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Developing functional relationships between temperature and cover crop species vegetative growth and development

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Abstract

Cover crops planted in the offseason are subjected to uncontrollable weather variables that limit agro-ecological services through modifications in growth and development. The growth of five cover crop species was investigated in response to an array of day/night temperatures, 17/9, 22/14, 27/19, 32/24, and 37/29 ˚C. Shoot and root parameters were measured 33 d after planting. Quadratic functions best described most of the root and shoot dynamics in response to increasing temperatures except for a linear response of plant height in crimson clover (*Trifolium incarnatum*) and mustard (*Brassica juncea*). Temperature minimum (Tmin), maximum (Tmax), and optimum (Topt) for shoot traits varied from 9.8 to 10.6, 37.5 to 43.2, and 23.9 to 26.5 ˚C, respectively. The Tmin for root traits varied significantly, ranging from 8.5 to 10.8 ˚C. Topt and Tmax ranged from 22 to 25.7 and 35.2 to 40.6 ˚C, respectively. On average, the Topt for root traits was significantly lower than shoot traits in four of five species. Regardless of temperatures, cover crop species recorded higher biomass partitioning to shoot (62%) than to root, with a maximum proportion of biomass partitioned to shoot in crimson clover and Mighty Mustard Pacific Gold (80%) than other species (64–70%). The results of this study will help growers choose mixes of cover crops with the same temperature range to plant in the same climatic conditions during fallow periods. The cardinal temperatures and functional algorithms for growth and developmental traits could be used to develop models for cover crops under different temperature conditions.

1 | INTRODUCTION

Cover crops span a diverse range of species and plant types commonly grown for soil and water conservation (Clark, 2015). Growing cover crops during fallow periods can increase nitrogen for cash crops, improve cash crop yield (Tonitto et al., 2006), and provide multiple benefits to soil health (Dabney et al., 2001; Fageria et al., 2005). Essential benefits of cover crops are to cover the soil over the winter to protect the surface from erosion, high-velocity precipitation, and provide a high-humidity environment for bacteria, fungi, and invertebrates to break down the stubble remaining from the previous cash crop (Wienhold et al., 2018; Clark, 2015).

Cover crop species planted in early or late fall experience a range of air and soil temperatures (Blanco-Canqui et al., 2014). Extreme temperatures (sub- and supra-optimal) during the early seedling stage significantly affect the growth

Abbreviations: DAP, days after planting; SPAR, soil–plant–atmosphere research; Tmax, maximum temperature; Tmin, minimum temperature; Topt, optimum temperature.

and development of plants (Li et al., 2014; Lynch & Clair, 2004). Research on cash crops has shown that the temperature optimum (Topt) varies among species and determines adaptability of different species to different climatic zones (Gray & Brady, 2016; Nagai & Makino, 2009; Reddy et al., 2017; Tribouillois et al., 2016). Crop growth and development typically follow a positive linear function between minimum temperature (Tmin) and Topt. A negative linear function is observed between Topt and beyond Topt in many crops (Wheeler et al., 2000). The ability of plant species to withstand changing microclimatic conditions depends on their thermal adaptation ability (Luo, 2011; Urban, 2015). A range of crop species has been evaluated for their adaptability and response to temperature changes by considering physiological, root and shoot parameters (Luo, 2011; Luo et al., 2020; Nagai & Makino, 2009; Reddy et al., 2017). However, similar thermal adaptation studies are limited in cover crops. Recently, germination response to temperature changes and water potential has been reported using a wide range of cover crop species (Tribouillois et al., 2016). To help select the most appropriate cover crops for planting as a function of temperature, germination response to temperature alone is insufficient. Cover crops are exposed to extreme, both sub- and supra-optimal, temperatures due to the diversity of planting dates throughout the United States. These extreme temperatures can prevent cover crops from producing enough biomass to keep the land covered (Weil & Kremen, 2007), limiting the expected agroecological services from the cover crops.

Cover crops are being incorporated into cropping systems to scavenge nitrogen from the soil profile and use the scavenged nitrogen for cash crop growth (Nevins et al., 2020; Singh et al., 2018). Cover crop root biomass physically binds, anchors, and stabilizes soil particles; provides a food source to soil organisms; and increases microbial biomass (Blanco-Canqui et al., 2014). The significance of belowground cover crop biomass for building soil organic matter has been reported across species (Austin et al., 2017). Root biomass often decomposes faster than aboveground biomass and plays an essential role in structuring the soil and improving soil health (Sievers & Cook, 2018). Certain cover crop species with vigorous root growth in favorable areas of the soil profile may provide more benefits than other species by improving nutrient utilization and mobilizing from deeper layers (Rosolem et al., 2002) and can maintain a better shoot–root balance.

Early development of root systems is critical in seedling establishment and achieving the desired functionality throughout the fallow period. The temperatures that occur during the early growing season are very influential on the cover crop. Changes in growing temperature can induce significant biomass accumulation changes and their allocations (Boese & Huner, 1990; Nagai & Makino, 2009). There have been reports describing how extreme temperatures affect plant growth and development at various stages. Studies have used leaf, shoot, and root properties to explain the functional relationship between temperature and growth (Luo et al., 2020; Reddy et al., 2017). Shoot and root responses to temperature changes can be species-specific and different species are often known to have different Topt for shoot and root growth traits (Gray & Brady, 2016; Reddy et al., 2017). However, we are aware of no information describing the effects of temperature on the shoot and root morphological traits of cover crops at the early growth stage. This information is critical to understand how plants adjust their biomass allocation between shoot and root (Aidoo et al., 2016) and cardinal temperatures for selecting site suitability of specific cover crop species (Tribouillois et al., 2016).

On the other hand, field studies for understanding the effect of temperature on the cover crop is tedious, inconsistent, and seasonally limited. Therefore, there is a need for simple, rapid, and reliable techniques to understand cover crops' responses to temperature. The soil–plant–atmosphere research (SPAR) systems have the advantage of precise control of air temperature, CO_2 concentration, and air humidity under natural solar radiation compared to other controlled-environment facilities (Allen et al., 2020). Functional algorithms developed from studies using sunlit plant growth chambers helped improve the crop models (Reddy et al., 1997a, 1997b) used for field applications and the policy arena (Liang et al., 2012). Here, we used the SPAR systems to quantify the effect of gradient temperatures on the growth and development of cover crops, a prerequisite for modeling studies.

This study used five different cover crop species since they are widely grown in the United States and worldwide during the fallow season. The present study hypothesized that physiological, above- and belowground related parameters in cover crops would have different temperature thresholds or cardinal temperatures. The specific objectives of this study were to (a) quantify the effects of gradient temperature on aboveground and belowground traits, and (b) calculate the cardinal temperatures (Tmin, Topt, and maximum temperature, Tmax) for the shoot and root traits.

Core Ideas

- Functional relationships of cover crop species growth to temperature are needed to develop models.
- Determine the response of vegetative growth of several cover crop species to temperature.
- Estimate cardinal temperatures for the shoot and root traits.
- Among the species tested, mustard consistently provided higher biomass across a wide range of temperatures.

TABLE 1 The environmental parameters, average day, night, day/night temperatures, average day chamber CO_2 concentration, and average day/night vapor pressure deficit (VPD) were recorded during the 25 d for each treatment

Set temperature	Measured temperature ˚C			CO_2 µmol mol^{-1}	VPD kPa	
Day/Night	Day	Night	Day/Night	Day	Day	Night
17/09	16.85 ± 0.11	10.22 ± 0.21	13.07 ± 0.14	429.29 ± 1.53	0.62 ± 0.00	0.57 ± 0.01
22/14	21.44 ± 0.07	14.22 ± 0.03	17.32 ± 0.04	427.66 ± 0.91	0.66 ± 0.01	0.60 ± 0.00
27/19	25.88 ± 0.05	18.68 ± 0.04	21.78 ± 0.03	428.71 ± 0.69	0.73 ± 0.02	0.65 ± 0.01
32/24	30.48 ± 0.10	23.20 ± 0.04	26.34 ± 0.05	429.60 ± 1.55	0.77 ± 0.03	0.68 ± 0.01
37/29	35.15 ± 0.06	27.78 ± 0.04	30.96 ± 0.03	428.88 ± 0.81	0.86 ± 0.05	0.75 ± 0.03

2 | MATERIALS AND METHODS

2.1 | Crop husbandry

This study included four cool-season cover crops (cereal rye [*Secale cereale*], crimson clover [*Trifolium incarnatum*], triticale [*Triticum* x *Secale*], and winter wheat [*Triticum aestivum*]) and one warm-season cover crop (Mighty Mustard Pacific Gold, *Brassica juncea*). The experiment was carried out in the controlled environment facility (SPAR units) at the Environmental Plant Physiology Laboratory, Mississippi State University (33˚28′N, 88˚47′W), Mississippi State, MS. The specifications and operation of SPAR units have been detailed in Reddy et al. (2001).

Seeds of five cover crops were sown in 30.5- by 15.2-cm (height by diameter) polyvinyl chloride pots filled with a soil medium consisting of 3:1 sand/topsoil (v/v). The pots were placed in SPAR units set at 27/19 ˚C day/night temperatures with 70% relative humidity for 7 d to facilitate uniform emergence under natural daylengths (photoperiod of 12/12h light/dark). The seedlings were thinned down to one plant per pot before the start of actual temperature treatments. The plants were watered and fertilized with full-strength Hoagland nutrient solution (Hewitt, 1952) based on evapotranspiration measured daily (Reddy et al., 2001). The experiment consisted of two factors (5 levels of temperature treatments × 5 species) with six replications. The pots were randomly arranged within each SPAR unit to avoid positional effects. In this study, 150 plants (5 cover crops × 5 treatments × 6 replications) were used to estimate the five different cover crop species' cardinal temperatures.

2.2 | Variable temperature treatments

Upon emergence, temperature setpoints were adjusted to five different day and night temperatures (17/09, 22/14, 27/19, 32/24, and 37/29 ˚C) and maintained for 25 d (Table 1). In all the temperature treatments, the maximum temperature was maintained from sunrise to sunset (photoperiod of 12/12 h light/dark), and the minimum (night) was held from 1 h after sunset to sunrise with a 30-min transition period between maximum to minimum temperatures and vice versa. In all the SPAR units, microclimatic conditions such as temperature (HMV 70Y, Vaisala, St. Louis, MO), CO_2 (model LI-6252, LI-COR, Lincoln, NE), and vapor pressure deficit (estimated following Murray, 1967) were monitored at 15-min intervals throughout the experiment. The plants were grown in a SPAR unit under natural daylengths in Starkville (33˚28′N, 88˚47′W), Mississippi State, MS. Each SPAR unit consists of a 1.27-cm thick Plexiglas, allowing 97% of the visible solar radiation to pass without spectral variability in absorption. The set and measured environmental variables in this study using five different SPAR units are provided in Table 1.

2.3 | Measurements

Several physiological (leaf chlorophyll, leaf flavonoid index, and nitrogen balance index), aboveground (height, main stem or axis leaves, whole-plant leaf area, shoot dry weight, and whole plant dry weight), and belowground parameters (root tips, root forks, root crossings, total root length, root volume, root surface area, and root dry weight) were recorded from all five treatments.

2.4 | Physiological and shoot parameters

Leaf chlorophyll content, flavonoids index, and nitrogen balance index (the ratio of chlorophyll content/flavonoids) were measured on the uppermost, fully expanded leaf, second from the top, across all treatments using a handheld Dualex Scientific instrument (Force A DX16641, Paris, France) at 32 d after planting (DAP). The following morning (33 DAP), all plants were hand-harvested, plant height (cm) was measured, main stem or axis leaves number were counted, and then total leaf area (cm^2 plant^{-1}) was determined using LI-3100 leaf area meter (LI-COR, Lincoln, NE). Plant components such

as shoot dry weights (leaf weight [g plant^{-1}] + stem weight [g plant^{-1}]) and root weight (g plant^{-1}) were determined by drying the samples at 80 ˚C until a constant weight was reached.

2.5 | Root morphology

Individual plants were harvested, and the roots were separated from the shoot. Any soil that remained adhered to the roots was washed thoroughly with a mild speed water stream. Roots were floated in 5 mm of water in a 0.4- by 0.3-m glass tray and were separated and untangled using plastic forceps to minimize any root overlap. The roots were scanned with an Epson Expression 11000XL scanner at a resolution of 800 dots per in, and images were analyzed using WinRHIZO Pro 2009C software (Regent Instruments, Québec, Canada). The digitized images were used to determine gradient temperature effects on root development (number of root tips, number of root forks, and number of crossings per plant) and growth parameters such as total root length (cm plant^{-1}), root volume (cm^3 plant^{-1}), and root surface area (cm^2 plant^{-1}).

2.6 | Statistical analysis

The experimental layout was a split plot with a complete randomized block design, considering temperature treatment as the whole plot and species as the subplot. The variance analysis was performed to test the effects of temperature treatments, species, and their interactions on the measured traits using SAS 9.2 (SAS Institute, Cary, NC). The fit of each regression equation for all parameters' response to temperature was determined by comparing r^2. The best-fit regression function was used to estimate cardinal temperatures (Tmin, Topt, and Tmax) for all the measured parameters among five cover crops. The cardinal temperatures were estimated following a similar procedure described by Seepaul et al. (2011) for a quadratic response. The Tmin and Tmax define the limits of growth and development of different cover crops and Topt at which the response (growth and development) of a cover crop is maximal. Graphs were generated using Sigma Plot 13.0 (Systat Software, San Jose, CA).

3 | RESULTS AND DISCUSSION

This study compared five different cover crop species for their adaptive responses of both above- and belowground parameters to temperature (Figure 1; Tables 1, 2). To our best knowledge, this is the first study that tests different cover crop species across a wide range of growing temperatures (daily average temperature from 13 to 31 ˚C). Growing plants at a wide range of temperatures allowed us to calculate cardinal temperatures and develop functional relationships for various growth and developmental processes at the early seedling stage (Tables 1, 2, 3). Knowledge of cover crop performance in response to temperature changes will help select a cover crop best suited for fallow planting depending on local climatic conditions. On average, all the treatments' day and night temperatures were ±0.1 ˚C of the target temperatures (Table 1). At the same time, the vapor pressure deficit was slightly lower (0.24 kPa) with a cooler temperature (13.7 ˚C) compared to a higher temperature (31 ˚C).

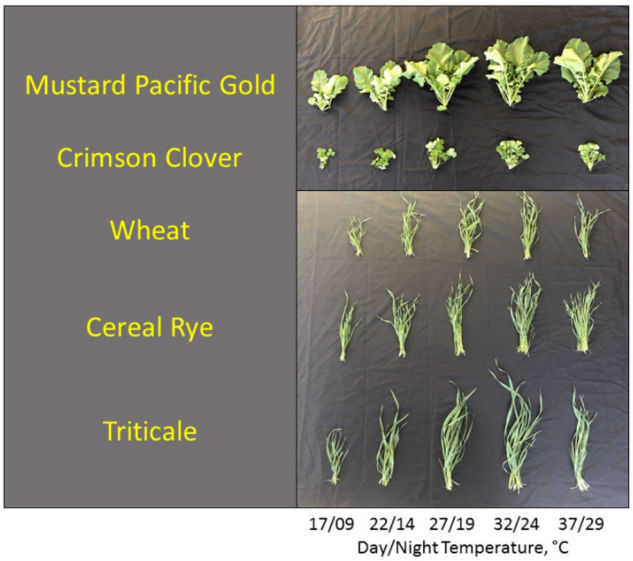

FIGURE 1 Pictorial representation of temperature effects on shoot growth and development of five cover crops measured 33 d after planting or 25 d after temperature treatment

3.1 | Physiological parameters

Chlorophyll content, flavonoids index, and nitrogen balance index were affected significantly by temperature treatments and species (Table 2). The interaction of treatment × species for chlorophyll content was significant, whereas the interactions for the flavonoids index and nitrogen balance index were non-significant (Table 2). A decreasing trend in chlorophyll content with increasing temperature was observed in all species (Figure 2a). A decrease in chlorophyll content may be due to heat-stress induced premature loss of chlorophyll or accelerated chlorophyll degradation under high-temperature stress (Feierabend, 1977). On average, across species, a higher chlorophyll (33.6) and flavonoid index (0.96) was observed at low temperature (13 ˚C), whereas at high temperature (33 ˚C), they decreased by 14 and 43%, respectively. Under

TABLE 2 Summary of analysis of variance across the temperature treatments (T), species (S), and their interaction (T × S) on different root and shoot growth, physiological, and developmental traits measured at 33 d after planting. Plant height (PH), number of leaves (LVS), leaf area (LA), chlorophyll content (CC), flavonoids index (FI), nitrogen balance index (NBI), root tips (RT), root forks number (RF), root crossing number (RC), root length (RL), root volume (RV), root surface area (RSA), root dry weight (RDW), shoot dry weight (SDW) and whole plant dry weight (TDW)

Source	PH	LVS	LA	CC	FI	NBI	RT	RF	RC	RL	RV	RSA	RDW	SDW	TDW
Temperature (T)	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
Species (S)	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
T × S	***	***	***	*	**NS**	**NS**	***	***	***	**	***	***	***	***	***
Temperature															
17/09[a]	a[b]	a	a	a	a	a	a	a	a	a	a	a	a	a	a
22/14	b	b	b	a	b	b	b	b	bc	b	a	b	b	b	b
27/19	c	c	c	a	bc	b	c	c	c	c	b	c	c	c	d
32/24	c	d	c	a	c	b	d	d	d	d	b	c	c	d	d
37/29	b	c	d	b	c	b	ab	b	b	a	a	ab	b	c	c
Species															
Cereal Rye	d	d	b	b	a	c	c	c	c	c	b	c	c	c	c
Crimson Clover	a	a	a	a	ab	a	a	a	a	a	a	a	a	a	a
Mighty Mustard Pacific Gold	e	e	c	a	bc	d	d	d	d	d	c	d	d	d	d
Triticale	c	c	b	c	c	c	b	b	b	b	b	bc	c	c	c
Wheat	b	b	a	b	c	b	b	b	b	b	b	b	b	b	b

*Significant at the .05 probability level; **Significant at the .01 probability level; ***Significant at the .001 probability level; NS non-significant. [a]Day/night temperatures in °C. [b]Temperature and species with a common letter are not significantly different based on the t-test at $P < .05$.

TABLE 3 Quadratic equation constants (a, b, and c); regression coefficients (r^2); and minimum, optimum, and maximum temperatures (Tmin, Topt, and Tmax, respectively) for the shoot and root parameters of five cover crops species. Maximum trait value (MTV) at Topt for each of the parameters is measured in all five species. All the trait values are expressed on a per plant basis

	Equation constants				Cardinal temperatures			
					˚C			
Parameter	a	b	c	r^2	Tmin	Topt	Tmax	MTV
Cereal Rye								
Leaf number, no.	−48.03	6.0804	−0.10631	.9	9.5	28.6	47.7	38.9
Leaf area, cm^2	−520.29	64.6701	−1.32794	.81	10.2	24.3	38.5	267.1
Aboveground weight, g	−2.59	0.3194	−0.00624	.88	10.1	25.6	41.1	1.5
Total dry weight, g	−3.67	0.463	−0.00936	.85	9.9	24.7	39.5	2.1
Root crossings, no.	−9,426.5	1,180.6	−26.4	.83	10.4	22.3	34.3	3,765.1
Root forks, no.	−84,896.4	10,570.8	−235.0	.8	10.5	22.5	34.5	33,983.8
Root tips, no.	−28,498.4	4,139.6	−93.7	.85	8.5	22.1	35.7	17,237.1
Root dry weight, g	−0.92	0.1193	−0.0026	.98	9.9	23	36.1	0.4
Root length, cm	−8,378.3	1,130.3	−25.2	.83	9.4	22.4	35.5	4,303.7
Root surface area, cm^2	−999.7	134.7	−3.006	.83	9.4	22.4	35.4	509.8
Root volume, cm^3	−9.62	1.2912	−0.02883	.83	9.4	22.4	35.4	4.8
Crimson Clover								
Leaf number, no.	−22.43	2.8312	−0.05458	.92	9.8	25.9	42.1	14.3
Leaf area, cm^2	−247.91	28.6546	−0.57415	.89	11.1	25	38.8	109.6
Aboveground weight, g	−0.92	0.1076	−0.00209	.9	10.8	25.7	40.7	0.5
Total dry weight, g	−1.09	0.1315	−0.00261	.98	10.5	25.2	39.8	0.6
Root crossings, no.	−3,209.7	351.5	−7.03	.77	12	25	38	1183
Root forks, no.	−26,630.5	3,045.1	−64.37	.83	11.6	23.7	35.7	9,382.8
Root tips, no.	−8,831.0	1,207.7	−26.13	.45	9.1	23.1	37.1	5,125.8
Root dry weight, g	−0.21	0.0253	−0.00055	.86	10.6	23	35.4	0.1
Root length, cm	−4,023.9	496.8	−10.3	.78	10.3	24.1	37.8	1,950.6
Root surface area, cm^2	−460.96	59.84	−1.29	.82	9.8	23.2	36.6	231.9
Root volume, cm^3	−4.27	0.583	−0.01304	.78	9.2	22.3	35.5	2.2
Mighty Mustard Pacific Gold								
Leaf number, no.	−3.1	0.8181	−0.01446	.93	4.1	28.3	52.5	8.5
Leaf area, cm^2	−2,345.47	263.42	−5.32	.92	11.6	24.8	37.9	915
Aboveground weight, g	−9.65	1.0588	−0.01984	.91	11.7	26.7	41.7	4.5
Total dry weight, g	−12.22	1.3472	−0.02574	.93	11.7	26.2	40.7	5.4
Root crossings, no.	−6,409.4	793.4	−13.67	.82	9.7	29	48.4	5,106.3
Root forks, no.	−163,877.4	18,017.6	−343.2	.93	11.7	26.2	40.8	72,602
Root tips, no.	−18,603.7	2,463.6	−46.1	.93	9.1	26.7	44.3	14,276.8
Root dry weight, g	−2.57	0.2857	−0.00587	.83	11.9	24.3	36.7	0.9
Root length, cm	−8,229.6	1,089.8	−21.68	.87	9.3	25.1	41	5,464.2
Root surface area, cm^2	−2,540.1	291.0	−5.94	.86	11.4	24.5	37.6	1,023.9
Root volume, cm^3	−54.99	5.94	−0.12371	.77	12.5	24	35.5	16.3
Triticale								
Leaf number, no.	−12.76	2.3912	−0.04248	.96	6	28.1	50.3	20.9
Leaf area, cm^2	−811.56	91.9592	−1.94193	.95	11.7	23.7	35.6	277.1
Aboveground weight, g	−3.04	0.3544	−0.00693	.97	10.9	25.6	40.2	1.5
Total dry weight, g	−3.86	0.4704	−0.00949	.97	10.4	24.8	39.2	2
Root crossings, no.	−4,488.3	595.1	−12.9	.57	9.5	23.1	36.6	2,370.7

(Continues)

TABLE 3 (Continued)

Parameter	Equation constants a	b	c	r^2	Cardinal temperatures ˚C Tmin	Topt	Tmax	MTV
Root forks, no.	−55,950.8	7,201.7	−159.9	.76	10	22.5	35.1	25,130.1
Root tips, no.	−14,496.3	2,423.4	−55.3	.92	7.1	21.9	36.6	12,037.6
Root dry weight, g	−0.64	0.093	−0.00206	.79	8.5	22.5	36.5	0.4
Root length, cm	−4,236.48	688.4903	−15.47935	.75	7.4	22.2	37.1	3,419.2
Root surface area, cm^2	−689.91	103.947	−2.36769	.88	8.2	22	35.8	451
Root volume, cm^3	−8.56	1.2253	−0.02818	.91	8.7	21.7	34.7	4.8
Wheat								
Leaf number, no.	−33.75	4.5931	−0.09018	.98	8.9	25.5	42	24.7
Leaf area, cm^2	−400.58	47.6359	−1.01935	.96	11	23.4	35.7	155.9
Aboveground weight, g	−2.4	0.2842	−0.00602	.99	11	23.6	36.2	1
Total dry weight, g	−3.19	0.3917	−0.0084	.95	10.5	23.3	36.1	1.4
Root crossings, g	−4,752.6	645.0	−14.7	.97	9.4	22	34.6	2,332
Root forks, no.	−49,438.0	6,493.8	−148.3	.98	9.8	21.9	34	21,646.4
Root tips, no.	−11,255.6	1,984.8	−45.1	.49	6.7	22	37.3	10,563.3
Root dry weight, g	−0.68	0.0876	−0.00192	.98	9.9	22.8	35.8	0.3
Root length, cm	−5,326.5	797.4	−18.2	.93	8.2	21.9	35.6	3,403.6
Root surface area, cm^2	−681.2	100.3	−2.3	.96	8.4	21.7	35	408.2
Root volume, cm^3	−6.95	1.0074	−0.02336	.99	8.6	21.6	34.5	3.9

low temperature, triticale recorded the highest chlorophyll content (Figure 2a) and flavonoid index (Figure 2b). Conversely, increased chlorophyll content and decreased leaf flavonoids were recorded in Mighty Mustard Pacific Gold (Figure 2a, b). Under high temperature, wheat recorded the highest leaf chlorophyll and flavonoids, followed by triticale, cereal rye, and crimson clover (Figure 2a, 2b). The nitrogen balance index (ratio of chlorophyll/flavonoids) increased quadratically with increasing temperature in all species, except Mighty Mustard Pacific Gold. The maximum nitrogen balance index was observed at 27/19 ˚C in cereal rye, 32/24 ˚C in triticale, crimson clover, and wheat, and 37/29 ˚C in Mighty Mustard Pacific Gold (Figure 2c). The adverse effects (% decrease from Topt) of Tmin and Tmax on nitrogen balance index were most significant for crimson clover (31%) and cereal rye (20%), respectively. These results indicate that plants grown under extreme temperatures may partition more carbon to synthesize polyphenols than chlorophyll (Li et al., 2015). Similar to other abiotic stress studies (Liu et al., 2013; Ma et al., 2014; Yuan et al., 2012), our results indicate that total flavonoid accumulation was most significant in response to low and high temperatures for all species (Figure 2b). These results suggest that flavonoids may serve a protective role by preventing the generation and scavenging of reactive oxygen species when exposed to extreme events (Agati & Tattini, 2010; Jaakola & Hohtola, 2010).

3.2 | Root morphology of cover crops

The spatial configuration of the root system architecture in the soil is important because it can play an essential role in increasing the soil organic carbon concentration along with optimizing the acquisition of water and nutrients by plants in response to different environments (Bardgett et al., 2014; Zhu et al., 2011). Significant ($P < .001$) effects of temperature, species, and the interaction between temperature and species were observed for root morphological parameters (Table 2). Variation in the root traits of cover crop species in response to temperature change might signify adaptive significance at the seedling stage, as similarly observed in other crops (Luo et al., 2020). The root development (tips, forks, and crossings) traits gradually increased from the minimum temperature (Tmin) to the optimal temperature (Topt) and then sharply decreased at the highest temperature (Figure 3). The quadratic functions best described, the root tips (Figure 3a), forks (Figure 3b), and crossing (Figure 3c) dynamics in response to increasing temperature treatments (Table 3). This quadratic trend resulted in the different cardinal temperatures for the number of root tips, forks, and crossings (Figure 3, Table 3). Based on the fits, the mean Topt of all cover crop species was 23.1 ˚C for root tip (ranged from 21.9 ˚C for triticale to 26.7 ˚C for Mighty Mustard Pacific Gold), 23.4 ˚C for root forks (ranged from 21.9 ˚C for wheat to 26.2 ˚C for Mighty Mustard Pacific Gold), and 24.3 ˚C for root crossing (ranged from 22 ˚C for wheat to

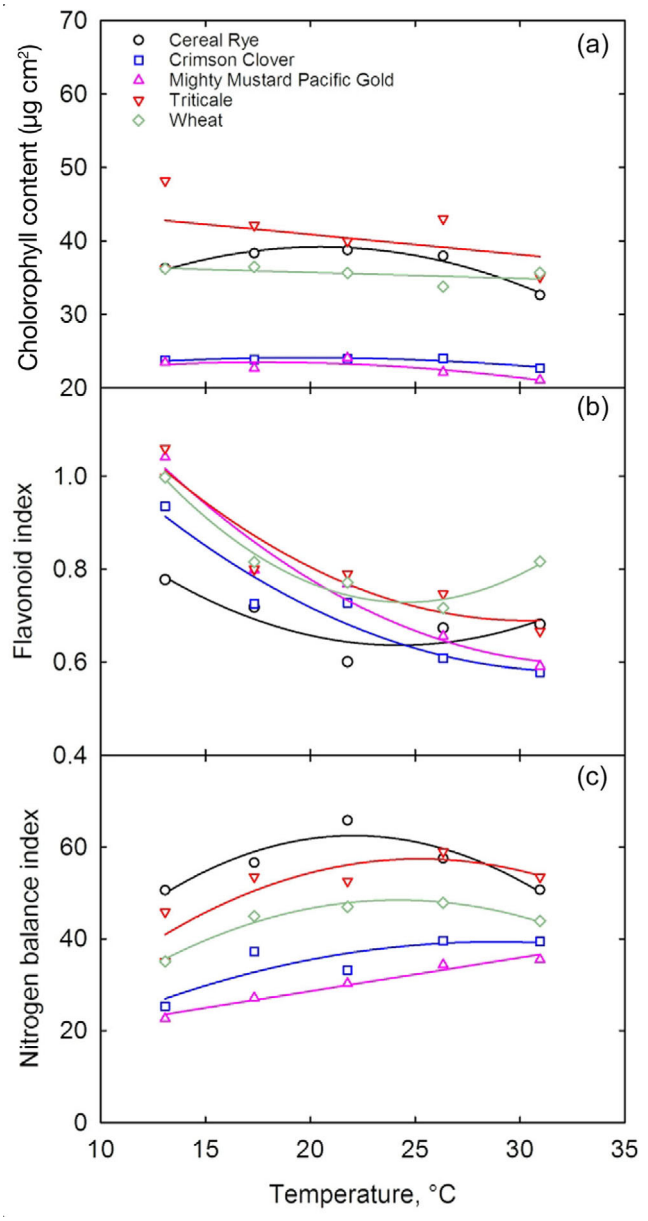

FIGURE 2 Temperature effect on chlorophyll content (a), flavonoid index (b), and nitrogen balance index (c) measured 33 d after planting or 25 d after temperature treatment. Values are the mean of six replications for each cover crop at each of the temperature treatment

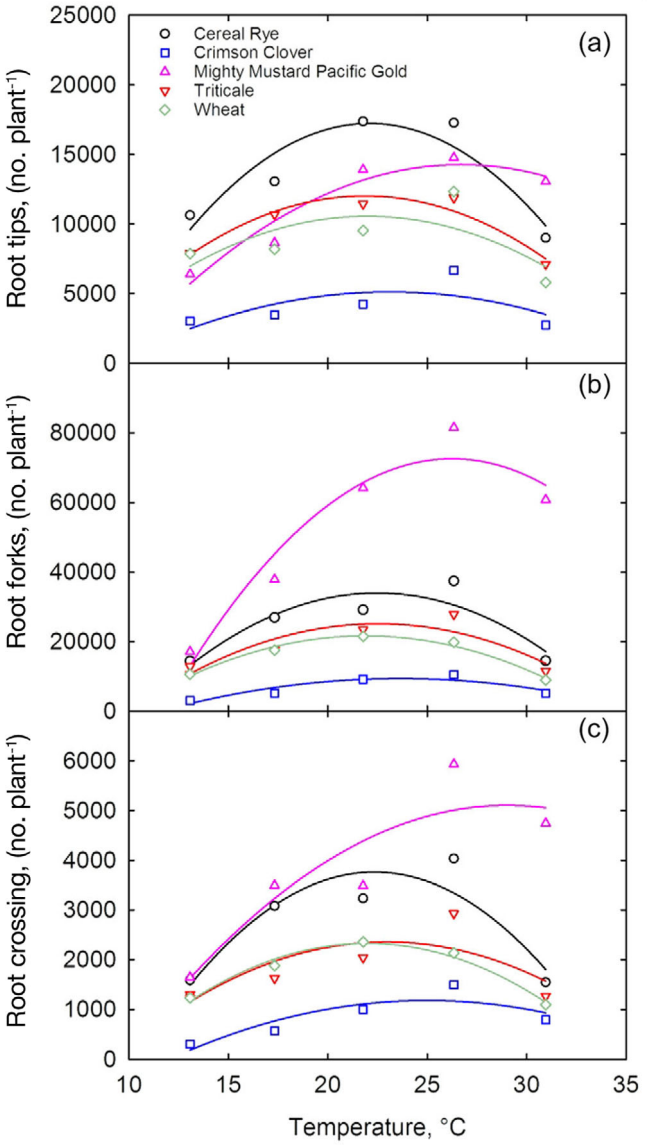

FIGURE 3 Temperature effects on root tips (a), root forks (b), and root crossings (c) measured 33 d after planting or 25 d after temperature treatment. Values are the mean of six replications for each cover crop at each temperature treatment, and the curves are fitted lines using quadratic functions

29 ˚C for Mighty Mustard Pacific Gold; Figure 3; Table 3). Similar to rice (*Oryza sativa*; Luo et al., 2020) and other studies (Gray & Brady, 2016), our results showed the existence of different Topt for root growth for different species. Mighty Mustard Pacific Gold had a higher Topt and a greater percentage of root forks (31%) and crossings (47.2%) than that of other species (Figure 3; Table 3). Wheat had a lower Topt (4.4–7.1 ˚C) than the Mighty Mustard Pacific Gold for root tips (Topt = 26.7 ˚C; Figure 3a), forks (Topt = 26.2 ˚C; Figure 3b) and crossings (Topt = 29 ˚C; Figure 2c). At Topt, the maximum number of root tips production was found to be at 21.1 ˚C in cereal rye and the minimum number of root tips in crimson clover at 23.1 ˚C (Figure 3a; Table 3). For Tmax, Mighty Mustard Pacific Gold recorded a smaller reduction in the number of root tips (6%), forks (10%), and crossings (1%) than other species compared to its Topt (Figure 3). For Tmin, the maximum reduction in the number of root tips (60%) and the number of root forks (82%) was observed in Mighty Mustard Pacific Gold compared to its Topt. It suggests that Mighty Mustard Pacific Gold may be more highly sensitive to cold temperatures than other cover crops. Root growth in response to extreme temperatures can be inhibitive or promotive (Luo et al., 2020). This observed root growth

phenomenon in our study under sub- and supra-optimal temperatures might be due to delayed or inhibited root meristem cell division (Francis, & Barlow, 1988; Zhukovskaya et al., 2018). This result implies that different cover crop species exhibit a differential adaptive response to low and high temperatures; thus, their performance would vary as growing temperature varies. For example, a cover crop with more branching throughout the root system may provide a greater ability to scavenge for nutrients and water from the soil profile than a species with less branching (Varney et al., 1993) at any given temperature.

Total root length, root volume, and root surface area are indicators of root size and play an essential function in water and nutrient uptake as well as resource use efficiency under varied abiotic stress conditions in crops (Calleja-Cabrera et al., 2020; Costa et al., 2002; Hammer et al., 2009), including in cover crops (Dabney et al., 2001). Our study revealed significant treatment, species, and treatment × species interaction ($P < .001$) for root length and root volume (Table 2). Similar to other studies (Luo et al., 2020; Reddy et al., 1992, 2017), root traits were significantly affected by temperature, while the magnitude of the temperature effect differed by species (Figure 4). Root length, volume, and surface area followed a quadratic trend in response to an increase in temperatures (Figure 4; Table 3) similar to root development traits. Among the cover crop species, Topt ranged from 21.9 (wheat) to 25.3 ˚C (Mighty Mustard Pacific Gold) for root length, 21.6 (wheat) to 24 ˚C (Mighty Mustard Pacific Gold) for root volume, and 21.7 (wheat) to 24.5 ˚C (Mighty Mustard Pacific Gold) for root surface area (Table 3; Figure 4). Mighty Mustard Pacific Gold exhibited a greater maximum total root length (5,464.2 cm, Topt = 25.1 ˚C; Figure 4a), root volume (16.3 cm^3, Topt = 24 ˚C; Figure 4b), and root surface area (1,023.9 cm^2, Topt = 24.5 ˚C; Figure 4c) than the other four species. On average, the plants grown at Tmin had lower total root length (51%), root volume (56%), and root surface area (54%) than the plants grown at Topt (Figure 4; Table 3). Similar to Tmin, the Tmax also significantly lowered the root length along with root volume and root surface area by 32, 45, and 38% compared to its Topt (Figure 4). Triticale (2.6 cm^3), cereal rye (2.3 cm^3), and wheat (2.2 cm^3) had higher root volume at Tmin than the other two species at the same temperature (Figure 4b). Mighty Mustard Pacific Gold showed significantly higher root surface area (Figure 4c) at all temperatures compared to crimson clover at 33 DAP. Overall, a decrease in total seedling root length was accompanied by a massive reduction of root volume and surface area (Figure 4), indicating reduced root biomass allocation per unit root length (Figure 4). These results mean that extreme temperatures not only affect seed germination events (Tribouillois et al., 2016), but they also have a significant negative effect on the partitioning of resources during growth and development in cover crops. The nutrient retentions in the root zone and their losses

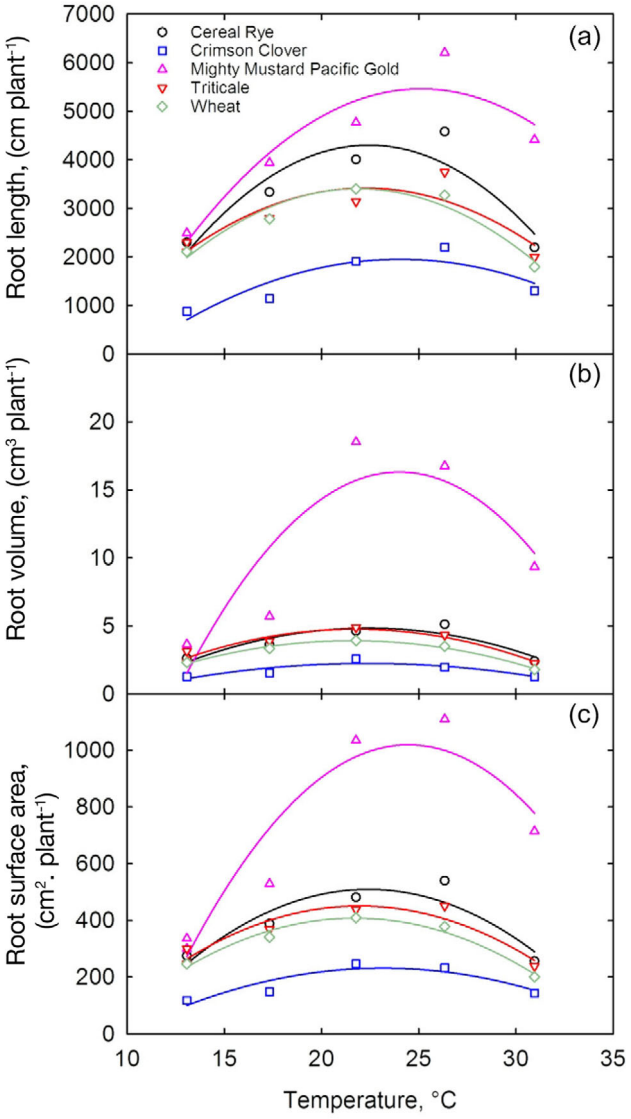

FIGURE 4 Temperature effects on cover crop root length (a), root volume (b), and root surface area (c) measured 33 d after planting or 25 d after temperature treatment. Values are the mean of six replications for each cover crop at each temperature treatment, and the curves are fitted lines using quadratic functions

from the fields are predicted to be controlled by the root system architecture of cover crops. Therefore, the inclusion of cover crops with a vigorous root system may alleviate soil compaction by acting like bio-drills and enhance forage for resources (Cresswell & Kirkegaard, 1995).

When comparing the root growth and development traits, there is clear evidence that sub- and supra-optimal temperatures suppressed most of the measured root parameters (Figures 3, 4). In agreement with the root volume and surface area results, root branching traits (tips, forks, and crossings) of cover crops also exhibited high sensitivity to temperature change (Figure 3). Suppression of root development and growth under sub- and supra-optimal temperatures could

be due to reduced water permeability of the root, decreased hydraulic conductivity, increased root respiration, and an imbalance of phytohormones (Ali et al., 1998; Fatichi et al., 2014; Huang, 1991; Luo et al., 2020; Morales et al., 2003; Steffens & Rasmussen, 2016). Other studies have reported that plants are grown in the field with different soil temperatures and diurnal oscillations strongly affect root growth (Stone & Taylor, 1983; Walter et al., 2009) by changing their root morphology, physiology, anatomy, and cellular components (Calleja-Cabrera et al., 2020; Nagel et al., 2009; Walter et al., 2003). During the fallow planting in most of the United States and other parts of the temperate world, extreme temperatures may coincide with a rainfall shortage. In such environments, cover crops with a more in-depth rooting system could help overcome the negative effect of combined water deficit and high-temperature stresses (Calleja-Cabrera et al., 2020; Sievers & Cook, 2018). Our results suggest that Mighty Mustard Pacific Gold may have better adaptive potential to combat water deficit with its more in-depth root system (Figure 3, 4). Evaluation of root traits provides better insights to distinguish root growth and development at the Topt. Better root traits enable maximization of soil carbon sequestration, nitrogen acquisition (Kristensen & Thorup-Kristensen, 2004), and controls the dynamics of the carbon and nitrogen ratio (Justes et al., 2009) which ultimately benefits the following cash crops (Blanco-Canqui et al., 2014; Tonitto et al., 2006). The assumption is that cover crops with higher total root length, volume, and surface area coupled with active developmental traits (more tips, forks, and crossings) would maximize resource uptake more readily than a species with fewer numbers of those traits under unfavorable environments. The cardinal temperatures identified for root growth and development in this study can help select the right cover crop according to local climatic conditions.

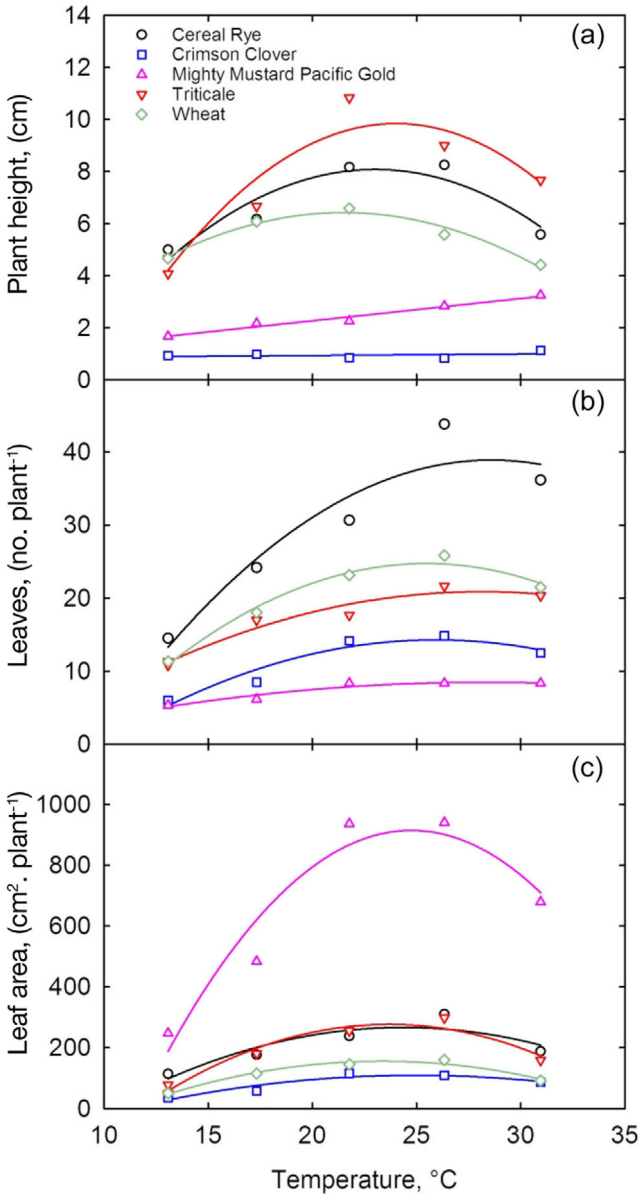

FIGURE 5 Temperature effect on plant height (a), main stem and/or axis leaves (b), and whole-plant leaf area of five cover crops measured 33 d after planting or 25 d after temperature treatment. Values are the mean of six replications for each cover crop at each temperature treatment, and the curves are fitted lines using quadratic or linear (plant height, triticale, and wheat) functions

3.3 | Aboveground morphology parameters

There is no doubt that the selection of cover crop species for fallow planting is dependent on several factors. Among all, species choice largely depends on the climatic conditions of the site and the characteristics of the cover crop to produce high biomass (Blanco-Canqui et al., 2014). It is crucial to know the cardinal temperatures for aboveground traits (leaf number, leaf area, and biomass) to select the most appropriate species to plant during the fallow season. Plant height, number of leaves, and leaf area parameters were significantly affected by treatment, species, and interaction (Table 2). All three parameters increased quadratically across the temperatures in triticale, cereal rye, and wheat (Figure 5; Table 3). A similar quadratic trend has been observed between temperature and leaf traits in other crops (Luo et al., 2020; Reddy et al., 1992; Reddy et al., 1993), whereas a linear increase or no change in the height of seedlings were recorded in response to increasing temperature in Mighty Mustard Pacific Gold and crimson clover (Figure 5a). Therefore, we have not emphasized the plant height parameter in this report. The Topt for the number of leaves varied from 24.5 (wheat) to 28.6 ˚C (cereal rye), wherein cereal rye significantly outperformed all other species (Figure 5b).

Interestingly, Mighty Mustard Pacific Gold exhibited the lowest temperature (4 ˚C) limits for leaf number, followed by triticale (6.0 ˚C). In contrast, the remaining three species

showed a minimum temperature of slightly above 8.9 ˚C (Table 3). Mighty Mustard Pacific Gold recorded the highest leaf area per plant at all temperatures than the other four species (Figure 5c). Averaged across species, increased temperature from Topt to Tmax decreased leaf number by 5% (ranged from 11 to 1%; Table 3) and whole plant leaf area by 28% (varied from 38 to 19%; Figure 5c, Table 3). Likewise, plants grown at Tmin exhibited a decrease in both leaf number (54%) and leaf area (73%) compared to the Topt (Table 3). The adverse effects (% decrease from optimum) of Tmax on leaf area were most pronounced in wheat (38%) followed by triticale (37%), and thus were classified as highly sensitive to high temperature (Figure 5c; Table 3). The adverse effects (% decrease from Topt) of Tmin on leaf area were most significant in triticale (79%), and thus classified as highly sensitive to low temperature (Figure 5c). Leaf area development depends on multiple processes such as initiation of the axillary shoot, initiation of new leaves, and leaf expansion. Generally, extreme temperatures are known to affect the rate of leaf initiation and expansion. Sub-optimal temperatures reduce the number of leaves due to the slowing of the rate of leaf initiation and delayed cell division and elongation (Ben-Haj-Salah & Tardieu, 1995); such events are known to decrease leaf area and final dry weight of plants (Wijewardana et al., 2015). Our results suggest that the leaf initiation event in cover crops may better withstand supra-optimal temperature compared to sub-optimal temperatures as we did not see a significant reduction in leaf number above Topt (Figure 5b).

3.4 | Temperature effects on root and shoot biomass

Cover crops with superior growth or faster shoot and root growth seem to have greater potential to scavenge residual soil resources that contribute to overall sustainability (Faé et al., 2009; Lehman et al., 2014; Sainju et al., 1998). At harvest (33 DAP), the amount of total dry biomass (i.e., aboveground and root biomass) was mostly dependent on the temperature treatment (Figure 6). Shoot, root, and total dry weight indicate the seedling vigor; these parameters were significantly affected by treatment, species, and interaction (Table 2). Shoot, root, and total dry weight per plant increased quadratically in response to increasing temperature in all species (Figure 6; Table 3). Maximum shoot dry weight per plant was observed in Mighty Mustard Pacific Gold (4.8 g plant^{-1} at 28 ˚C) followed by triticale (1.7 g plant^{-1} at 28 ˚C) and cereal rye (1.6 g plant^{-1} at 28 ˚C; Figure 6a). In Mighty Mustard Pacific Gold, shoot dry weight decreased (73%) dramatically in the plants grown at Tmin compared with Topt (Table 3). Conversely, under Tmax, the same species recorded the lowest reduction (18.6%) in shoot dry weight, and the highest reduction (34.8%) was recorded in wheat compared to Topt

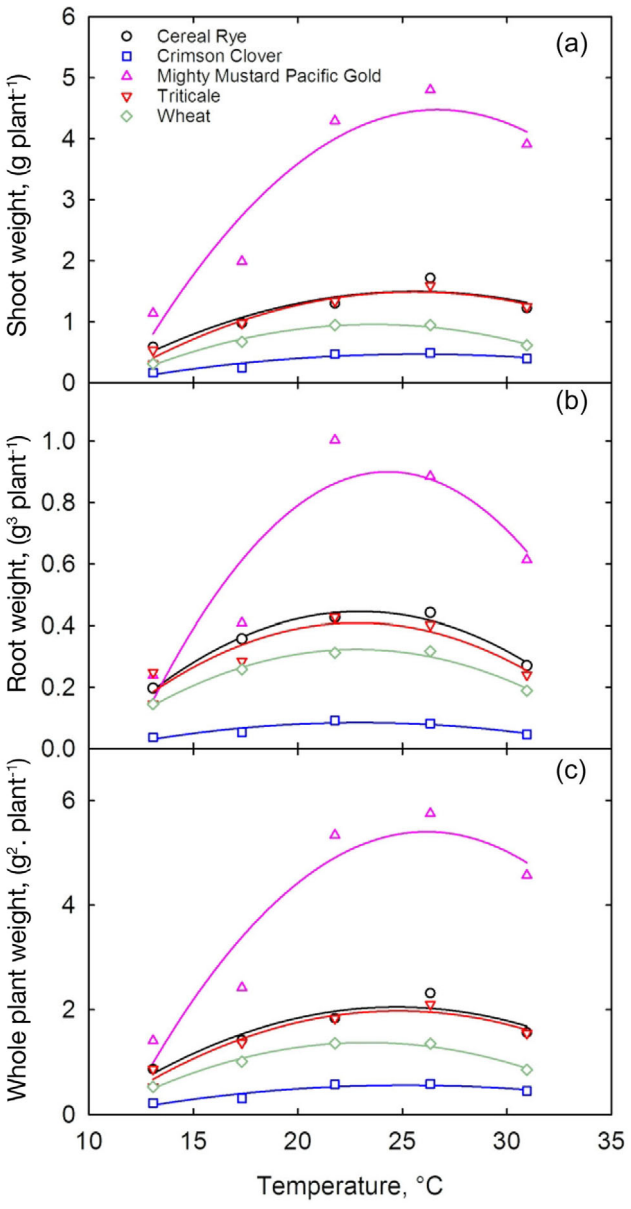

FIGURE 6 Temperature effect on shoot weight (a), root weight (b), and whole-plant dry weight (c) measured 33 d after planting or 25 d after temperature treatment. Values are the mean of six replications for each cover crop at each temperature treatment, and the curves are fitted lines using quadratic functions

(Figure 6a; Table 3). Root dry weight showed a similar pattern to shoot dry weight in both species (Figure 6b; Table 3). Among the five species, the Topt for root weight ranged from 22.5 (Triticale) to 24.3 ˚C (Mighty Mustard Pacific Gold). Under Topt, the highest and lowest maximum root dry weight was observed in Mighty Mustard Pacific Gold (at 24.3 ˚C) and cereal rye (at 22.9 ˚C), respectively (Figure 6b; Table 3). Also, there were considerable differences (46–83%) in the root dry weight between the Tmin and Topt treatments (Table 3). As expected, whole-plant dry weight showed a similar pattern to other dry weights among the species. Biomass production was

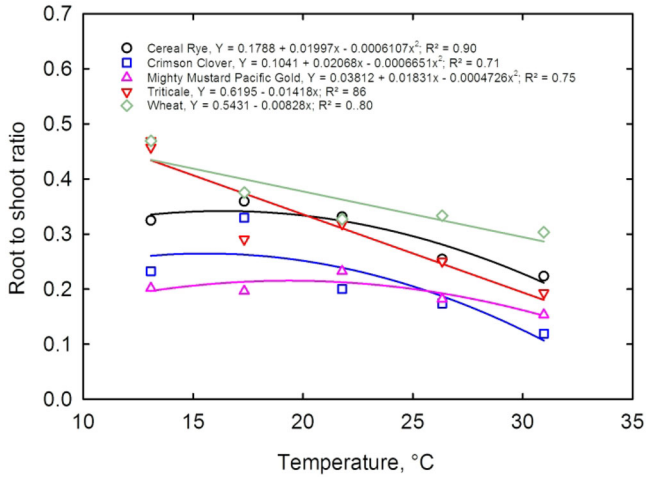

FIGURE 7 Temperature effect on the root/shoot ratio measured 33 d after planting or 25 d after temperature treatment. Values are the mean of six replications for each cover crop at each of the temperature treatment

highest at Topt and decreased with rising temperatures (Figure 6c). On average, Tmin decreased total dry weight from 82 to 62%; under Tmax, the total dry weight dropped from 36 to 11% from its Topt (Table 3). The negative effect (% decrease from optimum) of Tmin on total dry weight was greatest in Mighty Mustard Pacific Gold (81%) followed by crimson clover (68%), and thus can be classified as highly sensitive to low temperature (Figure 6c, Table 3). The negative effect (% decrease from Topt) of Tmax on total dry weight was greatest in wheat (36%) followed by cereal rye (18%) and triticale (18%), and thus classified as highly sensitive to high temperature (Table 3). Under Tmax, the smallest percent decreases were in Mighty Mustard Pacific Gold (11%) followed by crimson clover (16%), indicating that mustard was the most tolerant to supra-optimal temperatures (Table 3). Observed reduced leaf area (Figure 5c) development in both Tmin and Tmax may partially explain the decreased biomass during early seedling stages in all species.

Pooled over all species, the root/shoot ratio parameter measured at 33 DAP decreased quadratically (cereal rye, crimson clover, and Mighty Mustard Pacific Gold) or linearly (triticale and wheat) in response to increasing temperature (Figure 7). Regardless of cover crop species, the root/shoot ratio was higher under low sub-optimal temperatures than supra-optimal temperatures (Figure 7). On average, across species, an increase in temperatures from 13 to 31 ˚C decreased the root/shoot ratio from 34 to 20%. Regardless of temperatures, all cover crop species recorded higher biomass partitioning to the shoot (62.3%) than to roots, with a maximum proportion of biomass partitioned to shoot in Mighty Mustard Pacific Gold (81%) and crimson clover (79%) than other species (64−70%). At the same time, higher biomass partitioning to roots was observed in species with a fibrous root system (cereals), with a maximum proportion of biomass partitioned to root in wheat (47 and 33%) followed by triticale (46 and 25%) and cereal rye (32 and 25%) at extreme temperatures (Tmin and Tmax, respectively). As shown in previous studies, suppression of root morphological traits (tips, forks, and branching root length, volume, and surface area) along with other root anatomical changes may partially explain the reduced root growth and development in response to extreme temperatures (Bheemanahalli et al., 2019; Luo et al., 2020; Steffens & Rasmussen, 2016). On the other hand, a balance between carbon supplied (leaf area) and carbon used for growth and respiratory costs of cover crops are strongly affected under sub- and supra-optimal temperatures (Figures 3, 4, 5). Differential partitioning of resources (root/shoot ratio) describes changes in growth and development of shoot and root at extreme temperatures (Parent et al., 2010). Regardless of species, more narrow ranges of cardinal temperatures were observed for shoot traits than for root traits (Table 3). Overall, the Tmin for root traits (averaged across root tips, root forks, root crossings, total root length, root volume, root surface area, root dry weight) varied significantly and ranged from 8.5 ˚C (triticale) to 10.8 ˚C (Mighty Mustard Pacific Gold); Topt ranged from 22 ˚C (wheat) to 25.7 ˚C (Mighty Mustard Pacific Gold); and Tmax from 35.2 ˚C (heat) to 40.6 ˚C (Mighty Mustard Pacific Gold; Table 3). The Topt for root traits was significantly lower than shoot traits (averaged across leaf numbers, leaf area, and shoot dry weight) in all the species, except Mighty Mustard Pacific Gold. Wheat, triticale, and cereal rye had lower Tmin, Topt, and Tmax than the other two species for root traits (Table 3).

Growing cover crops in the fallow period can regulate the gains and losses of organic carbon in the soil, depending on local climatic conditions such as air or soil temperature and rainfall (Poeplau & Don, 2015). Under harsh environmental conditions, cover crops with higher biomass (shoot and root) provide added opportunities to enrich soil organic carbon content (Blanco-Canqui et al., 2013; Schomberg et al., 2007). Interestingly, cover crops with superior root growth have been shown to have a positive correlation with nitrogen scavenging and mycorrhiza load in the soil (Sainju et al., 1998). It can be hypothesized that cover crops with superior growth (root and shoot) under any given temperature condition have the potential to increase the beneficial microbial load or soil carbon along with other ecological services. Such combinations are shown to positively affect the succeeding cash crop's growth and yield (Alvarez et al., 2017; Andraski, & Bundy, 2005; Bergtold et al., 2012). Our results confirm that extreme temperatures (low and high) negatively affect the growth and development of cover crops. Therefore, for colder (sub-optimal) climatic conditions, cereal rye would usually be the best species to grow. At warmer climatic regions (Topt and above), crimson clover and Mighty Mustard Pacific Gold may yield higher biomass and be the best selections. However, in all treatments, Mighty Mustard Pacific Gold was top among

the five species in root and shoot growth. With the results presented here, a producer could choose potential species to grow based on local climatic conditions.

4 | CONCLUSIONS

Our results demonstrated different cardinal temperature requirements for the growth and development of several cover crop species. Our study suggests that cover crops' characterization for root and shoot traits could be used as potential parameters to quantify sub- and supra-optimal temperature tolerance of cover crops. As we tested different species with the same range of temperatures, the identified cardinal temperatures for growth and development traits can be used in crop models to simulate the crop species' biomass production under different climatic conditions. The study aids in selecting mixes of cover crops with the same temperature range to plant at the same climatic conditions during fallow periods. However, the wide range of cardinal temperatures of the studied species, cereal rye and Mighty Mustard Pacific Gold seems to have consistently exhibited superior shoot and root traits at Topt. As a result, these two species could provide better ecological services by rapidly acquiring resources after sowing and establishing aerial cover faster than other species. The characteristic changes in shoot and root morphology in response to extreme temperatures are likely associated with the disruption of physiological and biochemical processes. Thus, we suggest that future studies primarily address the thermal limits of enzymes involved in carbohydrate metabolites to clarify the biochemical puzzle.

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CONFLICT OF INTEREST

The authors report no conflict of interest.

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