

Sweetpotato [*Ipomoea batatas* (L.) Lam.] Response to S-Metolachlor and Rainfall under Three Temperature Regimes

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Abstract

The S-metolachlor is used to control/suppress yellow nutsedge, annual grasses, and several broad-leaf weeds in sweetpotato. However, when used under adverse environmental conditions, it may lead to crop injury. Information is limited on the effect of S-metolachlor application followed immediately by rainfall on sweetpotato growth and development under different temperature regimes. The objective of this study was to determine sweetpotato response to S-metolachlor under low, optimum, and high temperatures with no rainfall and rainfall immediately after application. Sweetpotato slips were transplanted to sandy loam soil-filled pots. Half of the pots were subjected to 38 mm rainfall at 50.8 mm·h⁻¹ intensity within the first 24 h after POST-transplant S-metolachlor application at 0, 0.86, 1.72, 2.58 and 3.44 kg·ha⁻¹. The pots were moved into sunlit, computer-controlled plant growth chambers that were maintained at their respective temperatures for 61 days. Plant growth, development and plant-component dry weights and quantity of storage roots were recorded at harvest. Storage root yield was highest at the optimum temperature and declined at low and high temperature conditions. Shoot, root, and total plant biomass yield declined with increasing concentration of S-metolachlor across temperature conditions. In addition, storage root yield decline was S-metolachlor rate-dependent and aggravated by a rainfall event immediately after herbicide treatment across temperatures tested. These results can be used to weigh the risk of potential crop injury against the benefits of S-metolachlor when making management decisions as well as considering weather forecast information to avoid herbicide application coinciding with adverse weather conditions such as excessive rainfall event.

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Keywords

Growth, Development, Rainfall, Temperature, S-Metolachlor, Storage Roots, Sweetpotato

1. Introduction

Sweetpotato is a valuable crop producing the highest root dry matter for animal and human consumption, as well as industrial uses [1] [2]. It provides more or equal calories at $152 \text{ MJ ha}^{-1}\text{-day}^{-1}$ than cassava, wheat, and rice which provide 121, 135, and $151 \text{ MJ ha}^{-1}\text{-day}^{-1}$ calories, respectively [3] [4]. Storage roots are the leading economic product from sweetpotato for the consumer market in the United States, but other plant parts are used in other countries for other purposes. Adventitious roots emerge from root primordia on nodes and cut ends of slips within a few days after transplanting [5]-[7]. Under unfavorable conditions, these roots will become fibrous roots through secondary growth and lignification of the stele [8] [9]. However, when conditions are favorable, adventitious roots with pentarch and hexarch steles will develop into well-shaped economically important storage roots through proliferation of cambial cells that form starch-accumulating parenchymatous cells [7] [10] [12]. The storage root formation process involves a series of steps such as cessation of root elongation, initiation of primary and secondary vascular cambia, development of anomalous and interstitial cambia, increasing of radial growth, cell proliferation and expansion, and massive accumulation of starch and proteins [1] [6] [13]. Various factors such as grower expertise chemical weed control, slip quality, soil factors, cultivar genetic characteristics and environmental factors such as temperature and soil moisture have profound impacts on these steps, thus affecting the number and quality of storage roots [14]-[17].

Weed competition and interference are major factors that challenge sweetpotato production systems, particularly for high yielding cultivars such as Beauregard that are susceptible to weed competition [18]. Sweetpotato storage root yield and quality reductions due to weed competition and interference have been reported in several studies from the tropics to the temperate regions of the world. Weed competition and interference studies in the US indicate a 36% total marketable yield loss with a low density (0.5 m^{-1}) of palmer amaranth (*Amaranthus palmeri*) in North Carolina [19], and a yield loss ranging from 14% to 68% due to a mixed species of weeds in Louisiana and South Carolina [20] [21]. In addition, sweetpotato storage root yield can be reduced from 22% to 91% in more tropical environments such as Nigeria, Hawaii and the West Indies due to weed competition and interference [22].

Efficient weed management within the critical weed-free period of 2 - 6 weeks after transplanting is an important practice in sweetpotato production systems [23]. Sweetpotato growers usually use a combination of mechanical, manual and chemical practices to manage weeds. Mechanical cultivation is not very effective due to the prostrate growth habit of sweetpotato and hand weeding is not a good option due to increasing cost and shortage of labor. Therefore, the use of herbicides for weed control is essential. Among the few herbicides labeled for use in sweetpotato, S-metolachlor effectively controls or suppresses some of the most common and/or problematic weeds [24]. S-metolachlor is labeled for use in sweetpotato production systems to control or suppress yellow nutsedge, annual grasses, and several broadleaf weeds. It is generally pre-emergent to weeds and post-transplant to sweetpotato slips of the cultivar, Beauregard [24]. S-metolachlor is physically and chemically equivalent to metolachlor, but is more active at the site of action in susceptible plants and allows for lower use rates [25]. Plants absorb S-metolachlor through roots and shoots, but shoot tissues are generally more sorptive, and it is also the site of herbicidal activity [26] [27]. It is mostly transported upwards after absorption and its primary mode of action remains undefined even though major metabolic pathways are impaired in susceptible plants [28]. S-metolachlor is categorized as a mitosis inhibitor as it affects the synthesis of several plant components such as fatty acids, lipids, proteins, isoprenoids, and flavonoids in susceptible plants [25] [28]. Although, S-metolachlor is effective in controlling most problematic weeds in sweetpotato fields, the potential for injury does exist under certain environmental conditions. Prior studies reported that metolachlor was phytotoxic to sweetpotato at $3.4 \text{ kg}\cdot\text{ha}^{-1}$ usage rates [29] and storage root shape quality was affected at rates of $4.5 \text{ kg}\cdot\text{ha}^{-1}$ and higher usage rates [30]. Similarly, Porter [31] observed rounder and shorter storage roots from sweetpotato plants treated with $2.19 \text{ kg}\cdot\text{ha}^{-1}$ metolachlor compared with storage roots from an untreated check and those treated at lower metolachlor rates.

Environmental factors such as rainfall and temperature have a major impact on crop growth and development, as well as how the crop responds to herbicides in the chloroacetamide family [32]–[35]. Rainfall occurring shortly after an S-metolachlor application can result in movement of the herbicide into the root zone leading to increased absorption and severe sugarbeet (*Beta vulgaris* L.) injury [36]. In a growth chamber experiment, low soil temperature (15°C) increased metolachlor injury to corn and delayed plant emergence 1 to 2 days as well as the time needed to reach the first leaf stage by 2 days compared with plants grown in a 30°C soil environment [32]. Increased soybean and dry edible bean injury have been reported with increasing soil moisture and PRE applications of dimethenamid and metolachlor at high rates [33] [37].

Even though, S-metolachlor controls yellow nutsedge (*Cyperus rotundus*), annual grass and certain broadleaf weed species, some growers are skeptical of utilizing this herbicide in weed management programs, because injury to storage roots has been attributed to its use under certain environmental conditions. To our knowledge, the effect of S-metolachlor application followed immediately by a rainfall event on sweetpotato growth and development under different temperature conditions has not been documented. Therefore, the objective of this study was to determine interactive effects of S-metolachlor application rates, temperature and rainfall on sweetpotato growth and development, and storage root formation and bulking.

2. Materials and Methods

2.1. Experimental Facilities

This experiment was conducted from 16 May to 16 July 2012 in nine sunlit computer-controlled plant growth chambers known as Soil-Plant-Atmosphere-Research (SPAR) units at Rodney Foil Plant Science Research Center, Mississippi State University, Mississippi State (33°28'N, 88°47'W), MS, USA. The environmental control and operation of the facility was described in detail by Reddy *et al.* [38]. Briefly, each SPAR chamber consists of a steel soil bin (1 m depth by 2 m length by 0.5 m width) to accommodate the root system, a Plexiglas chamber (2.5 m height by 2 m length by 1.5 m width) to accommodate aerial plant parts, an environmental control and monitoring system and a cooling and heating system. The Plexiglas transmits 97% of the visible solar radiation to pass without spectral variability in absorption [39]. The heating and cooling system is connected to air ducts that pass conditioned air through the plant canopy with sufficient velocity (4.7 km·h⁻¹) to cause leaf flutter, mimicking field conditions. Chilled ethylene glycol was supplied to the cooling system via several parallel solenoid valves that opened or closed depending on the cooling requirement. Two electrical resistance heaters provided short pulses of heat, as needed, to fine-tune the air temperature control. Chamber air temperature, carbon dioxide concentration, and irrigation in each SPAR unit, as well as continuous monitoring of all-important environmental and plant gas exchange variables, were controlled by a dedicated computer system [38]. Variable density shade cloths (Hummert Seed Co., St. Louis, MO, USA) that surrounds the plant canopy to simulate canopy spectral properties was adjusted regularly to match canopy height and eliminate the need for border plants.

2.2. Experimental Design and Growth Conditions

The experimental design was a completely randomized block with four replications. Treatment combinations were five rates of S-metolachlor (Dual Magnum[®], Syngenta Crop Protection Inc., Greensboro, NC, USA) (0.0, 0.86, 1.72, 2.58 and 3.44 kg·ha⁻¹), two levels of rainfall (0 and 38 mm) and three levels of day/night temperatures, low, 25/17°C, optimum, 30/22°C, and high, 35/27°C. The no S-metolachlor treatment in each temperature level and rainfall treatment were considered as an untreated check and used for comparison. Sweetpotato cultivar, Beauregard (B14) slips cut from field seedbeds were transplanted into white polyvinyl chloride pots (20 cm diameter and 30 cm height) on 16 May, 2012. A total of 126 pots, 4 pots for each treatment with 6 extra pots for the control, were arranged in 9 SPAR units (3 SPAR units per temperature treatment) in 7 rows, 26.6 cm row spacing and placed at 25 cm apart within the row. Each pot, fitted with a detachable plastic bottom and filled with coarse gravel (600 g) at the bottom, allowed excess water and nutrients to drain with a small hole at the bottom of the pot. A single slip containing four nodes was transplanted into each pot with two nodes below the soil surface and two nodes above the soil surface. Nodes above the soil surface contained two recently fully expanded leaves.

S-metolachlor was applied POST and half of the pots were subjected to 38 mm of simulated rainfall at 50.8 mm·h⁻¹ intensity within 24 h after herbicide applications. S-metolachlor was applied in water as a carrier with a

tractor-mounted, compressed-air spraying system using Teejet 8002 XR flat fan nozzles (Teejet Spraying Systems Co., Wheaton, IL, USA) that delivered $140 \text{ L} \cdot \text{ha}^{-1}$ at 180 kPa. At the time of herbicide treatments, the relative humidity was 51%, wind was blowing NE at 1 mph and prevailing air temperature was 28°C . The rainfall simulator used was modeled after one described by Meyer and Harmon [40] which reproduced droplet size, fall velocity, and kinetic characteristics similar to a natural rain event. Droplets of rain were delivered from a height of 2.4 m [41]. Prior to the treatment, the flow of the water was adjusted based on the measurements of rainfall amount at the plant height level using rain gauges. All potted plants after the herbicide and rainfall treatments were transferred into the SPAR chambers.

Evapotranspiration rates (ET) expressed on a ground area basis ($\text{L} \cdot \text{d}^{-1}$) throughout the treatment period was measured in each SPAR unit as the rate at which condensate was removed by the cooling coils at 900-s interval by measuring the mass of water in collecting devices connected to a calibrated pressure transducer [38] [42]. Based on evapotranspiration values recorded on previous day, the amount of water provided to each treatment was adjusted by making changes in the time and duration of irrigation provided at each temperature treatment. The plants were irrigated with full-strength Hoagland nutrient solution [43] through automated drip irrigation system, one dripper per pot with each dripper emitting 50 mL per minute. Air temperature treatments in each SPAR unit were monitored and adjusted every 10 s throughout the day and night and maintained within set points $\pm 0.5^\circ\text{C}$. The daytime temperature was initiated at sunrise and returned to the nighttime temperature 1 h after sunset. The carbon dioxide in each SPAR unit was monitored and adjusted every 10 s throughout the day, and maintained at $400 \pm 10 \mu\text{mol} \cdot \text{mol}^{-1}$. The relative humidity (RH) of each chamber was monitored with a humidity and temperature sensor (HMT 70Y, Vaisala Inc., San Jose, CA, USA) installed in the returning path of airline ducts. The vapor pressure deficits (VPD) in the units were estimated from these measurements as per Murray [44]. The measured environmental variables such as temperatures, CO_2 concentrations, vapor pressure deficits and daily evapotranspiration values during the experimental period were summarized and are presented in Table 1.

3. Data Collection and Statistical Analysis

Growth and yield measurements were recorded at 61 days after transplanting (DAT). Vine length and number of leaves were collected from two branches identified as branch 1 and 2. Branch 1 originated from the first node near the soil surface and branch 2 was from the second node. Total vine length per plant was described as the sum of the lengths of branch 1 and 2 on each plant. Total number of leaves per plant was also described as the sum of the leaves on branch 1 and 2 on each plant. Plant component parts were separated and leaf area measurements were taken using a Li-COR 3100 leaf area meter (LICOR, Inc., Lincoln, NE, USA). Fresh storage roots were counted and weighed. Plant component parts were bagged separately, oven-dried at 80°C for >72 h and weighed for biomass determination.

The data were subjected to analysis of variance (ANOVA) using the General Linear Model (GLM) procedure of the Statistical Analysis System [45] to determine main factor effects and treatment interactions. Means were separated by Fisher's protected LSD test at the $p < 0.05$ confidence level. Whenever there was a statistically significant difference between rainfall and no-rainfall treatments, data were separated by rainfall and no-rainfall, and treatments within each S-metolachlor level were separated according to the Fisher's protected LSD ($p <$

Table 1. Mean air temperature, carbon dioxide [CO_2] vapor pressure deficit (VPD), evapo-transpiration (ET) during the experimental period for each temperature regime.

Set treatments		Measured variables*					
Day/Night	Temperature		[CO ₂]	VPD		Mean daily ET	
	Day	Night		Mean	Day		Night
	----- °C	-----		μmol·mol ⁻¹	----- KPa	-----	L·d ⁻¹
25/17	25.1 ± 0.08	17.5 ± 0.04	22.0 ± 0.07	404.2 ± 7	1.37 ± 0.03	1.11 ± 0.04	6.65 ± 0.38
30/22	29.5 ± 0.07	22.0 ± 0.05	26.5 ± 0.06	407.9 ± 5	2.18 ± 0.12	1.69 ± 0.08	9.84 ± 0.86
35/27	34.1 ± 0.17	26.6 ± 0.12	31.1 ± 0.15	415.3 ± 10	3.11 ± 0.23	2.47 ± 0.11	13.69 ± 1.32

*Each value represents the mean $\pm$ SE for carbon dioxide [CO_2], temperature, VPD and ET for 61 days, from 16 May to 16 July 2012.

0.05). Data on plant variables and S-metolachlor were regressed and graphical analysis carried out using SigmaPlot 11.0 (Systat Software Inc., San Jose, CA, USA). Coefficient of determination (R^2) and root mean square error (RMSE) were used to determine the best-fit equations between S-metolachlor rates and measured sweetpotato parameters at each temperature and rainfall treatment.

4. Results and Discussion

Aerial and soil environmental factors control sweetpotato growth and development, particularly storage root initiation during first 3-weeks of transplanting. Also, storage root bulking during mid- and late-season will also be affected by environmental factors. In this experiment, sweetpotato growth and development were monitored under well-controlled environmental conditions and in sunlit radiation environment similar to field settings. This is the first study that quantified the functional relationships of both aboveground plant growth and developmental processes and storage root formation and bulking in sweetpotato in response to a wide range of S-metolachlor rates and temperature levels with and without rainfall event immediately after transplanting and herbicide application. The data showed significant S-metolachlor damages to growth and development of sweetpotato, particularly storage root initiation and bulking, and intensity of the damage, however, was dependent on rates of herbicide and modulated by temperature and rainfall event immediately after the herbicide application. Therefore, the data obtained and functional relationships derived between S-metolachlor concentration and plant parameters in this study will be useful to assist growers to make appropriate S-metolachlor rate selection and management options such as planting dates and scheduling irrigation in sweetpotato production systems.

4.1. Vine Length and Leaf Area Growth and Development

There was no difference between the rainfall treatment levels for vine length at each temperature treatment and therefore the data were combined between rainfall treatments and analyzed as a function of S-metolachlor rate (Figure 1(A)). Vine length was not different between the two highest temperature (30/22°C and 35/27°C) grown

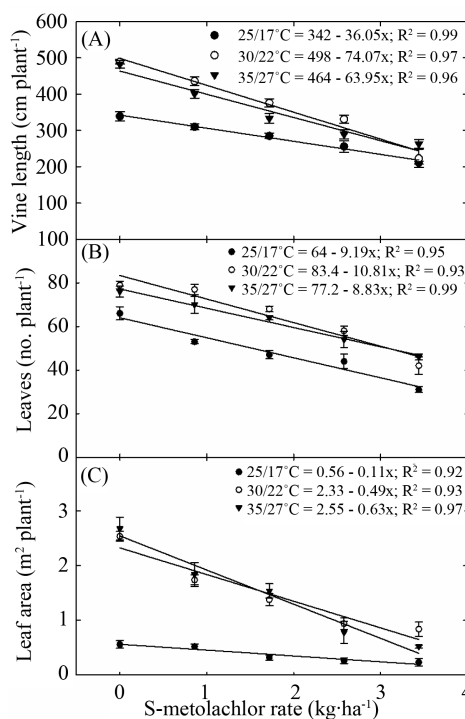


Figure 1. S-metolachlor and rainfall effects on (A) vine length, (B) leaf number, (C) leaf area of Beauregard sweetpotato grown in soil-plant-atmosphere-research growth chambers at 25/17°C, 30/22°C, and 35/27°C day/night temperatures and harvested 61 days after transplanting in 2012. Since there was no difference between rainfall treatment levels, the data on rainfall and no-rainfall were combined across S-metolachlor rates. Values represent the mean of eight plants and the error bars are $\pm$ SE of the mean.

plants, about 481 cm plant⁻¹ in the absence of S-metolachlor treatment, but vines were shorter at the lowest temperature (25/17°C) tested by 29% compared to values at the two other temperatures. Vine length, however, declined linearly across all temperatures with increase in S-metolachlor rates, and rates of decline were temperature dependent. The decline at the lowest temperature (25/17°C) was 36.05 cm plant⁻¹ kg⁻¹·ha⁻¹ S-metolachlor applied, and the decline was 91% more at the two high temperatures (30/22°C and 35/27°C), probably due to faster growth rates of the plants at these growing conditions as discussed later. Vine lengths decreased by 9%, 15%, and 37% at low (25/17°C), 13%, 23% and 52% at optimum (30/32°C) and 12%, 21% and 48% at high (35/27°C) temperatures for minimum (0.86 kg·ha⁻¹), maximum (1.43 kg·ha⁻¹) recommended label use rates and the highest (3.48 kg·ha⁻¹) rate of S-metolachlor used in this study, respectively (**Figure 1(A)**), for weed control measures in sweetpotato production systems in the US Midsouth. Similar to our results, Soltani *et al.* [46] reported 11% and 14% decline in sugarbeet (*Beta vulgaris* L.) plant height with PPI and PRE applications of 3.2 kg·ha⁻¹ S-metolachlor. Also, Grichar *et al.* [47] reported stunted growth in peanuts (*Arachis hypogaea* L.) with PRE application of S-metolachlor at 1.5 and 2.2 kg·ha⁻¹. Sakr [48] reported faster vine growth at 21°C to 25°C compared to 10°C to 15°C growth temperature conditions similar to our findings at various temperatures in sweetpotato. The greater injury to vine length at higher S-metolachlor rates was probably due to the inability of the plants to efficiently metabolize the herbicide at these higher concentrations. Since S-metolachlor affects mitosis and synthesis of several plant components such as fatty acids, lipids, proteins, isoprenoids, and flavonoids in susceptible plants [25] [28], the declining vine lengths in sweetpotato with increasing rates of S-metolachlor might have been due to its effects on cell division and elongation resulting in shorter plants.

Similar to vine length responses, no differences were detected between rainfall and no-rainfall treatments for number of leaves produced per plant at each of the temperature treatments. Therefore, data on rainfall and no-rainfall treatments were pooled across herbicide rates for analysis of the number of leaves per plant (**Figure 1(B)**). Plants grown at the two highest temperatures (30/22°C and 35/27°C) produced about 80 leaves plant⁻¹ during the 61-day period, on average, 1.3 leaves d⁻¹, in the absence of S-metolachlor application. Plants grown at the low temperature treatment (25/17°C), on the other hand, produced 15 fewer leaves plant⁻¹ than the other two temperatures. However, the rates of decline in leaf numbers were not much different among the temperature treatments; 9.19, 10.81 and 8.83 leaves plant⁻¹ kg⁻¹ S-metolachlor rate applied, for low, optimum and high temperature environments, respectively (**Figure 1(B)**).

Whole plant leaf area growth response was similar to that of vine growth responses to S-metolachlor levels, temperature and rainfall conditions (**Figure 1(C)**). Plants grown at low temperature treatment (25/17°C) and with zero S-metolachlor rate produced about 0.56 m² leaf area plant⁻¹, while plants grown at the two higher temperatures (30/22°C and 35/27°C) produced 2.4 times more leaf area than at the low temperature treatment indicating strong temperature effects on leaf area development, the product of individual leaf sizes and number of leaves produced, which were very temperature dependent. Similar to vine growth responses to S-metolachlor treatment, the rate of decline was lower, 0.11 m² leaf area plant⁻¹ kg⁻¹·ha⁻¹ S-metolachlor applied at the low temperature (25/17°C) than the rates of decline, 0.49 and 0.63 m² leaf area plant⁻¹ kg⁻¹·ha⁻¹ S-metolachlor applied, at the optimum (30/22°C) and high (35/27°C) temperature treatments, respectively. For the minimum (0.86 kg·ha⁻¹), maximum (1.43 kg·ha⁻¹) recommended label use rate and the highest (3.44 kg·ha⁻¹) S-metolachlor rate used in this experiment, leaf area was decreased by 17%, 28% and 68%, 18%, 30%, and 67% and 22%, 65% and 86% for plants grown at low (25/17°C), optimum (30/22°C) and high (35/27°C) temperature treatments, respectively (**Figure 1(C)**). Leaf area development was more responsive than vine length and leaf addition rates to S-metolachlor application across all temperature conditions (**Figure 1**). This could be due to S-metolachlor effects on cell division and cell expansion [25] [28]. Since vine length extension that includes all growing internodes, whole plant leaf area development that includes all the leaves on all vines, and leaf addition on all vines are recognized as basic phenomena of shoot morphogenesis and growth for effective capture and interception of solar radiation [49], any factor that affects growth and developmental processes of these organs will affect overall canopy development and finally yield of sweetpotato.

4.2. Storage Root Development

Representative pictures of root systems harvested at 61 DAT at a range of S-metolachlor concentrations and temperatures with and without rainfall events illustrate the damaging effects of S-metolachlor and the influence of temperature and rainfall on root morphology, storage root production and bulking (**Figure 2**). Like vine

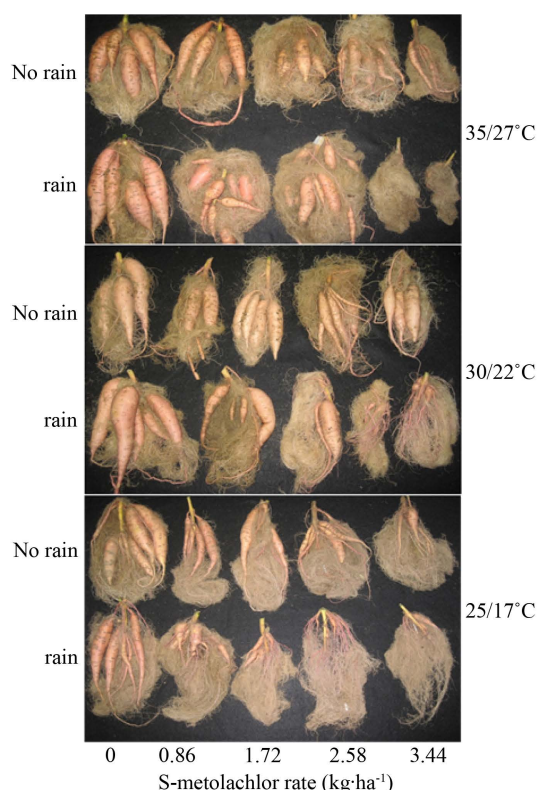


Figure 2. Pictorial representation of S-metolachlor and rainfall effects on the storage root system of Beaugard sweetpotato grown in soil-plant-atmosphere-research growth chambers at 35/27°C, 30/22°C, and 25/17°C day/night temperatures and harvested 61 days after transplanting in 2012.

length, leaf area growth and development, there was no difference between rainfall treatment levels for storage roots produced. Therefore, the data on rainfall and no-rainfall treatments were combined across S-metolachlor rates. Storage roots declined linearly and significantly with increase in S-metolachlor rates across all temperature treatments (**Figure 3**). Sosnoskie *et al.* [50] reported a decline in squash (*Cucurbita pepo* L.) fruit numbers with PRE and PRE followed by POST applications of S-metolachlor and this corroborates our findings in sweetpotato storage root production.

4.3. Biomass Production and Partitioning

Unlike vine and leaf area growth and development, and storage root responses, there was significant interaction between rainfall and S-metolachlor rates for leaf, stem, root and total biomass production across all growing temperatures ($p < 0.05$; **Figure 4**). Also, there was a S-metolachlor by temperature interaction for all biomass components and total biomass production (**Figure 4**). In the absence of S-metolachlor, low (25/17°C) temperature grown plants produced 21.7 g plant⁻¹ leaf biomass, which was 56% and 47% lower than leaf biomass production at optimum (30/22°C) and high (35/27°C) temperature environments, respectively. Leaf biomass declined linearly with S-metolachlor rates across all temperature treatments and both with and without rainfall treatments (**Figure 4(A)-(C)**). At optimum temperature, leaf biomass declined at a faster rate in the presence of rainfall, 10.3 g plant⁻¹ kg⁻¹·ha⁻¹ S-metolachlor than with no-rainfall treatment, 3.9 g plant⁻¹ kg⁻¹·ha⁻¹ S-metolachlor (**Figure 4(B)**). In the presence of rainfall, leaf biomass declined by 14%, 24% and 57% at low; 18%, 30% and 72% at optimum and 12%, 21% and 57% at high temperature conditions for minimum (0.86 kg⁻¹·ha⁻¹), maximum (1.43 kg⁻¹·ha⁻¹) recommended label use rates and at the highest rate (3.44 kg⁻¹·ha⁻¹) of S-metolachlor used in this study, respectively, when compared to the untreated check. However, with no rainfall event immediately after transplanting and herbicide application, leaf biomass declined by 12%, 21% and 50% for low; 7%, 11% and 27% for optimum, and 10%, 17%; and 40% for high temperatures, respectively (**Figure 4(A)-(C)**). Bellinder and Warholc [51] observed similar declines in cabbage head weight with preplant application of me-

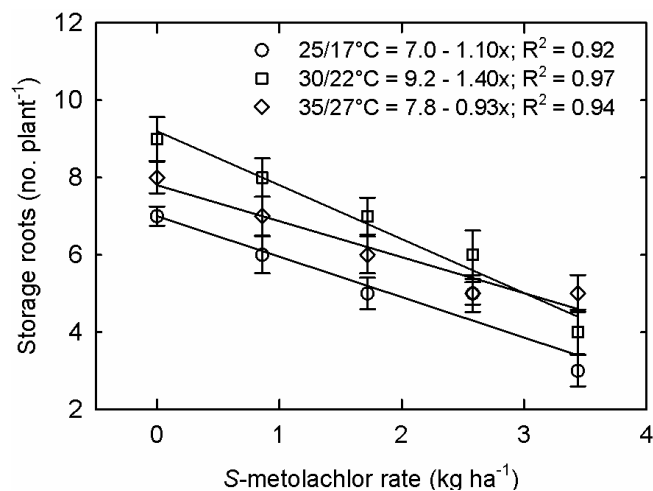


Figure 3. S-metolachlor and rainfall effects on storage roots of Beauregard sweetpotato grown in soil-plant-atmosphere-research growth chambers at 35/27°C, 30/22°C, and 25/17°C day/night temperatures and harvested 61 days after transplanting in 2012. Since there was no difference between rainfall treatment levels, data on rainfall, no-rainfall were combined across S-metolachlor rates. Values represent the mean of eight plants and the error bars are $\pm$ SE of the mean.

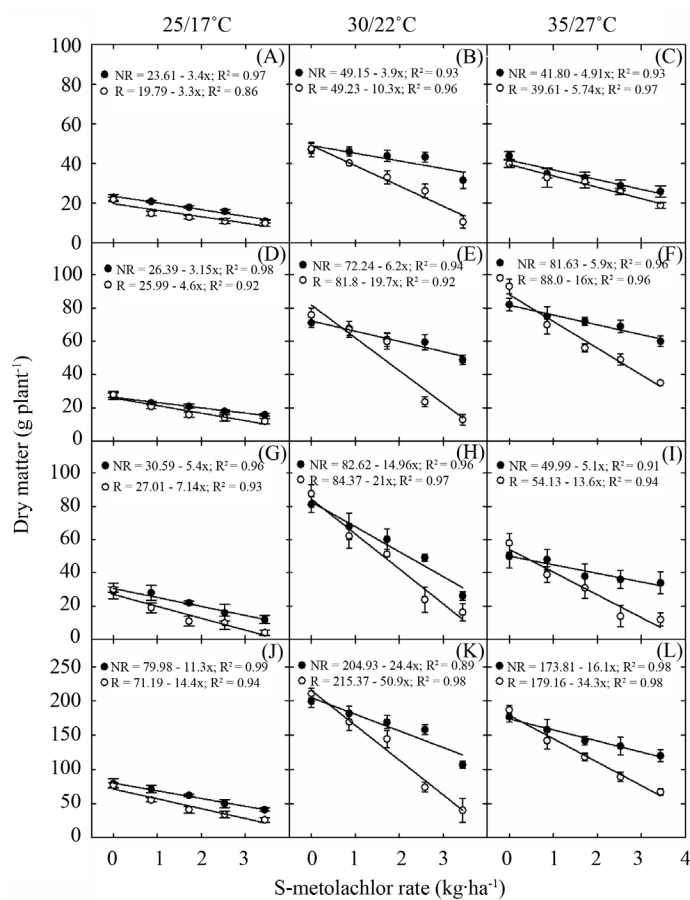


Figure 4. Effects of S-metolachlor with rainfall (R) and no rainfall (NR) on (A)-(C) leaf, (D)-(F) stem (G)-(I) root, and (J)-(L) total dry matter accumulation of Beauregard sweetpotato grown in soil-plant-atmosphere-research growth chambers at 25/17°C, 30/22°C, and 35/27°C day/night temperatures and harvested 61 days after transplanting in 2012. Values represent the mean of four plants and the error bars are $\pm$ SE of the mean.

tolachlor.

Even though 21%, 57% and 108% more stem biomass was produced compared to leaf biomass at low (25/17°C), optimum (30/22°C) and high (35/27°C) temperatures, respectively, in the absence of S-metolachlor application, the decline in stem biomass followed similar trends as observed in leaf biomass with S-metolachlor rates across all growth temperatures and rainfall treatments (**Figure 4(D)-(F)**). Similar to our findings, Harrison *et al.* [52] reported a 19% and 79% decline in collard “Georgia” seedling shoot weight with 6.0 kg⁻¹·ha⁻¹ metolachlor PRE in greenhouse and field studies, respectively, when compared to the untreated check. Plants grown at optimum and high temperatures produced 163% more stem biomass than plants grown at low temperature, when averaged over rainfall treatments in the absence of S-metolachlor application showing positive stem biomass response to higher temperatures. Stem biomass declined at a lesser rate in the low temperature (25/17°C) than at optimum (30/22°C) and high (35/27°C) temperature conditions with or without rainfall treatments (**Figure 4(D)-(F)**).

For both rainfall and no-rainfall, root biomass was higher for plants grown in optimum compared to high and low temperature environments, with higher biomass in high temperature compared to low temperatures (**Figure 4(G)-(I)**). In the absence of S-metolachlor and with no-rainfall, plants grown at optimum temperature (30/22°C) conditions produced 82.62 g plant⁻¹ which was 2.7 and 1.7 times more than root biomass produced at low (30.59 g plant⁻¹) and high (49.99 g plant⁻¹) temperatures, respectively. However, with rainfall treatment, root biomass production was, 27.01, 84.37 and 54.13 g plant⁻¹ for low, optimum and high temperature grown plants, respectively. The influence of S-metolachlor, in general, was more pronounced at the optimum temperature (17.98 g·kg⁻¹ S-metolachlor) than at low (6.25 g·kg⁻¹ S-metolachlor) or high temperature (9.35 g·kg⁻¹ S-metolachlor) treatments, when averaged across rainfall treatments (**Figure 4**). Root biomass production declined by 37%, 28% and 33% with rainfall, and 3%, 16% and 4% without rainfall after transplanting of slips and herbicide application at low, optimum and high temperature treatments, respectively, when compared to untreated checks for rain and no rainfall. At the lowest rate of S-metolachlor (0.86 g·kg⁻¹), root biomass declined 25%, 26% and 15% with no-rainfall, and 38%, 36% and 36% with rainfall at low, optimum and high temperatures, respectively. But when S-metolachlor was applied at nearly a 4× label use rate 3.44 kg·ha⁻¹, the decline in root biomass production was higher compared to the lower rate by 87%, 82% and 79% with rainfall and 59%, 68% and 32% without rainfall event, as growth temperatures increased.

Similar to plant component biomass responses, total biomass per plant was generally less in low temperature compared to optimum and high temperature environments, which was more pronounced with rainfall compared to no rainfall after transplanting and herbicide treatment across the three temperature treatments (**Figure 4(J)-(L)**). Compared to the untreated checks for both rainfall and no-rainfall treatments, total biomass was greater at optimum than at high temperatures, with biomass at high temperatures being greater than the low temperature environment (**Figure 4**). Similar to the decline in leaf, stem and root biomass, the decline in total biomass was linear across all temperatures with increasing concentration of S-metolachlor rate, suggesting that rates of decline were temperature dependent and modified by rainfall events. Total biomass production at low temperature in the absence of both S-metolachlor and rainfall event was 2.6 and 2.2 times lower when compared to optimum and high temperature, respectively, but when rainfall occurred immediately after transplanting, total biomass production was 3 and 2.5 times lower. Similar to the untreated checks, the rate of total biomass decline was higher with plants grown in optimum temperature compared to high and low temperatures, with a higher rate of decline in high versus low temperature environments. Total biomass decline was 11.3, 24.4 and 16.1 g plant⁻¹ with no-rainfall, versus 14.4, 50.9 and 34.3 g plant⁻¹ with rainfall, for low, optimum and high temperatures, respectively, with an incremental increase in S-metolachlor rate. When rainfall followed S-metolachlor treatments, total biomass production at low, optimum and high temperatures declined by 17%, 29% and 49%; 10%, 34% and 81%, and 16%, 27% and 66% at minimum, maximum recommended label use rates and the highest S-metolachlor rate used in this study, respectively, when compared to the untreated check. However, when no-rainfall followed herbicide treatment, total biomass declined by 12%, 20% and 49%; 10%, 17% and 41%; and 8%, 13% and 32% under the same temperature conditions and herbicide rates. Similar to vine and leaf growth, these results indicate that growth and development at low temperatures are slow compared to the warmer temperatures in this study, even in the absence of the herbicide. Harter and Whitney [53] reported slower growth of sweetpotato at 15°C compared to plants grown at higher temperatures, which corroborates our results.

In this study, sweetpotato leaf, stem and root biomass was less with higher rates of S-metolachlor followed by rainfall in all three temperatures. This is probably due to rainfall moving the herbicide into the root initiation

zone of transplanted slips making it available for plant uptake and over-whelming plant herbicide metabolism processes leading to impaired growth. Similar declines in growth have been reported in other studies, 16% decline in black bean biomass with $3.2 \text{ kg}\cdot\text{ha}^{-1}$ S-metolachlor PRE [46], 36% decline in sugarbeet biomass with $1.4 \text{ kg}\cdot\text{ha}^{-1}$ S-metolachlor PRE in a greenhouse study [54], and delayed emergence and reduced growth with S-metolachlor treatment followed by irrigation treatments in peanuts [55]. Similarly, Robinson and McNaughton [56] reported 27% and 29% decline in carrot shoot dry weight with 1.6 and $3.2 \text{ kg}\cdot\text{ha}^{-1}$ S-metolachlor POST, respectively, as well as 14% and 16% decline in red beet shoot dry weight with 1.6 and $3.2 \text{ kg}\cdot\text{ha}^{-1}$ S-metolachlor PRE, respectively, when compared to the untreated check under field conditions. In greenhouse study, Rowe and Penner [35] reported that corn hybrids evaluated were injured with a high metolachlor rate of $6.7 \text{ kg}\cdot\text{ha}^{-1}$, which is similar to our results with S-metolachlor treatments in sweetpotato. The decreased plant-component and total biomass with S-metolachlor rates, temperature levels, and rainfall events reflect the changes in the decline in leaf production, vine growth, leaf area development (Figure 1) and storage root production and bulking (Figure 2 and Figure 3) across all the treatments.

Environmental, cultural and cultivar differences can have pronounced effect on how assimilates are allocated in sweetpotato [57]. Biomass partitioning represents source-sink relationships in plants and growth plasticity of the whole plant in response to environment. Similar to root biomass responses to S-metolachlor rates and temperature treatments, the biomass allocation to roots declined with increasing S-metolachlor concentration across all temperatures (Figure 5). Similar to the decline in biomass of plant components, dry matter partitioning to

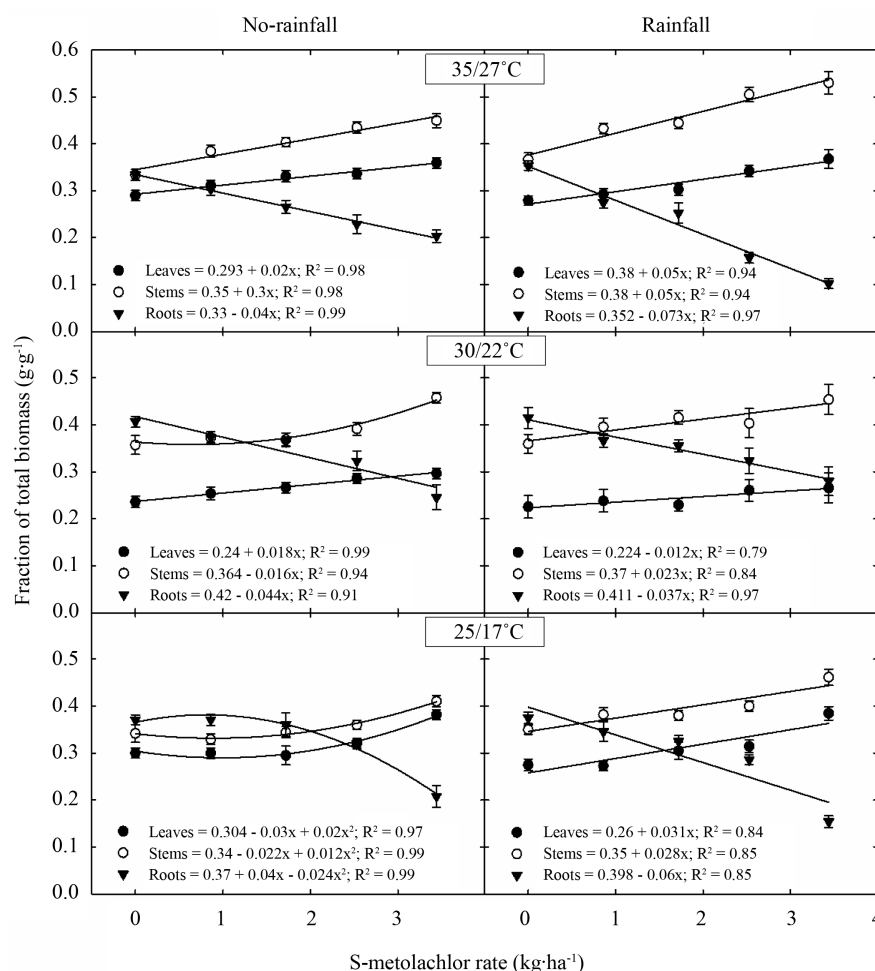


Figure 5. S-metolachlor and rainfall effects on biomass partitioning of Beauregard sweetpotato grown in soil-plant-atmosphere-research growth chambers at 25/17°C, 30/22°C, and 35/27°C day/night temperatures and harvested 61 days after transplanting in 2012. Values represent the mean of four plants and the error bars are $\pm$ SE of the mean.

roots declined linearly in all treatment combinations, except at low temperature with no-rainfall treatment where the decline was quadratic. However, biomass partitioning to stems and leaves increased with increased rates of S-metolachlor across the temperature treatments (Figure 5). Similar to the decline in biomass allocation to the roots, stems and leaves, allocation was linear with high temperature and both rainfall and no-rainfall, and optimum and low temperatures in the presence of rainfall. The increase in biomass allocation to the shoots with increasing concentration of S-metolachlor was however, quadratic at low temperature with no-rainfall. In the absence of the herbicide, more biomass (about 41% for optimum, 34% for high and 38% for low temperature) was partitioned to the roots in all three temperatures for plants harvested at 61 DAT. The biomass partitioning responses to temperature corroborate with a multi-locational field study conducted by Belehu [58] that showed 48% to 73% of dry matter was partitioned to storage roots among three cultivars measured at 150 days after transplanting. Since sweetpotato growth is very plastic, greater biomass was partitioned to leaves and stems because of impeded storage root initiation and development with higher rates of S-metolachlor.

Overall, comparing biomass allocation across the three temperature environments, plants grown at optimum temperatures partitioned a high proportion of biomass to roots, while those grown at high temperatures partitioned a high proportion of biomass produced to the shoots (stems and leaves) because storage root bulking became impaired at the higher temperature treatments. Similar trends in biomass allocation have been reported in potato (*Solanum tuberosum* L.) [59] and cotton [60] [61] under high temperature treatment. Knowledge of temperature effects on assimilates allocation coupled with seasonal temperature trends can be useful in timing of planting to enable the various phases to coincide with optimal temperature conditions.

4.4. Storage Root Fresh Weight

Storage root fresh weight showed interaction between S-metolachlor and rainfall treatments across all temperatures (Figure 6(A), Figure 6(C) and Figure 6(E)). The interaction indicated a linear response of increasing injury with increasing S-metolachlor concentration for no-rainfall and rainfall with R^2 values of at least 76%, for storage root weight. Storage root yield was less with rainfall than with no-rainfall across the three temperatures as S-metolachlor rate increased (Figure 6(A), Figure 6(C) and Figure 6(E)). In the absence of S-metolachlor, storage root weight for plants grown in the low temperature environment was 107.41 g plant⁻¹ with rainfall, which was 2.5 and 1.8 times less than storage root weight at optimum and high temperatures, respectively. However, when no rainfall occurred, storage root yield at low temperature was 161.52 g plant⁻¹ which was 3.6 and 2.5 times less than storage root yield at optimum and high temperatures, respectively. Storage root yield at optimum temperature conditions was 1.4 and 1.5 times greater than storage root yield at high temperatures with no-rainfall or rainfall, respectively. Rate of decline in storage root weight as S-metolachlor concentration increased was temperature dependent. In the presence of rainfall and low temperature growing conditions, storage root production declined 34.5 g plant⁻¹ with an incremental increase in S-metolachlor concentration, but the rate of decline was 72% and 60% more at optimum and high temperatures, respectively. However, when no-rainfall occurred, storage root production decline at low temperatures was 44.1 g plant⁻¹ as S-metolachlor rate increased incrementally, which was 1.9 times more at optimum temperatures, but not different compared to the high temperature environment (Figure 6).

In general, storage root weight was less at low temperature than at optimum and high temperatures. In comparison to the untreated check, storage root fresh weight declined by 23%, 17% and 17% with no rainfall and 28%, 27% and 28% with rainfall at the minimum recommended label use rate (0.86 kg·ha⁻¹) of S-metolachlor for low, optimum and high temperature conditions, respectively. When S-metolachlor was applied at the maximum recommended label use rate (1.43 kg·ha⁻¹), storage root weight declined by 39%, 29% and 28% with no-rainfall, and 46%, 45% and 46% with rainfall for low, optimum and high temperatures, respectively, when compared to the untreated check. However, at the highest S-metolachlor rate in this study (3.44 kg·ha⁻¹), storage root weight declined by 94%, 70% and 68% with no-rainfall; and 100%, 100% and 89% with rainfall, for low, optimum and high temperatures, respectively (Figure 6). Storage root weight declined with a steeper slope when S-metolachlor application was followed by rainfall than when no-rainfall occurred in all the three temperature treatments. This could probably be due to the low organic matter and clay content of the soil used in this experiment, which might have minimized herbicide adsorption and permitted herbicide mobility into the root zone of the soil profile. Low organic matter content (less than 2.0%), low clay mineral content and surface area enhances S-metolachlor solubility and mobility in the soil solution [25] [62]-[64]. In a field study, Robinson and

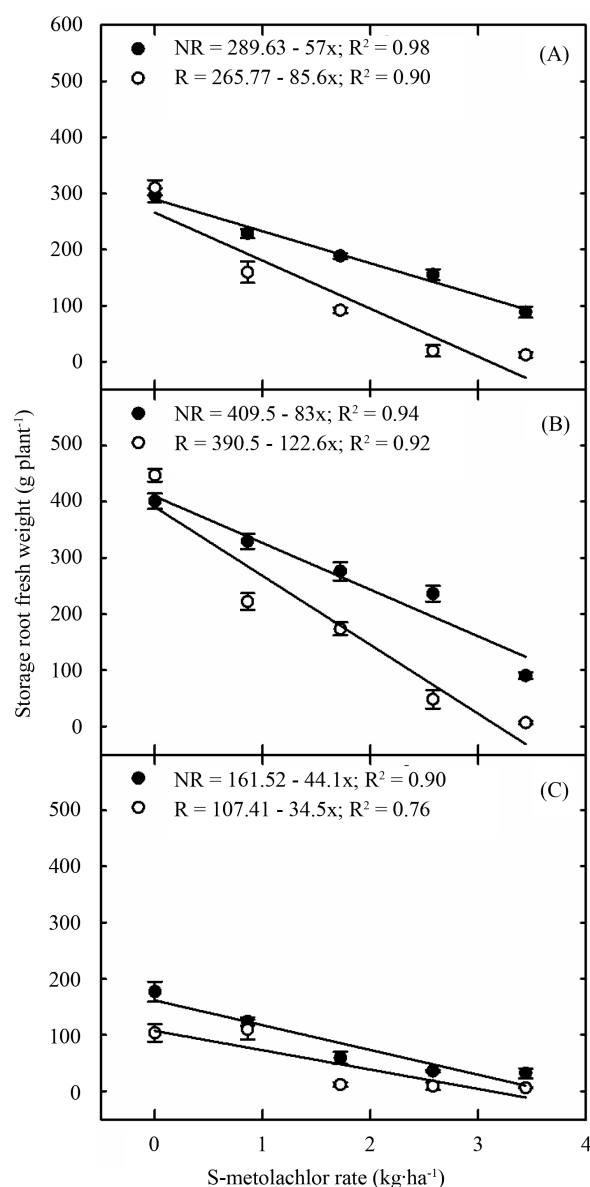


Figure 6. Effects of S-metolachlor with rainfall (R) and no rainfall (NR) on storage root fresh weight of Beauregard sweetpotato grown in soil-plant-atmosphere-research growth chambers at 25/17°C, 30/22°C, and 35/27°C day/night temperatures and harvested 61 days after transplanting in 2012. Values represent the mean of four plants and the error bars are ±SE of the mean.

McNaughton [56] reported 29% carrot marketable grade yield reduction resulting from late post-transplant (LPOST) application of S-metolachlor (1.2, 1.6 and 3.2 kg·ha⁻¹). They also reported red beet marketable yield reductions of 17% to 21% and 19% to 25% less than the untreated check for PRE and LPOST applications of S-metolachlor, and this is similar to our results. In another similar study, Bollman and Sprague [54] observed that rainfall event following PRE application of S-metolachlor enhanced absorption leading to death of sugar-beet plants. Furthermore, greater phytotoxicity of metolachlor in corn has been observed in wet locations than in dry locations and this was attributed to increased absorption due to more herbicide in soil solution as a result of the higher soil moisture content [65]. For rainfall and no-rainfall treatments, average storage root weight was higher in optimum temperature, followed by high and then by low temperature-grown plants. Harter and Whitney [53] reported that sweetpotato plants fail to survive when exposed to temperatures below 12°C, and growth increased from 15°C to 35°C and then suppressed at 38°C and this is similar to our observations.

5. Conclusion

Based on these predicted plant parameter loss data, growers are encouraged to select the lowest label use rate of S-metolachlor recommended for specific soil characteristics in order to minimize the potential risk of impaired growth and development in sweetpotato. Also, results from this study indicate that temperature, rainfall, and S-metolachlor application rate all play a role in the degree of S-metolachlor injury to sweetpotato. Across the three temperatures, sweetpotato growth and yield were affected by S-metolachlor and the degree of injury was S-metolachlor rate-dependent and more severe with a rainfall treatment immediately after transplanting and herbicide treatment. The herbicide was more injurious with the highest rate ($3.44 \text{ kg}\cdot\text{ha}^{-1}$) followed by rainfall across the three temperature treatments. Increasing S-metolachlor concentration induced a linear decline in vine elongation, leaf addition and leaf area expansion in all three temperatures. All these parameters were significantly less at low temperatures than at optimum and high temperatures. Leaf, stem and root dry matter accumulation declined linearly with increasing S-metolachlor rate and the response was steeper with a rainfall event at optimum and high temperatures. The partitioning of total biomass to roots declined with increased S-metolachlor dose with rainfall and no-rainfall treatments in all three growing temperatures, and this was reflected in the yield. Therefore, the rate response information in this study in conjunction with weather forecast data could be used to manage early season sweetpotato production practices such as transplanting time, S-metolachlor rates, and irrigation scheduling.

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