts to drought stress.

Table 2 Correlation analysis of physiological and biochemical metabolic indices of flax under drought stress

Note: and ** indicate significant and extremely significant correlations at the 0.05 and 0.01 levels (one-tailed), respectively. Pro, SP, Chl, MDA, CAT, POD, and SOD represent proline, soluble protein, chlorophyll, malondialdehyde, catalase, peroxidase, and superoxide dismutase, respectively.*

Discussion

Previous studies have constructed preliminary photosynthetic production and dry matter accumulation simulation models for flax under different fertilizer levels, planting methods, and densities. APSIM model has shown good performance in simulating spring wheat growth stages, grain number, thousand-grain weight, and yield under different drought conditions in dryland areas. Similarly, dynamic simulation models for rapeseed shoot dry matter partitioning have demonstrated good predictive capability when combined with variety genetic characteristics. In this study, the APSIM-based flax drought stress model achieved R^2 values of 0.8929–0.9894 for simulated yield, indicating high precision and suitability.

Our results showed that drought stress inhibited plant height, stem diameter, and root growth in three flax varieties, with varying degrees of inhibition across varieties and stress periods. Chlorophyll content directly reflects photosynthetic capacity. While some studies suggest drought inhibits chlorophyll synthesis and accelerates its decomposition, our findings indicate that flax leaf chlorophyll content increased across growth stages under drought stress, with the maximum increase (18.11%) occurring at the budding stage under severe stress. This may result from reduced leaf relative water content concentrating existing chlorophyll.

Osmotic regulation substances (proline, malondialdehyde, soluble protein) represent the most direct and important mechanisms for physiological adjustment under drought. Under severe stress, all three substances increased significantly, with proline and soluble protein showing maximum increases at the budding and final flowering stages, reflecting flax' s adaptive responses. Notably, proline increases were significantly higher than soluble protein increases. Malondialdehyde accumulation was relatively low at seedling and rosette stages but increased markedly at budding and final flowering stages, indicating greater drought tolerance during early growth stages.

Antioxidant metabolic indices (SOD, POD, CAT) scavenge reactive oxygen species and indicate stress resistance capacity. Under severe stress, SOD activity decreased while CAT and POD activities increased, with POD showing the greatest increase at the final flowering stage. This enzymatic response represents a key physiological reaction enabling flax to mobilize antioxidant protection and enhance drought resistance.

Conclusion

This study, using Longya 10 as the primary experimental material, established a flax drought stress model based on APSIM and investigated responses of physiological and biochemical metabolic indices to drought stress across different growth stages. The main conclusions are:

1. Using APSIM and field data from Xigongyi Town, Dingxi City, Gansu Province, we developed a flax drought stress model. Validation results showed the model effectively simulated changes in flax physiological and biochemical indices under different stress levels, with good fit and reliability (average $R^2 = 0.9387$).
2. Under severe drought stress, physiological and biochemical indices were significantly affected, particularly proline, soluble protein, and malondialdehyde. Osmotic regulation indices all increased, with maximum increases at the budding stage. Among antioxidant metabolic indices, SOD activity decreased (maximum reduction at budding stage), while POD activity increased (maximum increase at final flowering stage).
3. Correlation analysis revealed that under drought stress, proline content was extremely significantly correlated with chlorophyll, malondialdehyde, and CAT; soluble protein was extremely significantly correlated with malondialdehyde and CAT; and POD was significantly correlated with SOD.

These findings demonstrate that flax physiological and biochemical indices respond strongly to drought stress, and this model provides valuable theoretical support for efficient flax production management and agricultural system optimization.

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