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Effect of Temperature and Phosphorus Fertilization on Phosphorus and Nitrogen Uptake by Sorghum

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ABSTRACT

Temperature (T) and phosphorus (P) supply affect each of the mechanisms involved in P and nitrogen (N) uptake by grain sorghum [*Sorghum bicolor* (L.) Moench]. This study was conducted to assess the extent to which air temperature and P fertilizer influenced P and N uptake and partitioning in sorghum plant parts. Research was conducted in a climatic chamber, where plants (Venturoli Aralba hybrid sorghum) were grown in pots under a 14-h day/night photoperiod regime. Temperature regimes were kept constant for the entire life cycle at 21, 24, 27, and 30°C. The P fertilization rate was 0 and 150 mg P pot^{-1} as triple mineral perphosphate. Temperature and P supply controlled P and N concentration and content in all sorghum plant parts during the biological cycle. Whole plant, leaf, stem, and root P and N contents were highest at 27°C in growth Stages 3, 6, and 9 for both P-fertilized and unfertilized plants. Increased P supply resulted in greater P and N content in leaves and stems in all three stages and at all temperatures, while root P and N contents were unaffected. Panicle P and N contents were highest at 21 to 27°C in Stage 6 and at 24°C in Stage 9. The effect of T on increasing plant P and N contents was attributable primarily to higher P and N uptake rate per unit of root rather than to higher rate of root growth. Results do not support the view that poor growth at suboptimal temperatures is caused primarily by restricted P uptake, but that T and P supply limit growth independently, with additive responses.

PLANT COMPOSITION and nutrient absorption by grain sorghum may be influenced by many genetic and environmental factors. Of the environmental factors, nutrient availability and temperature are of prime importance because they affect key physiological and developmental processes determining plant growth, nutrient uptake, and grain yield.

Temperature influences mechanisms involved in plant phosphorus (P) uptake and phosphorus-deficient plants have been associated sometimes with low soil temperatures, suggesting that P supply to the root is restricted with low soil temperature (Barber, 1986).

Satisfactory plant P nutrition is related to the presence in soil of adequate quantities of $H_2PO_4^-$ and HPO_4^{2-} in soluble form (Mackay and Barber, 1984). An increase in soil temperature may increase the concentration of soluble soil and fertilizer P or the chemical decomposition rate of inorganic forms of P. High temperature may raise equilibrium P concentration and thus may affect plant growth by altering the availability and uptake of soil P. High temperature may also reduce P solubility by increasing the rate of immobilization and chemical fixation of P in soil (Singh and Jones, 1977).

Low temperature in the root zone reduces availability of P for wheat (*Triticum aestivum* L.) (Power et al., 1961), and high temperature increases the absorption of nitrogen and P by barley (*Hordeum vulgare* L.). In barley, the highest P absorption by roots occurs at soil temperatures of 7 to 11°C, declining sharply with higher soil temperature, while fertilizer P absorbed by tops is usually highest at a soil temperature of 11 to 15°C (Power et al., 1964).

Increasing temperature increases root growth, allowing plant roots to explore a larger volume of soil. This increases the P potentially absorbable (Stone and Taylor, 1983; Batten et al., 1986; Föhse et al., 1988).

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Abbreviations: GS1, Growth Stage 1; GS2, Growth Stage 2; GS3, Growth Stage 3; SAR, specific absorption rate; SDWI, specific dry weight increment; T, temperature.

Increasing temperature also increases the rate of physiological processes involved in plant growth, which determine nutrient absorption (Power et al., 1970; Tollenaar, 1989). Thus the ability of the root system to take up P from soil and accumulate it in the shoots (plant uptake efficiency) depends on the capacity of roots to absorb P, on the active life time of roots, and on the amount of root per unit of shoot. High P efficiency may also result from superior translocation or favorable partitioning. Power et al. (1970) showed that reduced growth rate of barley at low soil temperatures was due to slow translocation of P from roots to tops.

According to Föhse et al. (1988), P uptake efficiency depends on influx (uptake rate per unit of root length), root-shoot ratio and the period over which a root segment takes up P. In addition, at a given influx the uptake per plant depends on the size of the root system. Low uptake efficiency was shown to be associated both with a low root-shoot ratio and a low influx rate. Plants developed different strategies for P uptake from soil: some species increase the size of their root system, while others increase the uptake rate per unit of root. Increasing soil solution concentration led to an increase in influx rate and a decrease in root-shoot ratio for onion (*Allium cepa* L.), ryegrass (*Lolium perenne* L.), wheat, rape (*Brassica napus* L.), tomato (*Lycopersicum esculentum* L.), and spinach (*Spinacia oleracea* L.).

This research was conducted in controlled-environment chambers with the objective of studying the influence of constant air temperature and P supply on P and N absorptions and concentrations in the different plant parts of grain sorghum.

MATERIALS AND METHODS

Research was conducted in a climatic chamber, where sorghum plants were grown in pots containing 16.5 kg of soil. Soil chemical and physical properties were 77.6% sand, 13.9% silt, 8.5% clay, pH 7.8, 1.2% organic matter (Lotti method), 1.8% total nitrogen (Kjeldahl method), 12 μg g^{-1} assim. P_2O_5 (Olsen method), and 14 μg g^{-1} assim. K_2O (Dirks-Sheffer method). The Venturoli Aralba hybrid sorghum (class 400/500) was used. Three seeds per pot were planted, and seedlings were thinned at Stage 1 (scale of Vanderlip and Reeves, 1972) to one per pot. Plants were grown under a 14-h day/10-h night photoperiod regime. Sorrells and Myers (1982) reported that for the temperate sorghum group there is an interaction between variety, air temperature (night and day) and day-length, and that the number of days to floral initiation is shortest with a 10-h photoperiod. In Central Italy (43° N lat), sorghum is planted from about 15 April to 1 May. At this date, the photoperiod is more than 13 h long, increasing up to 21 June, when it peaks at 16 h. Lighting was provided by fluorescent lamps (Fluora 77, Osram, Germany) characterized by high emission in the blue and red bands. Photosynthetic photon flux density at the top of the plant canopy was 450 μmol m^{-2} s^{-1} measured with a hand-held spectroradiometer model LI-1800 (LI-COR Inc., Lincoln, NE). Relative humidity was kept at 65 ± 5%.

Treatments were air temperatures at 15, 21, 24, 27, 30, and 35°C and P fertilization rates at 0 and 150 mg pot^{-1} of P (4.4 g m^{-2}). The experiment was a split-plot design, with temperatures serving as main plots and P levels randomly assigned as sub-plots with five replications. Air temperature was kept constant throughout the trial period (entire life cycle of sorghum) and soil temperature was always about 3°C lower than that of air, owing to soil water evaporation. Phosphorus fertilizer (triple mineral perphosphate) was equivalent to 10 g m^{-2} of P_2O_5 and was uniformly distributed throughout the volume of soil. Nitrogen, as urea, and potassium, as K_2SO_4, fertilizers were applied before seeding at rates of 530 mg pot^{-1} of N (15 g m^{-2}) and 353 mg pot^{-1} of K_2O (8.3 g m^{-2} of K). Pots were watered regularly to ensure that no water limitation occurred.

According to Saeed et al. (1986), sorghum development is divided into three growth stages critical to yield: emergence to panicle initiation (GS1), panicle initiation to anthesis (GS2), and anthesis to physiological maturity (GS3). Dates of panicle initiation (Stage 3), anthesis (Stage 6), and physiological maturity (Stage 9) were recorded for plants in each pot. At each stage total and plant-component dry weights were determined. All plant parts were dried for dry weight determination at 75°C to constant weight. Plant samples were analyzed for P and N content, with total P determined colorimetrically in triacid extract by the ammonium-molybdophosphoric blue color method (Zandstra, 1968), and total N determined by the microKjeldahl method (Bremnar, 1965). Leaf, stem, panicle, and root P and N contents were calculated by multiplying the nutrient concentrations by dry weights. The total amount of P and N per plant was calculated by summing the content of each element in all plant parts.

The above-ground dry matter growth rate per unit weight of root (Specific Dry Weight Increment) was taken as the parameter for mineral nutrient demand per unit of root. In GS1, GS2, and GS3, this parameter was calculated by modifying the following formula of Engels (1993) as:

$$\mathrm{SDWI} = [(S_2 - S_1)/(t_2 - t_1)] \times [\ln(R_2/R_1)/(R_2 - R_1)],$$

where S_1 and S_2 are the above-ground dry weight (leaves + stem + panicle when present) and R_1 and R_2 are root dry weight at the beginning (t_1) and the end (t_2) of each growing stage respectively.

Specific absorption rates (SAR) of P and N in GS1, GS2, and GS3 were calculated according to Hunt's (1981) formula as:

$$\mathrm{SAR} = [(P_2 - P_1)/(t_2 - t_1)] \times [\ln(R_2/R_1)/(R_2 - R_1)],$$

where P_1 and P_2 are whole plant nutrient content and R_1 and R_2 are root dry weight at times t_1 and t_2 respectively.

Data were analyzed statistically by analysis of variance, performed separately for each harvest to test the effects of temperature, P supply, and temperature × P supply. In addition to the analyses of variance for individual stages, a combined analysis of variance over stages was conducted. Significantly different means were separated at the 0.05 probability level by the least significant difference test (Snedecor and Cochran, 1980).

RESULTS

Phosphorus Concentration

Optimal growth temperature for dry matter accumulation was 27°C for leaves and stems, and 21 to 24°C for panicles and roots (results not shown). Up to anthesis, the optimum temperature for whole plant growth was 27°C, since the plant was composed mainly of leaves and stems. After anthesis, optimum temperature dropped to 24°C, on account of extensive panicles and roots development. The P rate induced a slightly increased

Table 1. Effect of temperature on whole plant, leaf, stem, panicle, and root phosphorus concentration of sorghum. Values are mean of P levels.

Stage	Temperature	P concentration				
		Whole plant	Leaves	Stem	Panicle	Root
	°C	g kg^{-1}				
3	21	2.0a†	2.4a	2.1a	–	1.0a
	24	2.9b	3.7b	3.1b	–	1.6b
	27	2.8b	3.0c	2.8b	–	1.7b
	30	2.6b	3.2d	2.5ab	–	1.6b
6	21	1.5a	2.0a	1.2a	2.0a	1.1a
	24	2.4b	3.2b	2.1b	2.2b	1.3a
	27	3.1c	3.6b	2.8c	2.6c	2.4b
	30	2.6d	3.2b	2.1b	1.7d	1.3a
9	21	1.2a	1.1a	0.7a	1.9a	0.6a
	24	2.1b	2.5b	0.8a	3.2b	0.9a
	27	2.8c	3.2c	2.4b	3.6c	1.8b
	30	2.3b	2.7b	2.2b	2.5d	0.8a

† Means followed by the same letter, within the same column, are not significantly different at $P \leq 0.05$.

growth rate in all plant parts. Phosphorus concentration in sorghum the whole plant and in different plant parts was affected by temperature but not by P supply or by the temperature × P supply interaction.

Table 1 shows the effect of temperature on whole plant, leaf, stem, panicle, and root P concentrations in Stages 3, 6, and 9. At each temperature, maximum P concentration was detected in leaves in Stages 3 and 6, and in panicles in Stage 9. The lowest P concentration was found in roots at all three stages. In the panicle initiation stage, leaf P concentration was higher at 24°C than at the other three temperatures. Stem and root P concentration was also highest at 24°C, but no statistically significant differences were found between results obtained at 24, 27, and 30°C. As a consequence, whole plant P concentration was the same at 24, 27, and 30°C (approximately 2.7 g kg^{-1}).

From anthesis to physiological maturity, P concentration in all plant parts progressively increased with the increase in temperature from 21 to 27°C, and decreased thereafter. The increase was higher for stems (133% in Stage 6 and 243% in Stage 9) and for roots (118 and 200%) than for leaves (80 and 191%) or panicles (30 and 89%). Furthermore, the increase was higher for all plant parts in Stage 9 compared with Stages 3 or 6. From anthesis to physiological maturity, whole plant, leaf, stem (except at 30°C), and root P concentration decreased at each temperature, while panicle P concentration increased (except at 21°C).

Phosphorus Content

Leaf, stem, root, and whole plant P content was affected by temperature and P supply, while panicle P content was affected by the temperature × P supply interaction (Fig. 1). At Stage 3, maximum P content was achieved at 27°C for leaves, stems, and whole plant, and at 24 to 27°C for roots. At this stage plant biomass was low and temperature-induced variations in P content in all plant parts were negligible. Whole plant P content varied from 4 to 18 mg plant^{-1}.

In Stages 6 and 9, leaf and stem P content increased markedly from 21 to 27°C and decreased from 27 to 30°C. The increase was greater in leaves (455% in Stage 6 and 750% in Stage 9) than in the stems (319 and 447%, respectively), and in both these plant parts, the increase was greater from 24 to 27°C than from 21 to 24°C. In both stages, minimum leaf and stem P content was detected at 21°C. From anthesis to physiological

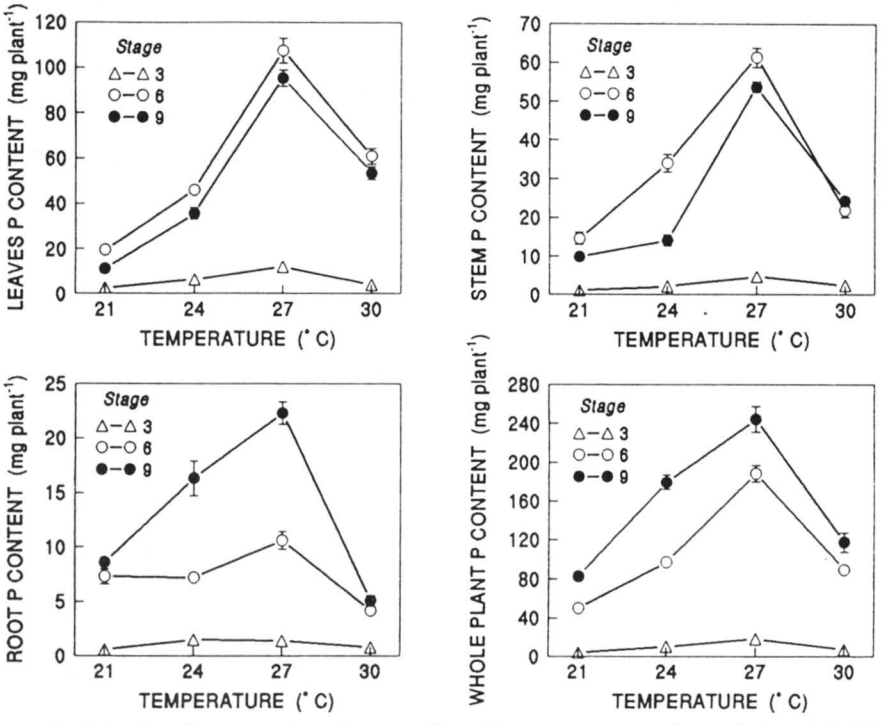

Fig. 1. Leaves, stem, root, and whole plant P content of sorghum as affected by temperature in Stages 3, 6, and 9. Values are mean of P level. Vertical bars represent ± SE of the mean for 10 plants. When not indicated error bar lies within the symbol.

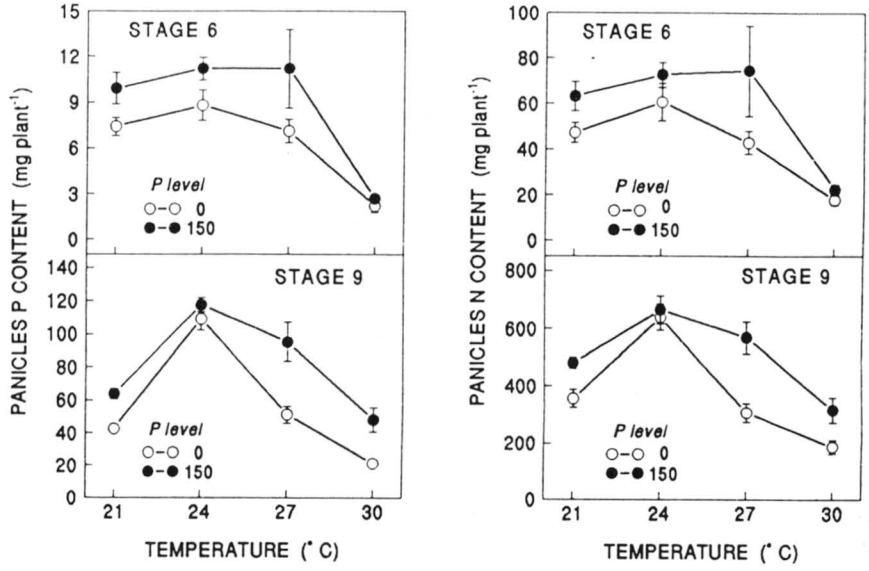

Fig. 2. Panicle P and N content of sorghum as affected by temperature × P level interaction in Stages 6 and 9. Vertical bars represent ± SE of the mean for five plants. When not indicated error bar lies within the symbol.

maturity, leaf and stem P content decreased slightly. In leaves, the decrease was the same at all temperatures (approximately 9.5 mg plant^{-1}), while in stems it was highest at 24°C (20 mg plant^{-1}). The decrease in leaf and stem uptake of P between Stages 6 and 9 is indicative of translocation into the panicles.

Root P content was highest at 27°C in both Stages 6 and 9, but in the Stage 6 the maximum and minimum value differed by only 6.4 mg plant^{-1}, while in the Stage 9, root P content increased by 13.7 mg plant^{-1} from 21 to 27°C and decreased abruptly by 17.2 mg plant^{-1} at 30°C (Fig. 1). Root P content at 24 and at 27°C was higher in Stage 9 than in Stage 6 (9.1 and 11.7 mg plant^{-1}, respectively), while at 21 and 30°C, the differences between the two stages were not noteworthy.

In Stage 6 temperature treatments, from 21 to 27°C, did not modify panicle P content of P-fertilized and unfertilized plants and P supply increased values (Fig. 2). From 27 to 30°C, on the other hand, panicle P content decreased and this decrease was higher for fertilized than for unfertilized plants. Thus at 30°C, there was no difference between fertilized and unfertilized plants. In Stage 9, panicle P uptake increased when temperature increased from 21 to 24°C and decreased thereafter. At all temperatures, P uptake was higher for P-fertilized than for unfertilized plants, but the difference was negligible at 24°C (Fig. 2).

As a consequence of leaf, stem, root, and panicle P uptake, the highest whole plant P content was found at 27°C in all three stages, and was higher in Stage 9 than in Stages 3 or 6 at all temperatures (Fig. 1).

Increased P supply resulted in greater leaf and stem P content in all three stages at all temperatures, while root P content was unmodified (Table 2). At physiological maturity, P content in P-fertilized plants was 95.5 mg plant^{-1} at 21°C, 183.7 mg plant^{-1} at 24°C, 273.4 mg plant^{-1} at 27°C, and 137.1 mg plant^{-1} at 30°C.

The P taken up by unfertilized plants represents soil P, and that taken up by fertilized plants represents both soil and fertilizer P. The difference between P content in the latter group and the former can thus be considered as the amount derived from fertilizer. The absence of P × temperature interaction indicated that with increasing temperature, P uptake from soil increased to the same extent as P uptake from fertilizer. Sorghum whole plant uptake of soil P exceeded that of fertilizer P and constituted up to 63% in Stage 3, 79% in Stage 6, and 81% in Stage 9 of total sorghum whole plant P uptake. This is probably because sufficient available P was present in the soil.

Table 2. Effect of P supply on P and N content of sorghum leaves, stem, root, and whole plant in stages 3, 6, and 9. Values are mean of temperature treatments.

		P content				N content			
Stage	P level	Whole plant	Leaves	Stem	Root	Whole plant	Leaves	Stem	Root
	kg ha^{-1}	mg plant^{-1}							
3	0	7.4a†	4.6a	2.1a	0.8a	78.6a	54.5a	17.8a	6.3a
	150	11.8b	7.2b	3.3b	1.2a	121.5b	83.7b	29.2b	8.6b
6	0	93.6a	51.6a	29.2a	6.5a	630.8a	423.9a	125.8a	39.0a
	150	118.7b	65.2b	36.7b	8.2a	762.6b	507.4b	150.5b	46.7b
9	0	139.7a	44.9a	24.5a	14.3a	917.7a	356.1a	93.1a	95.4a
	150	172.4b	52.9b	26.5b	11.8a	1087.2b	391.6b	98.9b	88.7b

† Means followed by the same letter, within the same column, are not significantly different at $P \leq 0.05$.

Table 3. Effect of temperature on P and N partitioning in sorghum leaves, stem, panicle, and root. Values are mean of P levels.

Stage	Temperature	P partitioning				N partitioning			
		Leaves	Stem	Panicle	Root	Leaves	Stem	Panicle	Root
	°C	% of whole plant							
3	21	59.1a†	27.3a	–	13.6a	68.6a†	26.9a	–	4.5a
	24	63.4b	21.8b	–	14.9a	68.7a	18.4b	–	13.0b
	27	65.9b	26.3a	–	7.8b	73.9b	20.1b	–	6.0a
	30	54.2c	34.7c	–	11.1c	64.0c	30.9c	–	5.1a
6	21	38.9a	29.3a	17.2a	14.6a	53.8a	19.1a	14.4a	12.7a
	24	47.3b	35.0b	10.3b	7.4b	62.7b	21.3b	9.2b	6.8b
	27	57.1c	32.5c	4.8c	5.6c	69.7c	20.5ab	5.5c	4.3b
	30	68.0d	24.6d	2.7d	4.7c	74.7d	17.5a	3.2c	4.6b
9	21	13.6a	11.8a	64.1a	10.4a	14.8a	6.1a	62.2a	16.9a
	24	19.8b	7.9b	63.3a	9.1b	27.4b	7.1a	55.7b	9.8b
	27	39.0c	21.9c	30.0b	9.1b	49.1c	12.7b	31.4c	6.8c
	30	45.4d	20.7c	29.6b	4.3c	50.6c	10.8c	32.8c	5.8c

† Means followed by the same letter, within the same column, are not significantly different at $P \leq 0.05$.

Similarly, efficiency of apparent fertilizer utilization, calculated at physiological maturity, as [(P uptake by fertilized plant − P uptake by unfertilized plant)/P supply] was the same at all temperatures, and was found to be 21.8% (32.7 mg plant^{-1}).

Phosphorus partitioning among the various plant parts was greatly influenced by temperature in Stages 6 and 9 and to a lesser extent in Stage 3 (Table 3). In this stage, stems accounted for 30% of whole plant P content, roots for 10% and leaves for approximately 60%. In Stages 6 and 9, the proportion of P in leaves increased, while that in panicles and roots decreased with increasing temperature. At physiological maturity, when temperature increased from 21 to 30°C, the proportion of leaf P rose from 14 to 45%, while panicle P decreased from 64 to 30%, and root P from 10 to 4%. Phosphorus supply had no significant effect on P partitioning among sorghum leaves, stems, roots, and panicles.

Nitrogen Concentration and Content

Similar to P concentration, sorghum whole plant and different plant part N concentrations were affected by temperature, but were not affected by P supply or by the temperature × P supply interaction. In the panicle initiation stage, leaf, stem, and whole plant N concentrations were maximum at 24°C (Table 4). During anthesis, maximum N concentration in leaves was detected at 24°C, and in the whole plant, stems, and panicles, at temperature ranging from 24 to 30°C. At physiological maturity the greatest N concentration in all aboveground plant parts was at 24 to 30°C. Root N concentration was not affected by temperature in Stages 6 and 9.

The response of leaf, stem, and whole plant N uptake to increasing temperature was similar to that of P uptake in all three stages in as much as values increased from 21 to 27°C and decreased thereafter (Fig. 3). In Stages 6 and 9, root N content did not change from 21 to 24°C, and decreased from 24 to 30°C. Root N content in Stages 6 and 9 was affected by the temperature × P supply interaction, and showed a pattern similar to P uptake (Fig. 2).

The increase in P availability increased N uptake by all plant parts with the exception of roots in Stage 9. The most pronounced increase was observed in leaves in Stage 6 (Table 2).

Temperature modified N partitioning similarly to P partitioning (Table 3). Thus, at physiological maturity, when temperature increased from 21 to 30°C, the proportion of N in leaves rose from 15 to 50%, while panicle N decreased from 62 to 32% and root N decreased from 17 to 6%. The proportion of N in leaves, stems, panicles, and roots was not affected by P supply.

Phosphorus and Nitrogen Uptake Indices

Table 5 shows the effect of temperature on shoot dry weight, increment and on specific P and N absorption rate in GS1, GS2, and GS3 and on root-shoot ratio and N-P ratio in Stages 3, 6, and 9.

Phosphorus uptake depends both on the amount of available P in soil and on plant properties. Thus the increase in plant growth with increasing temperature enhances a plant's ability to take up P from soil. Shoot dry weight increment represents the increase in shoot dry weight per unit of root dry weight. Engels (1993) used this parameter to quantify the mineral nutrient demand created by shoot growth that is imposed on each unit weight of the root system. In this research, SDWI was higher in GS2 than GS1 or GS3 due to extremely elevated

Table 4. Effect of temperature on whole plant, leaf, stem, panicle, and root nitrogen concentration of sorghum. Values are mean of P levels.

Stage	Temperature	N concentration				
		Whole plant	Leaves	Stem	Panicle	Root
	°C	g kg^{-1}				
3	21	24.7a†	35.3a	26.2a	–	4.9a
	24	32.0b	43.0b	28.4a	–	14.8b
	27	28.9b	35.5a	21.8b	–	13.1b
	30	23.1a	32.8a	19.0b	–	6.4a
6	21	11.4a	21.2a	5.8a	12.3a	7.4a
	24	17.5b	31.7b	9.2b	14.5ab	8.9a
	27	17.5b	24.7a	9.7b	16.1b	10.1a
	30	18.3b	24.4a	10.5b	14.0ab	8.9a
9	21	9.8a	9.8a	2.9a	14.4a	7.3a
	24	13.8b	22.2b	4.8ab	18.4b	6.5a
	27	16.2b	23.0b	7.6b	21.8b	7.5a
	30	15.1b	19.9b	7.5b	19.8b	6.7a

† Means followed by the same letter, within the same column, are not significantly different at $P \leq 0.05$.

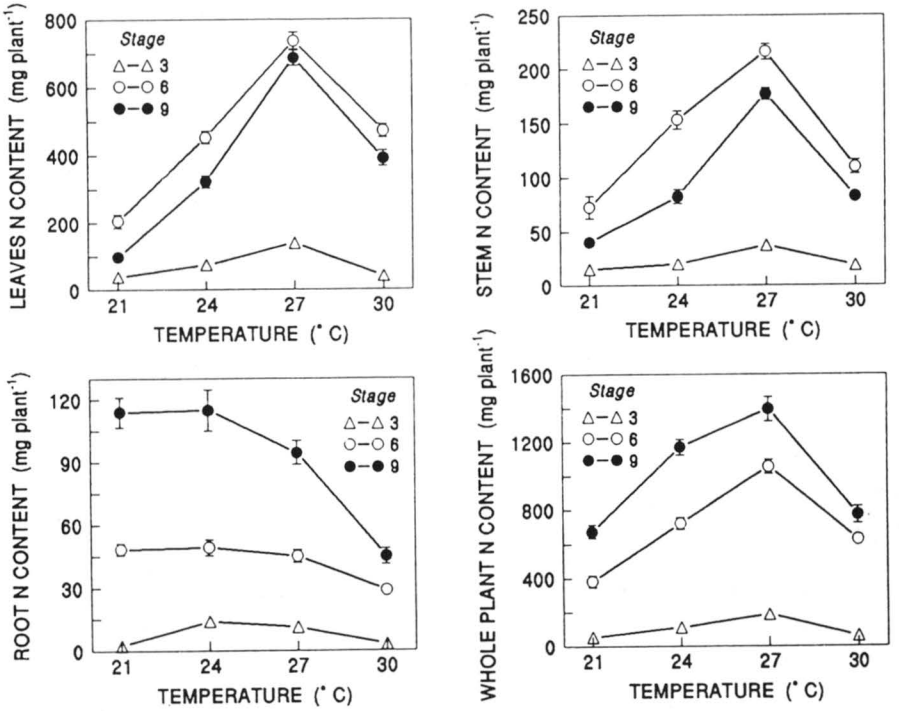

Fig. 3. Leaves, stem, root, and whole plant N content of sorghum as affected by temperature in Stages 3, 6, and 9. Values are mean of P level. Vertical bars represent ±SE of the mean for 10 plants. When not indicated error bar lies within the symbol.

growth of the above-ground part. Until anthesis, nutrient demand increased as temperature increased from 21 to 27°C, and decreased above 27°C. In contrast, after anthesis SDWI was consistently low and did not present any temperature-related variation. Shoot dry weight increment was not affected by P supply.

The P and N uptake rate per unit of root dry weight decreased at all temperatures with progression of the biological cycle of sorghum. As a mean of temperature and P supply, P SAR decreased from 1.8 g kg^{-1} in GS1, to 0.8 g kg^{-1} in GS2, to 0.1 g kg^{-1} in GS3, and N SAR decreased from 18.2 to 5.0 to 0.7 g kg^{-1}. Our data suggest that sorghum root P and N uptake efficiency decreased with plant aging and, until anthesis, was strongly influenced by temperature. Thus, until anthesis (GS1 and GS2), marked temperature-related variation was observed, with peak values at 27°C and lowest values at 21°C. In addition, greater differences between maximum and minimum values were found in GS1 (314% for P and 261% for N) as compared with GS2 (200 and 100%, respectively). Following anthesis, on the other hand, P and N SAR was not affected by temperature. The reduction in P and N SAR with plant aging could be attributable to an increase in percentage of older or suberized roots. Nitrogen and P SAR was unaffected by P availability.

DISCUSSION AND CONCLUSIONS

Temperature controlled P and N concentration and content of all sorghum plant parts during the biological

Table 5. Effect of temperature on sorghum Shoot Dry Weight Increment (SDWI), Specific P and N Absorption Rates in GS1, GS2, and GS3 and root-shoot dry weight ratio and N-P ratio in stages 3, 6, and 9. Values are mean of P levels.

Growing stage	Temperature	SDWI	SAR		Stage	Root-shoot ratio†	N-P ratio
			P	N			
	°C	mg mg^{-1}	g kg^{-1}			mg mg^{-1}	
GS1	21	0.3a††	0.7a	8.5a	3	0.39a	13.1a
	24	0.4a	1.6b	17.1b		0.37a	10.9ab
	27	0.9b	2.9c	30.7c		0.16b	10.5ab
	30	0.6ab	1.9b	16.6b		0.22b	8.7b
GS2	21	0.9a	0.4a	3.1a	6	0.25a	7.7a
	24	1.2ab	0.7ab	4.6ab		0.16b	7.4a
	27	1.8b	1.2b	6.2b		0.08c	5.6a
	30	1.3ab	0.8ab	5.9b		0.10bc	7.1a
GS3	21	0.6a	0.1a	0.7a	9	0.30a	8.2a
	24	0.6a	0.2a	1.0a		0.26a	6.5ab
	27	0.4a	0.1a	0.7a		0.18b	5.7b
	30	0.6a	0.1a	0.5a		0.16b	6.6ab

† On dry weight basis.
†† Means followed by the same letter, within the same column, are not significantly different at $P \leq 0.05$.

cycle, while P supply controlled only P and N content. Interaction between temperature and P supply was found only for panicle P and N content.

The effect of temperature differed in the different growth stages and plant parts. Whole plant maximum P and N concentration was obtained at 24 to 30°C in the panicle initiation stage and at 27°C at anthesis and physiological maturity. In Stage 3, shoot P and N concentration was highest at 24°C, and that of roots in the 24 to 30°C temperature range. In Stages 6 and 9, the highest P and N concentration in all plant parts was obtained at 27°C.

Whole plant, leaf, stem, and root P and N content was highest at 27°C during all biological cycle for both P-fertilized and unfertilized plants. Increased P supply resulted in greater leaf and stem P and N content in all three stages and at all temperatures, but did not modify root P and N content. Panicle P and N content was highest at 21 to 27°C until anthesis and at 24°C after anthesis; the increment due to P supply was highest at 27°C. Therefore, sorghum P and N absorption was maximum at temperatures optimal for dry matter production. The effect of temperature on increasing plant P and N content could be attributed to temperature-stimulated root growth, which would allow more thorough exploitation of a given volume of soil, a temperature-related increasing physiological capacity of roots to absorb nutrients, or both.

Until anthesis for both P fertilized and control plants, P and N uptake per plant conformed to the following order: 27 > 24 = 300 > 21°C. Since up to anthesis root dry weight decreased progressively from 21 to 30°C, the highest P and N uptake in sorghum was not dependent on root size. Rather, it was associated with improved root physiological nutrient uptake capacity. Uptake efficiency components are as follow: uptake rate per unit of root length, root-shoot ratio, and the period during which a root segment takes up nutrients. In this research, highest P and N uptake was associated with highest SDWI and SAR and lowest root-shoot dry weight ratio. Until anthesis, these peak values were observed at 27°C, and after anthesis SDWI and SAR did not change with temperature and the root-shoot ratio decreased progressively. In addition, at all temperature regimes, sorghum plants did not take up P or N after anthesis. Furthermore, during the period from panicle initiation to anthesis leaf and stem P and N content decreased. This was probably due to translocation into panicles, since an increase in panicle P and N content was observed.

Temperature did not modify utilization of fertilizer P, since at each temperature, P supply increased sorghum P uptake by the same amount. Phosphorus fertilization increased P and N uptake but did not modify SDWI, SAR, or root weight. Therefore, the increase was dependent only on the increase in fertilizer-derived soil P, which also stimulated plant growth.

Sorghum uptake of soil P exceeded that of fertilizer P and accounted for 63% of total P uptake in Stage 3, and for about 80% in Stages 6 and 9 at all temperatures. Similarly, efficiency of apparent fertilizer utilization was the same at all temperatures, and was found to be about 22%.

The results of this research do not support the view that poor growth at suboptimal temperatures is caused primarily by restricted P uptake. Thus, as suggested by Rahaman et al. (1974), it would appear that each factor (temperature and P supply) is able to limit growth independently, with additive responses.

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