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EFFECT OF SOIL TEMPERATURE AND SOIL WATER ON REPRODUCTION OF NEMATODE POPULATIONS INDIGENOUS TO THE COTTONWOOD SITE

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ABSTRACT

Effects of constant levels of soil temperature or soil water on reproduction of indigenous nematode populations were determined in soil blocks removed from range at the Cottonwood Site. Greatest reproduction of plant feeding forms occurred at 25°C. Little or no reproduction occurred at or below 15°C, and 35°C was lethal to most plant feeders. Reproduction of individual plant feeding taxa was in general agreement with that for the entire group. Highest populations of predaceous forms occurred at 30°C; overall, however, this group showed little response to temperature. Temperature had little influence on reproduction of saprophagous forms and substantial population increases over initial levels occurred at all temperatures.

Soil water appeared to be of lesser importance than temperature since significant reproduction of most taxa occurred at all water levels except 25% field capacity. Optimal reproduction of most taxa occurred at 75%, and 100% field capacity generally inhibited reproduction.

On the basis of Cottonwood abiotic studies it appears that plant feeding nematodes at the Cottonwood Site are appreciably active only from June through September. Overall absence of response of saprophagous forms to temperature indicates they possess a wider range of limits to activity than either plant feeders or predators.

INTRODUCTION

Nematodes are an important component of the belowground invertebrate biomass at the Cottonwood Site, and estimates of nematode intake indicate that plant feeding nematodes consume a significant amount of range vegetation (6). Soil water and temperature are important abiotic influences on nematode activity (1, 5, 7, 8), and a considerable amount of information is available concerning their effects. However, very little is known concerning the taxa that occur at the Cottonwood Site and, even when available, is of limited use since geographical location of a population may influence response to temperature (7).

In a previous study (6) it was assumed that nematodes remained active throughout the growing season. The method used in the study to calculate nematode intake compensated, in part, for temperature effects since nematode respiration is a part of the calculations. At low temperatures nematode respiration is near zero and increases rapidly with increasing temperature; however, high temperatures may be lethal. No attempt was made to compensate for effects of soil water.

The objectives of the present study were to determine the effects of constant levels of soil water or temperature on reproduction of nematodes indigenous to the Cottonwood Site and, using resulting of Cottonwood abiotic studies (2, 4), to determine the period of nematode activity.

METHODS

Sod pieces approximately 45 × 45 cm to a depth of 20 cm were removed by spade from grazed and ungrazed treatments at the Cottonwood Site on April 4, 1973. The sod was stored at 4°C until subdivided into blocks 6 × 6 cm square by 15 cm in length. Blocks were then double wrapped in aluminum foil and reinforced with tape.

Blocks for use in the temperature study were buried to within 1 cm of the top in sterile sand in metal containers which in turn were wrapped with heavy plastic. The containers were then placed in constant temperature tanks held at 10°, 15°, 20°, 25°, 30°, and 35°C. Water of the same temperature as that of the respective tank was applied when necessary. Care was taken to avoid overwatering of blocks since drainage was limited.

Material used in the moisture study was handled in a similar manner except only blocks from the grazed treatment were used and styrofoam strips were used to support them in metal containers. Field capacity was determined by thoroughly saturating six randomly selected blocks and allowing them to drain overnight in a cold room (4°C). Blocks were then weighed and dried at 60°C for 2 weeks and reweighed. Soil water in remaining blocks was maintained by daily weighings at 25%, 50%, 75%, and 100% field capacity. These levels correspond approximately to 7.1, 14.2, 21.3, and 28.4 cm of water to 60 cm depth (Vol. water/Vol. soil). The containers were arranged in a randomized complete block design in a glasshouse maintained at 25 $\pm$ 3°C. Blocks from the ungrazed treatment were not included in the moisture study because considerable difficulty was experienced in maintaining integrity of soil blocks during cutting, and necessary uniformity in weight was not obtained.

Treatments in both studies were replicated six times. Initial nematode populations were determined from six randomly selected blocks from both grazing treatments. Final nematode populations were assessed 6 months after treatments were initiated. Nematodes were extracted and counted in nine taxa groupings as previously described (6). Biomass as calculated from previously determined values (6).

Data were statistically analyzed by a least squares method by Dr. L. Tucker, S.D.S.U. Station Statistician. On the basis of previous studies (1, 5, 7, 8) it was assumed that nematodes would remain in a hypobiotic state at the lowest treatment levels in both studies for the duration of the experiments. Dunnett's d' at P = 0.05 was then used to compare treatment means to 10°C in the temperature study and to 25% field capacity in the moisture study. With this test, treatment means greater than Dunnett's d' were significant at $P \leq 0.05$.

RESULTS AND DISCUSSION

Temperature Study

The optimal temperature for reproduction of plant feeding nematodes in the grazing area appeared to be 25°C (Fig. 1). Significant differences when compared to 10°C occurred at 20°, 25°, and 30°C (Tables 1 and 2). Number of plant feeding forms in ungrazed blocks differed from 10°C only at 20°C (Fig. 1). In terms of biomass a similar peak at 25°C in both grazing treatments was noted (Fig. 2) and significant differences occurred at 20°, 25°, and 30°C. This range of optimal temperatures is in agreement with previous work (7).

The response of individual plant feeding taxa was generally in agreement with that for the entire group. The number of *Tylenchorhynchus* spp. was greatest at 25°C in grazed blocks (Fig. 3). Few of these nemas occur in the ungrazed area and thus there were no differences in the ungrazed blocks. The predominant species in the *Tylenchorhynchus* group is *T. robustoides* (6) and previous work (*unpublished results*) indicates that 25°C is the optimal temperature for reproduction of this species.

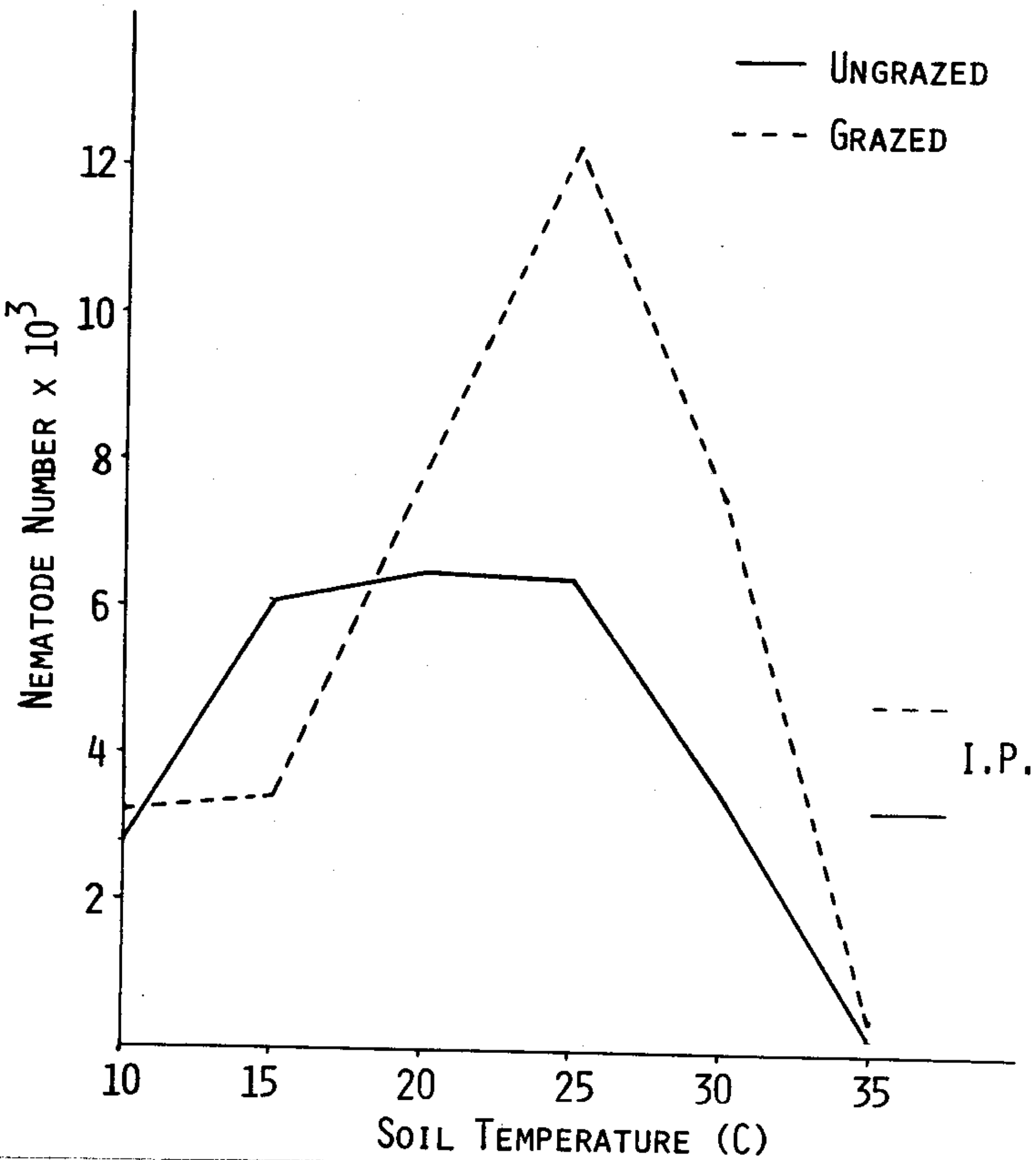

Fig. 1. Effect of soil temperature on number of plant feeding nematodes in soil blocks removed from grazed and ungrazed range at the Cottonwood Site. (I.P. = Initial Population)

Table 1. The effect of constant soil temperatures on reproduction of indigenous nematode populations in soil blocks removed from Cottonwood range.

Treatment	Soil temp. (°C)	Taxa grouping: *Tylenchorhynchus*	*Helicotylenchus*	*Paratylenchus*	Tylenchinae-Psilenchinae	*Xiphinema*	*Pratylenchus*	Dorylaimida	*Mononchus*	Rhabditida
		Initial population								
Grazed	--	669[a/]	423	1,472	2,064	17	27	358	3	1,147
Ungrazed	--	5	344	1,177	1,445	144	49	306	154	1,404
Grazed	10	391[a/]	158	554	1,885	11	0	550	65	3,145
	15	577	45	613	1,967	34	11	404	66	2,867
	20	1,470	121	1,399	4,477	45	32	1,047	44	2,074
	25	3,491	67	2,112	6,032	44	33	1,147	11	2,065
	30	1,233	11	3,943	1,601	11	11	1,847	32	3,254
	35	57	11	145	167	0	0	281	11	3,367
Ungrazed	10	32	303	811	1,407	32	33	647	21	2,981
	15	57	145	1,914	3,510	32	81	757	11	3,611
	20	57	257	2,344	3,167	223	77	878	0	3,637
	25	101	521	491	3,981	634	11	1,501	23	2,627
	30	132	222	581	1,087	134	267	1,881	53	3,913
	35	67	0	45	91	0	0	101	11	6,101
Dunnett's d' [b/] at P = 0.05		1,431	264	1,819	1,872	160	--	1,035	--	3,002

[a/] Average of six replications.

[b/] For comparisons within grazing treatments to 10°C.

Table 2. Effect of soil temperature on reproduction of plant feeding, predaceous, and saprophagous nematodes in soil blocks removed from Cottonwood range.

Soil temperature (°C)	Plant feeding		Predaceous		Saprophagous	
	Number	Biomass	Number	Biomass	Number	Biomass
			Grazed			
10	3,219	192.01[a]	395	369.23	3,145	250.03
15	3,409	194.91	308	290.18	2,867	227.93
20	7,963	454.81	672	620.04	2,074	164.88
25	12,238	689.84	699	640.61	2,065	164.17
30	7,549	451.18	1,140	1,046.41	3,254	258.69
35	492	49.13	180	165.57	3,367	267.68
Dunnett's d'[b] at P = 0.05	3,545	224.00	610	--	3,002	--
			Ungrazed			
10	2,877	193.80	409	376.73	2,981	236.99
15	6,042	269.82	465	426.68	3,611	287.07
20	6,476	417.56	527	481.63	3,637	289.14
25	6,339	796.26	924	847.26	2,627	208.85
30	3,532	452.58	1,182	1,086.88	3,913	311.08
35	264	24.40	72	66.83	6,101	485.03
Dunnett's d' at P = 0.05	3,545	224.00	610	--	3,002	--

[a] Dry wt in µg.

[b] For comparisons within grazing treatments to 10°C.

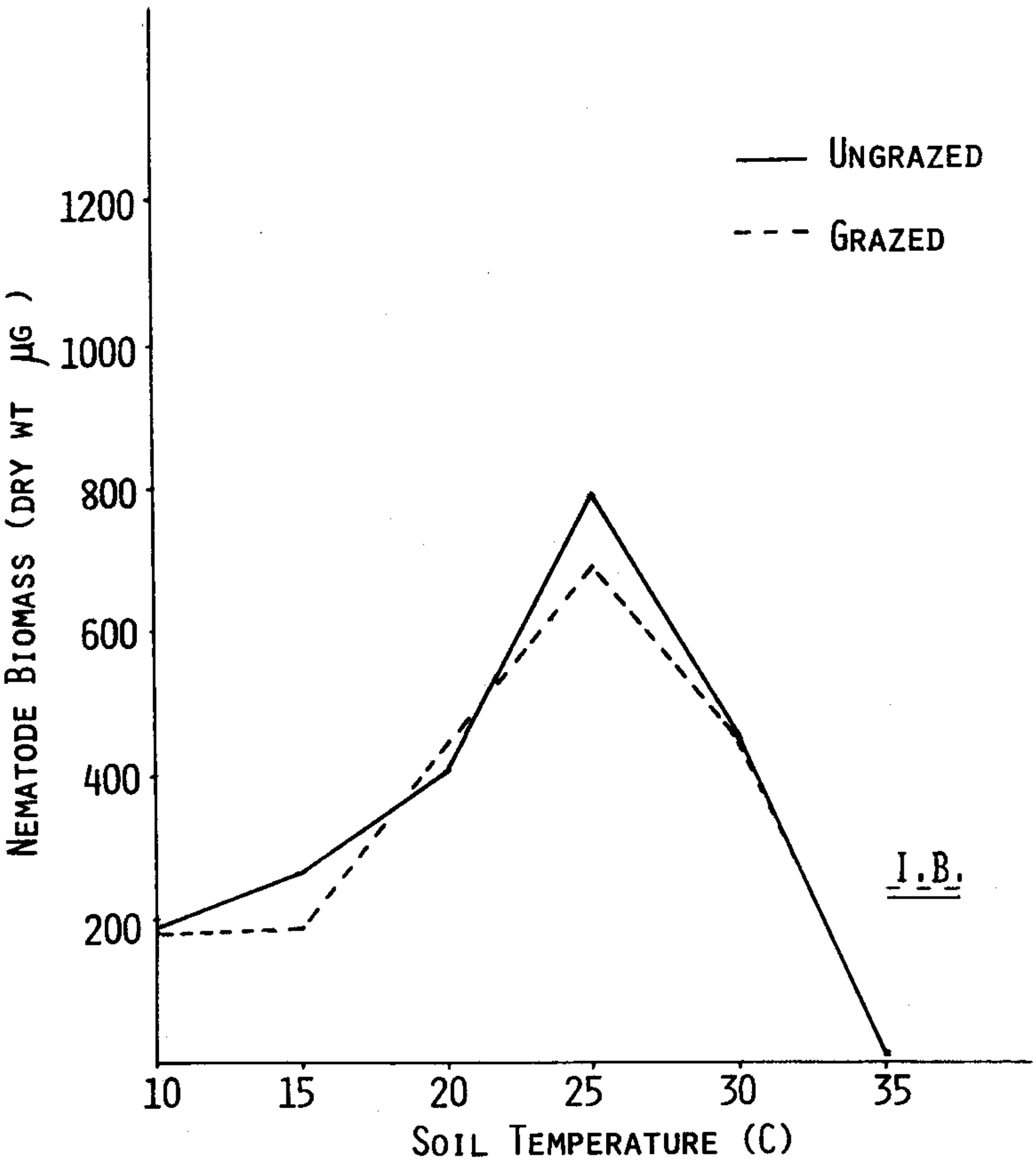

Fig. 2. Effect of soil temperature on biomass of plant feeding nematodes in soil blocks removed from grazed and ungrazed range at the Cottonwood Site. (I.B. = Initial Biomass)

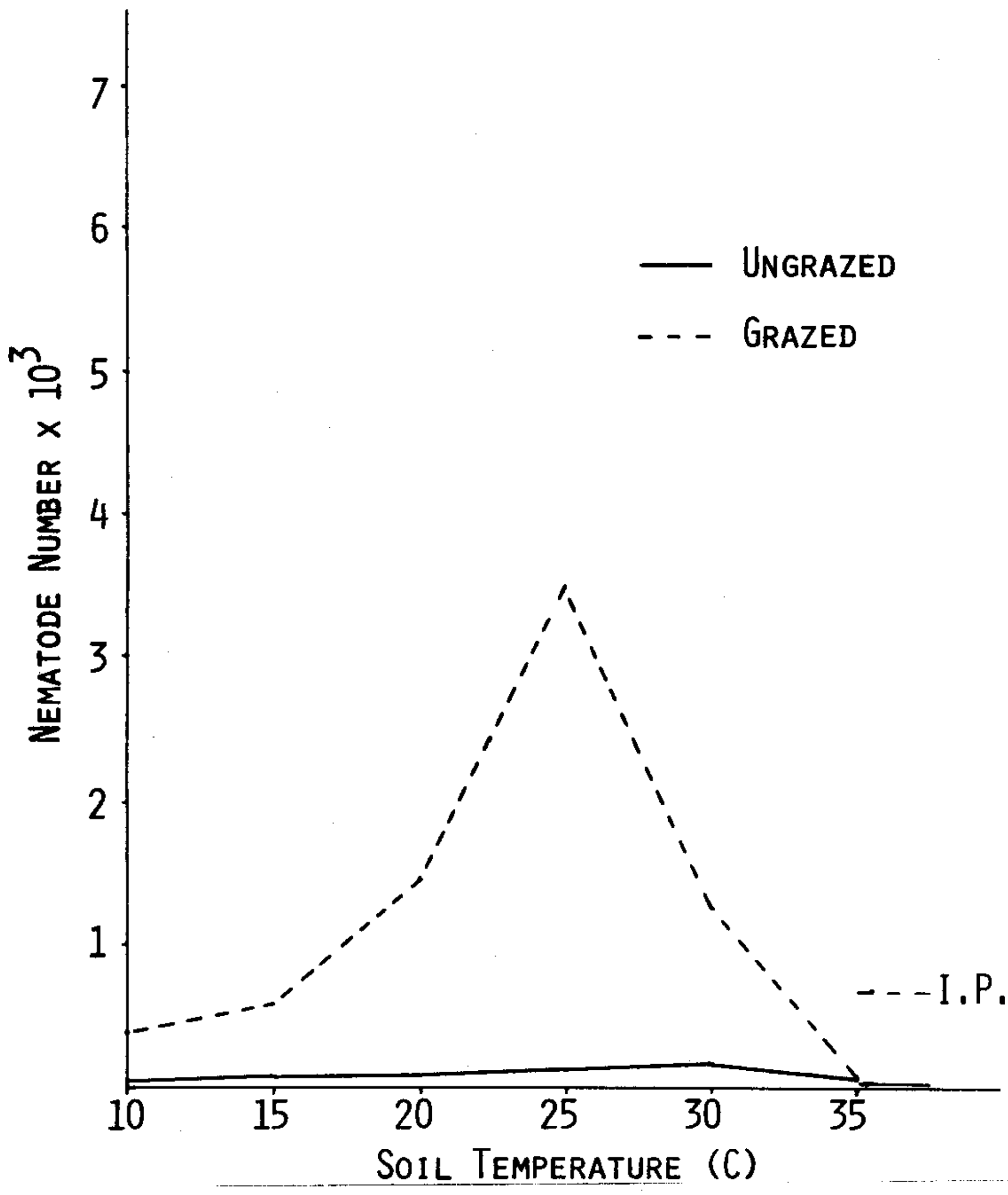

Fig. 3. Effect of soil temperature on number of *Tylenchorhynchus* spp. in soil blocks removed from grazed and ungrazed range at the Cottonwood Site. (I.P. = Initial Population)

The greatest number of *Xiphinema* spp. also occurred at 25°C (Fig. 4). This taxa group is most prevalent in the ungrazed treatment (6) and it is probable that these large nemas are primarily responsible for the biomass peak at 25°C noted earlier (Fig. 2). The response of Tylenchinae-Psilenchinae was somewhat erratic (Fig. 5), especially in the ungrazed blocks where significant differences occurred at 15° and 25°C. In the grazed blocks significant differences compared to 10°C occurred at 20° and 25°C with the greatest number occurring at 25°C (Fig. 5). A substantial number of species is included in this taxa group (6) which may account for the erratic response.

The reproduction of the *Paratylenchus* spp. was strikingly different in the grazed and ungrazed blocks (Fig. 6). A significant increase occurred at 30°C in the grazed blocks whereas numbers were highest at 20°C in the ungrazed. It appears that different species are involved; however, this was not observed in an earlier study (6). In addition, this taxon did not increase substantially above the initial population in either grazing treatment (Fig. 6) which might also explain the unusual response.

The effects of constant temperature on reproduction of predaceous and saprophagous forms were also determined. The numbers and biomass of predaceous forms were significantly greater only at 30°C (Fig. 7 and 8). The very sharp drop in reproduction of predaceous forms from 30° to 35°C, especially apparent in terms of biomass (Fig. 8), suggests that the true optimal temperatures lie between 25° and 30°C. Numbers of predators did not substantially exceed initial levels at most of the temperatures (Fig. 7). Predaceous nematodes are not dependent solely on other nematodes for sustenance as has been previously discussed (6), and it

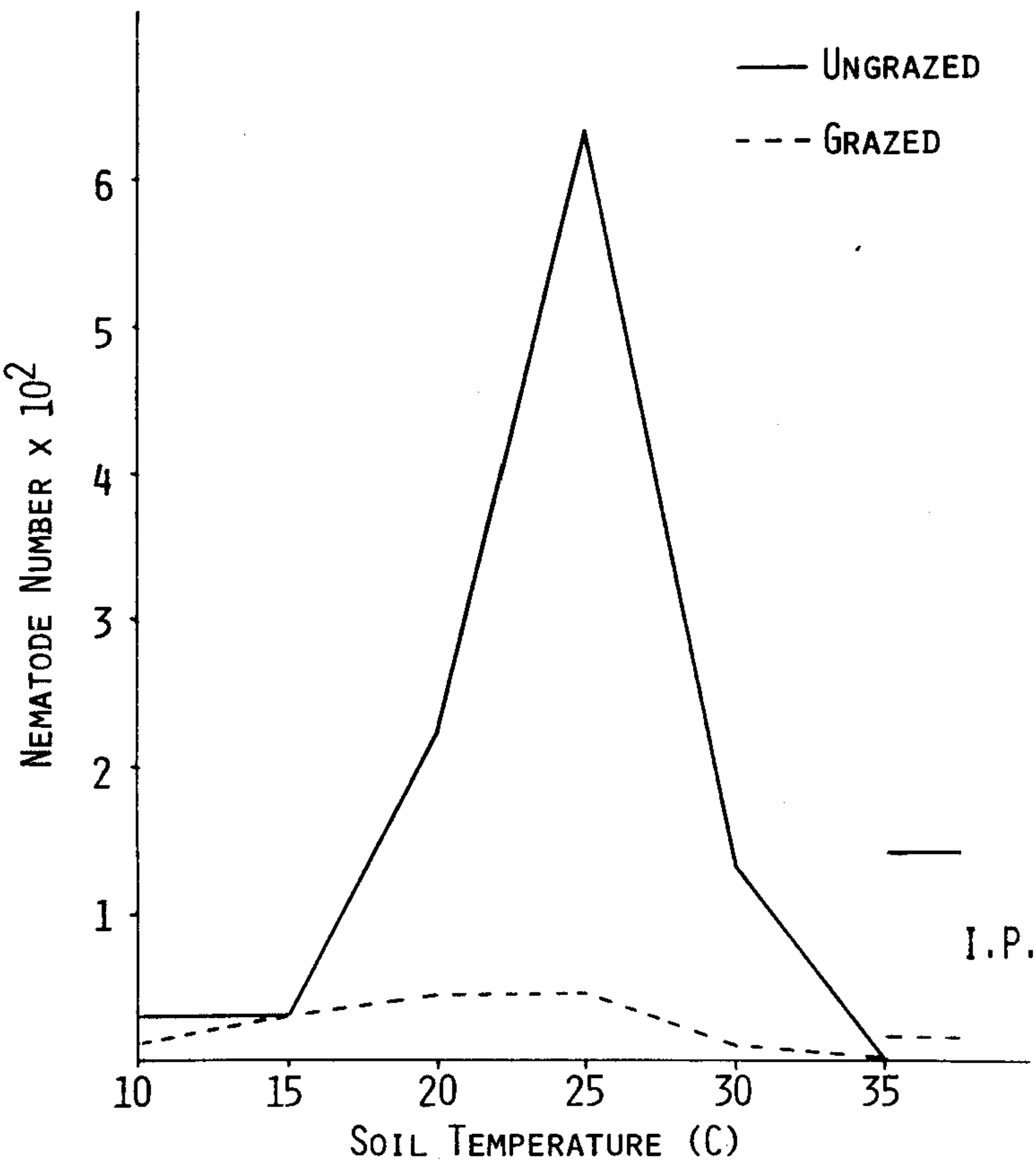

Fig. 4. Effect of soil temperature on number of *Xiphinema* spp. in soil blocks removed from grazed and ungrazed range at the Cottonwood Site. (I.P. = Initial Population)

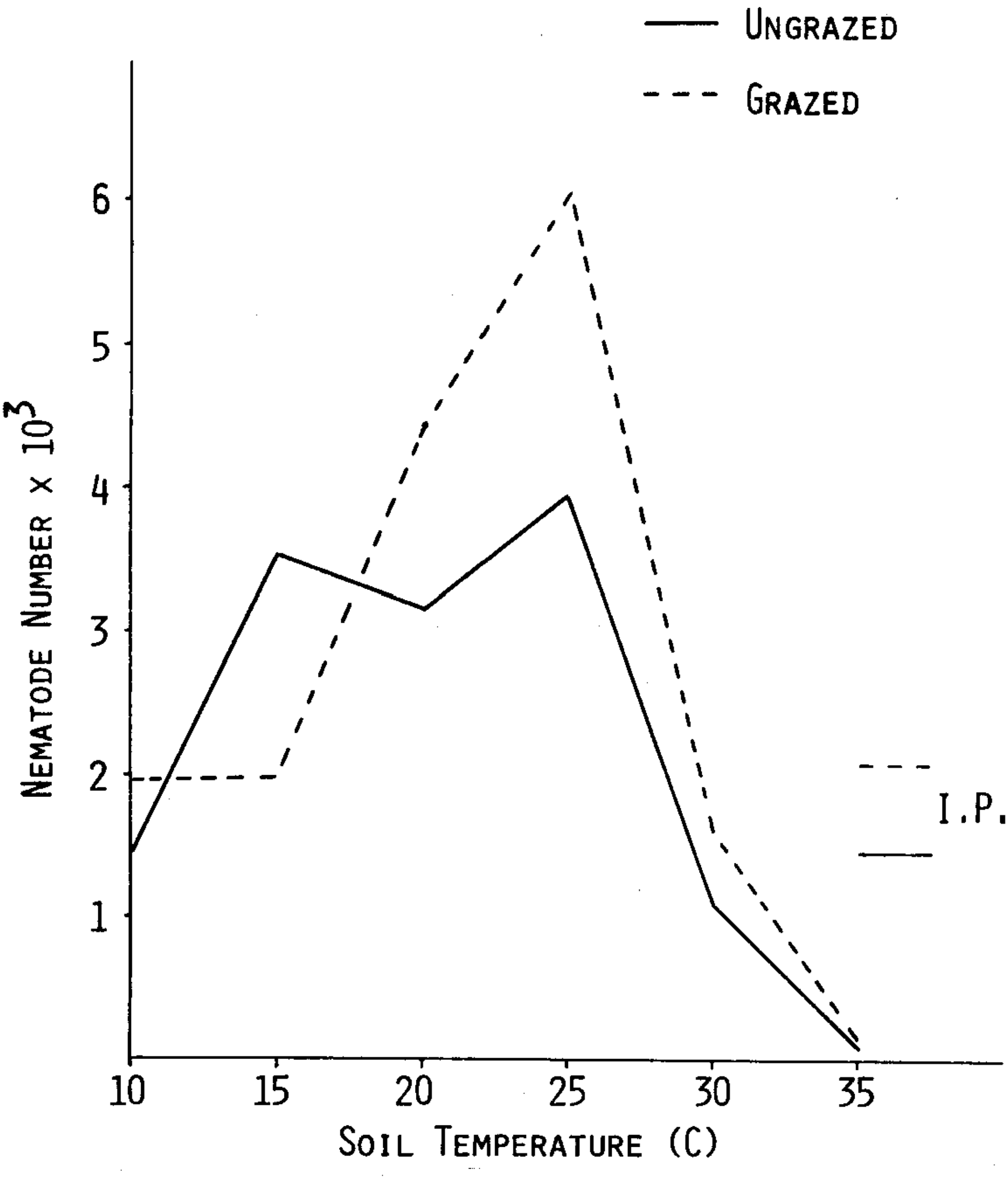

Fig. 5. Effect of soil temperature on number of Tylenchinae-Psilenchinae spp. in soil blocks removed from grazed and ungrazed range at the Cottonwood Site. (I.P. = Initial Population)

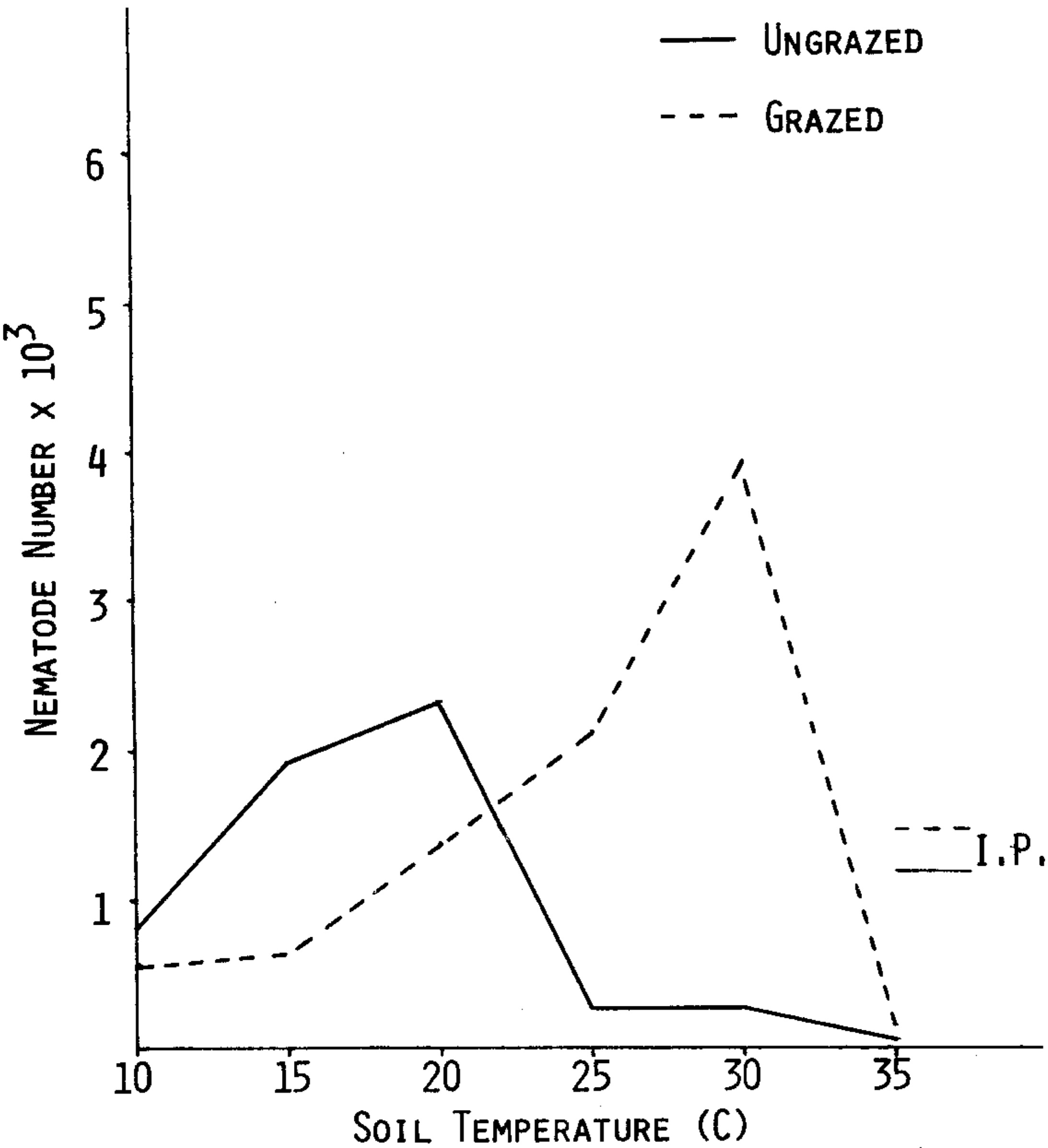

Fig. 6. Effect of soil temperature on number of *Paratylenchus* spp. in soil blocks removed from grazed and ungrazed range at the Cottonwood Site. (I.P. = Initial Population)

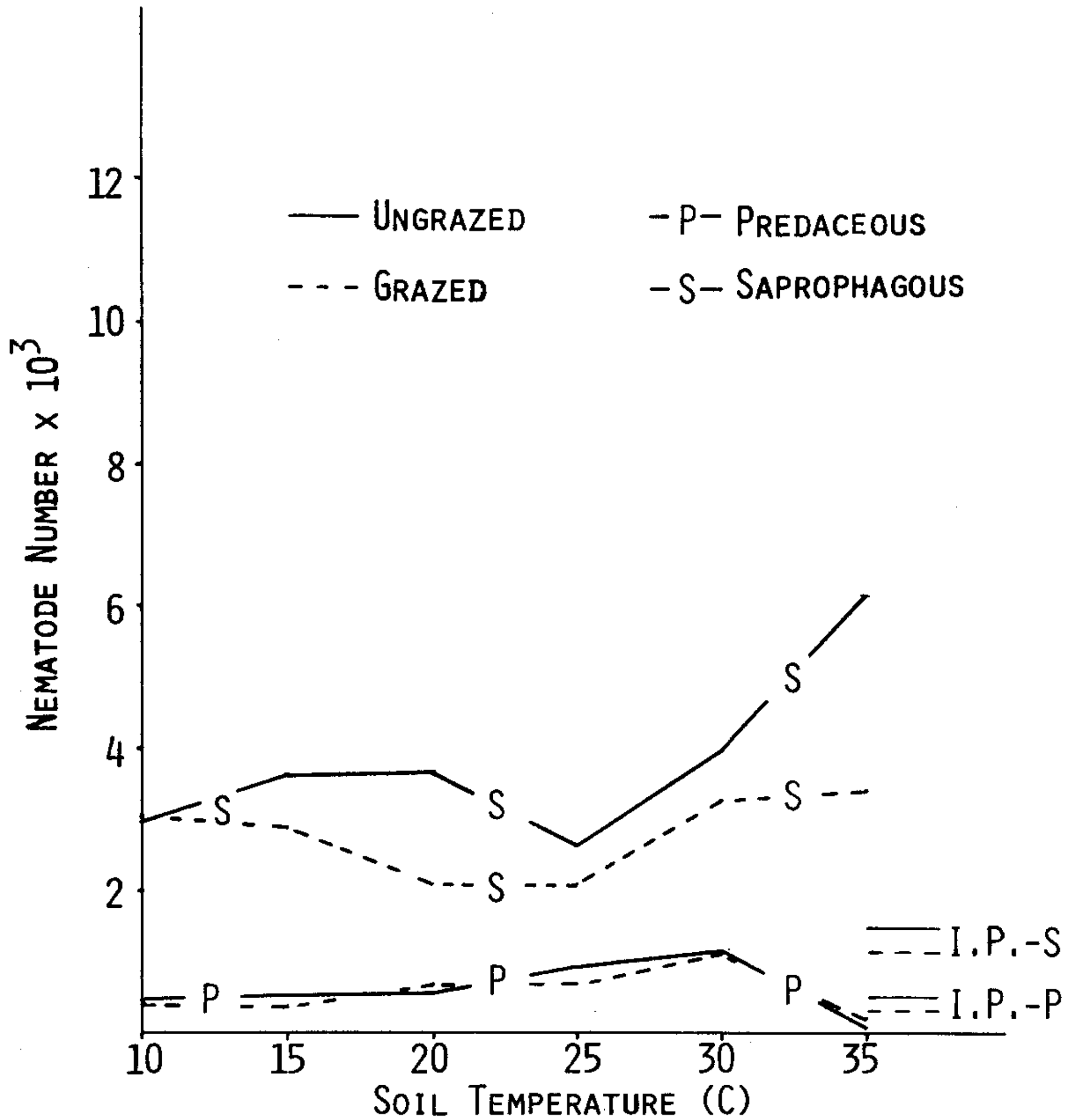

Fig. 7. Effect of soil temperature on number of predaceous and saprophagous nematodes in soil blocks removed from grazed and ungrazed range at the Cottonwood Site. (I.P. = Initial Population)

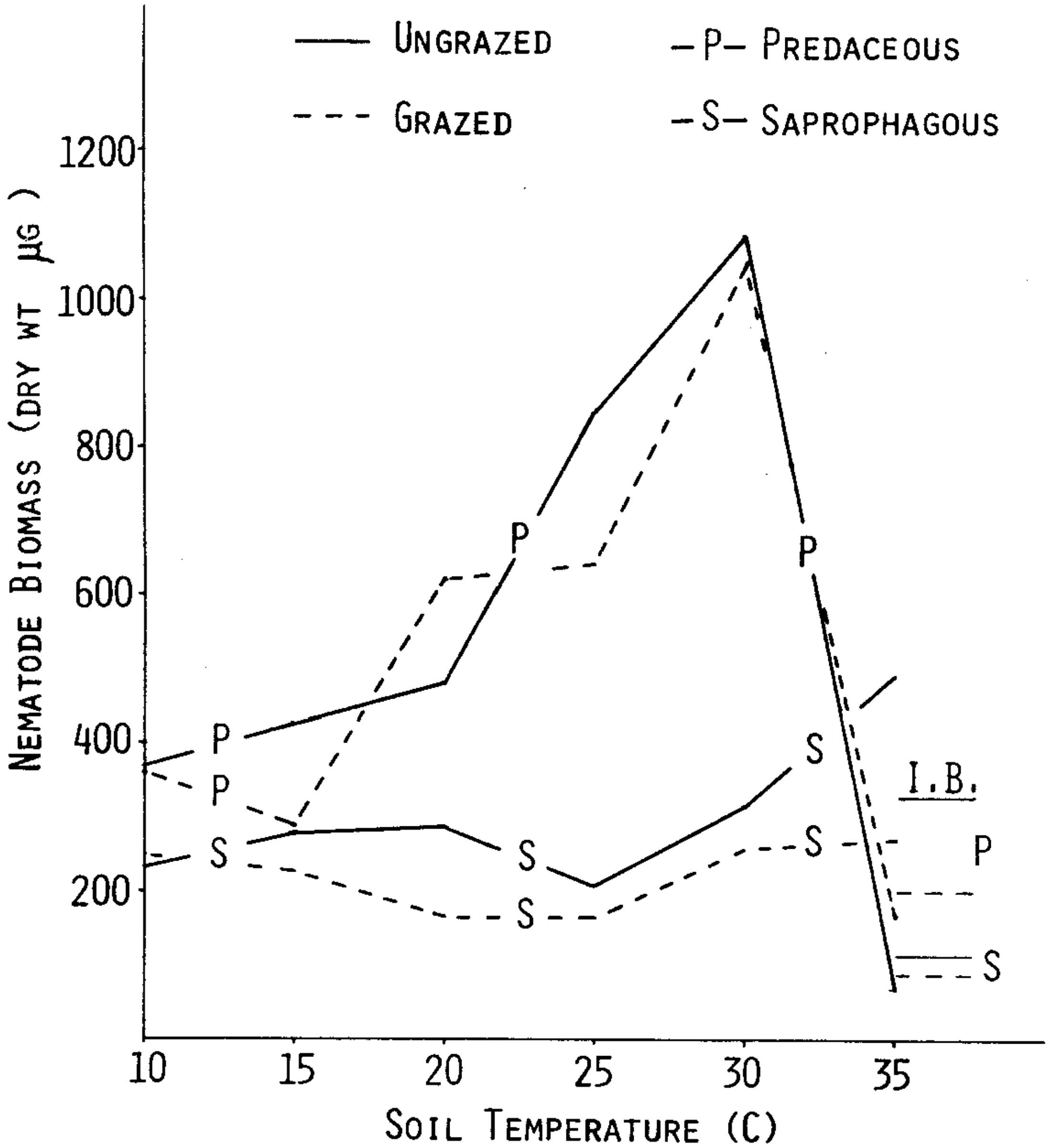

Fig. 8. Effect of soil temperature on biomass of predaceous and saprophagous nematodes in soil blocks removed from grazed and ungrazed range at the Cottonwood Site.
(I.B. = Initial Biomass)

is possible that conditions in this study interfered with reproduction of other prey and thus hindered predator reproduction. The only significant difference compared to 10°C in reproduction of saprophagous forms occurred at 35°C in the ungrazed blocks (Fig. 7 and 8). The number of saprophagous forms increased above the initial levels at all temperatures (Fig. 7). The large number of species included in the saprophagous taxa grouping (6) may account for the general absence of temperature response; however, no attempt was made to determine if a species or a group of species responded differentially to the range of temperatures.

The growth of grasses in soil blocks generally increased with increasing temperature (Fig. 9). Growth in ungrazed blocks was greater than grazed at lower temperatures, whereas at higher temperatures growth in grazed blocks increased substantially above the ungrazed. This might be expected since vegetation in the ungrazed treatment is dominated by a cool season grass *Agropyron smithii* Rydb. while warm season grasses *Buchloe dactyloides* (Nutt.) Engelm. and *Bouteloua gracilis* (H.B.K.) Lag. ex. Steud. dominate the grazed treatment (3).

Soil Water Study

Optimal reproduction of all trophic levels occurred at 75% field capacity (Fig. 10). Reproduction was significantly greater (Table 3) at 50, 75 and 100% for plant feeding and saprophagous forms compared to 25% field capacity. Significant increase in reproduction of predaceous forms occurred only at 75% (Fig. 10).

Response of individual plant feeding taxa generally corresponded to that of the trophic level as a whole (Fig. 11). Number of Tylenchinae-Psilenchinae was significantly greater at 50 and 75% field capacity and

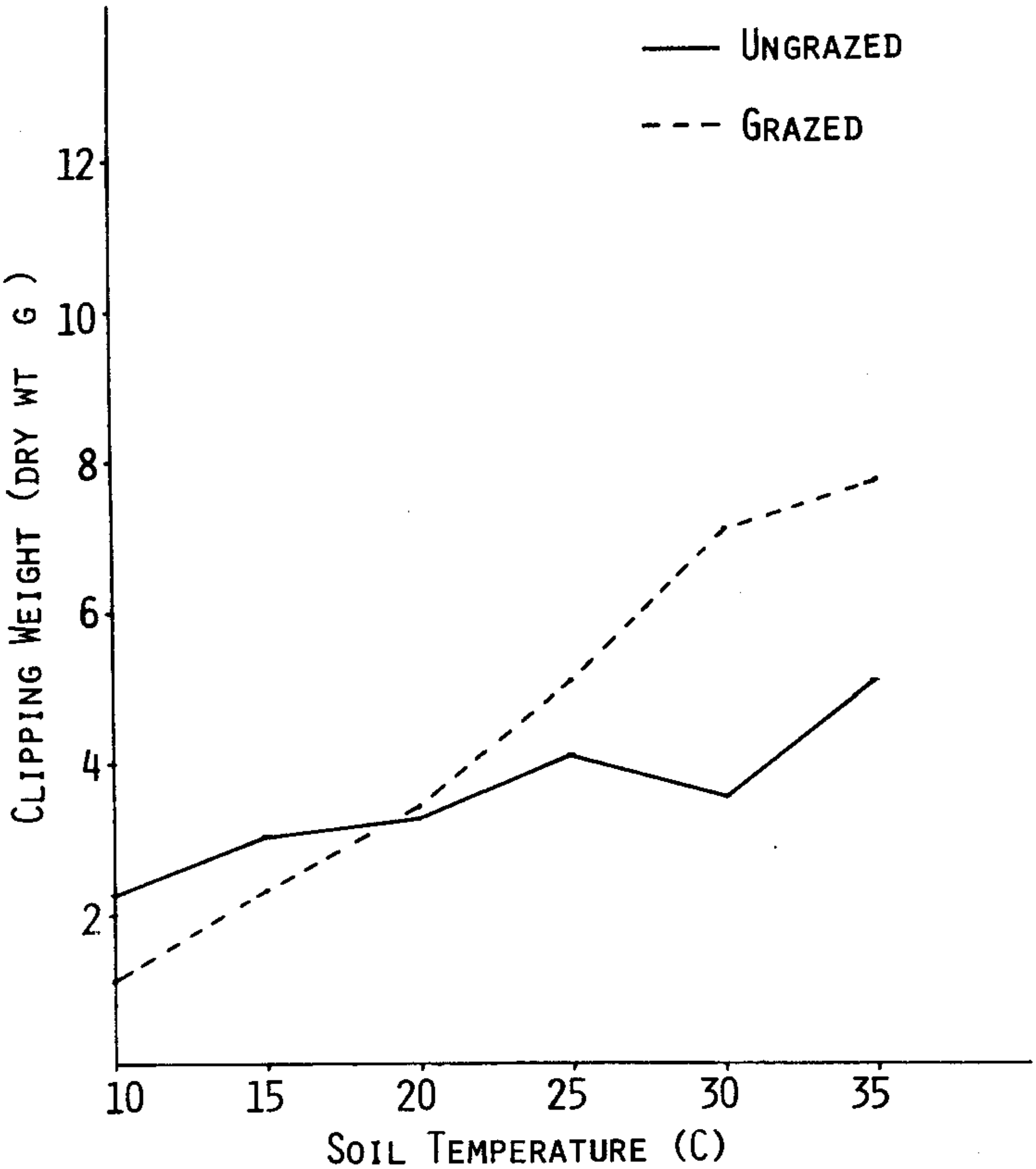

Fig. 9. Effect of soil temperature on growth of grasses in soil blocks removed from grazed and ungrazed range at the Cottonwood Site.

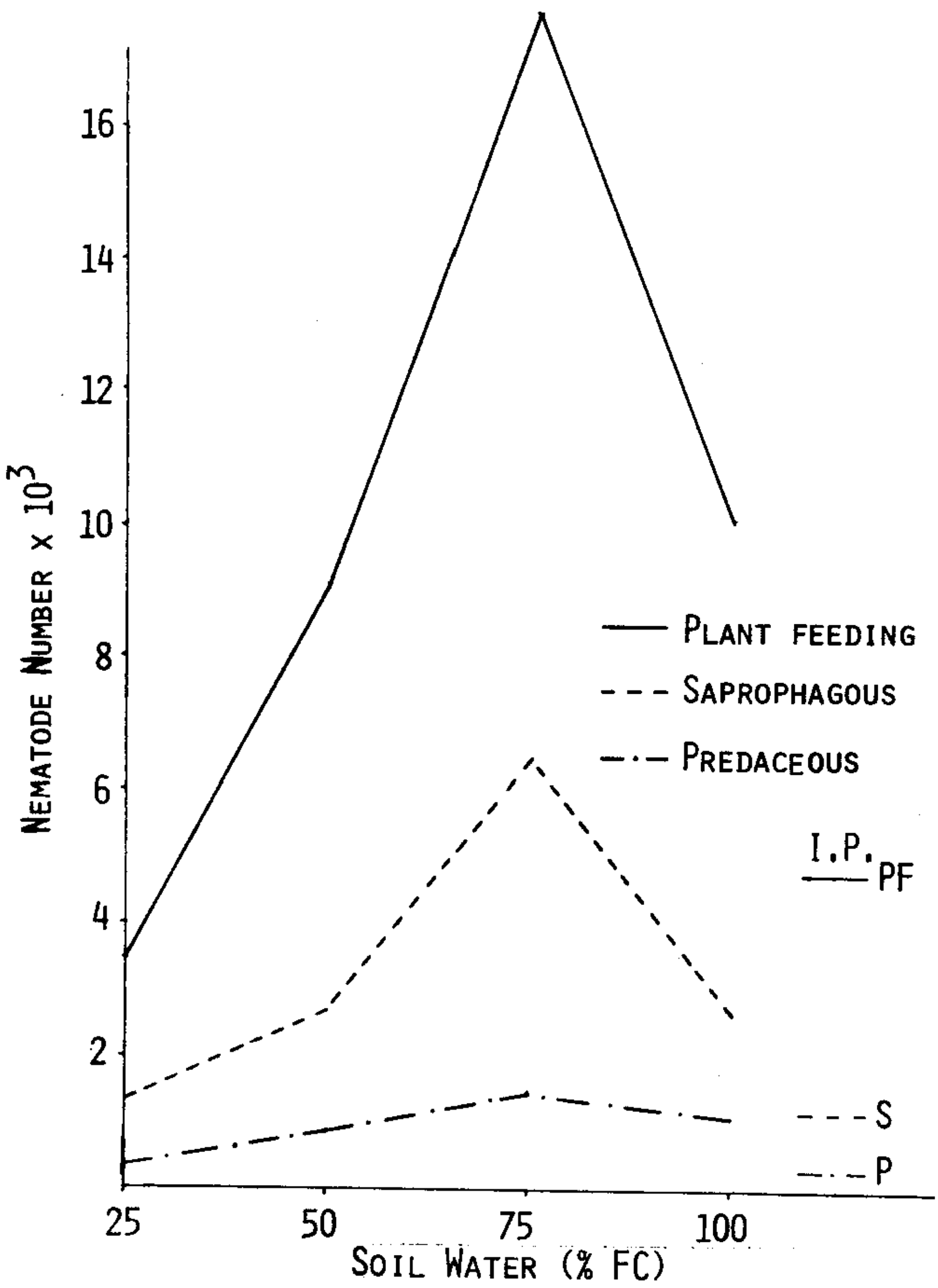

Fig. 10. Effect of soil water on numbers of plant feeding, predaceous and saprophagous nematodes in soil blocks removed from grazed range at the Cottonwood Site. (I.P. = Initial Population)

Table 3. Effect of soil water on reproduction of nematodes in soil blocks removed from grazed range at the Cottonwood Site.

Soil water field capacity (%)	*Tylenchorhynchus*	*Helicotylenchus*	*Paratylenchus*	Tylenchinae-Psilenchinae	*Xiphinema*	*Pratylenchus*	Dorylaimida	*Mononchus*	Rhabditida
	Taxa grouping								
	Initial population								
	669[a]	423	1,472	2,064	17	27	358	3	1,147
25	224[a]	89	637	2,153	0	0	447	88	1,335
50	842	301	1,988	5,403	11	21	1,224	98	2,621
75	3,990	480	3,747	9,225	11	201	2,247	89	6,425
100	4,301	67	609	4,670	0	11	1,534	257	2,737
Dunnett's d' at P = 0.05	1,738	--	1,873	2,598	--	--	1,065	--	1,324

Soil water field capacity (%)	Trophic level					
	Plant feeding		Predaceous		Saprophagous	
	Number	Biomass	Number	Biomass	Number	Biomass
25	3,282	158.49[b]	356	336.44	1,335	106.13
50	9,056	456.48	832	772.86	2,621	208.37
75	18,553	1,019.25	1,437	1,324.86	6,425	510.79
100	10,295	723.23	1,177	1,108.09	2,737	217.59
Dunnett's d'[c] at P = 0.05	2,936	193.00	839	--	1,324	--

[a] Average of six replications.

[b] Dry wt in µg.

[c] For comparisons to 25% field capacity.

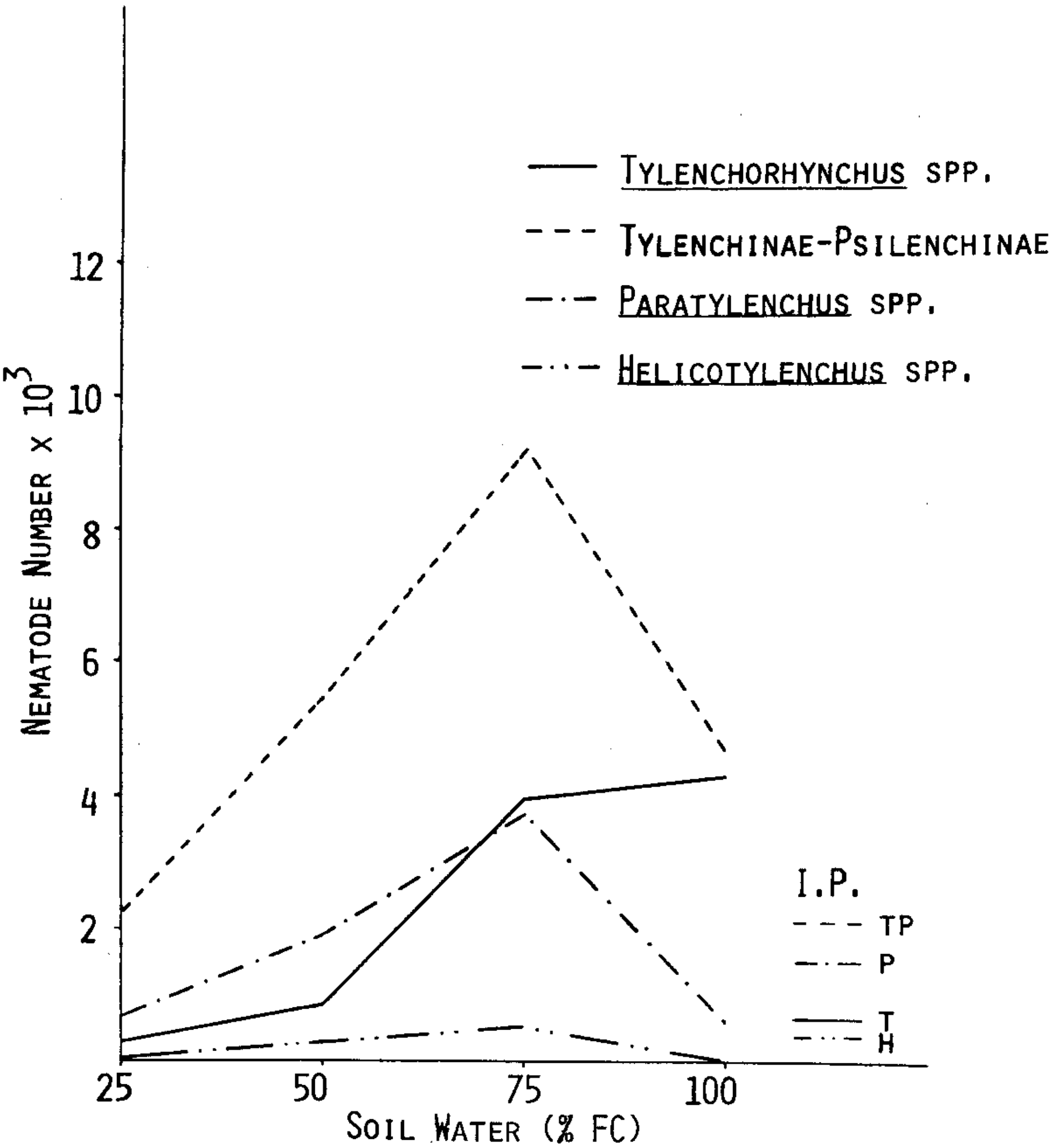

Fig. 11. Effect of soil water on numbers of *Tylenchorhynchus* spp., *Helicotylenchus* spp., *Paratylenchus* spp., and Tylenchinae-Psilenchinae in soil blocks removed from grazed range at the Cottonwood Site. (I.P. = Initial Population)

number of *Paratylenchus* spp. was greater at 75%. There were no differences in reproduction of *Helicotylenchus* spp. (Fig. 11). The majority of this taxa group occur below 10 cm soil depth (6) and thus very few were included in the soil blocks. Numbers of *Tylenchorhynchus* spp. increased significantly only at 75 and 100%. The increase in numbers of *Tylenchorhynchus* spp. from 75 to 100%, which is the reverse occurrence for all other taxa, may be due to the preference of this group for the upper soil layers (6). It is very probable that oxygen was in short supply in the lower layers of the soil blocks held at 100% field capacity, and inadequate aeration apparently suppressed all other taxa.

The growth of the grasses in the soil blocks increased with increasing soil water content (Fig. 12). Vegetation in the blocks held at 25% field capacity failed to even green during the 6-month study period. This might be expected since this soil water level is well below the wilting coefficient for soil at Cottonwood.

CONCLUSIONS

The optimal temperature for reproduction of most plant feeding nematodes was 25°C. Little or no reproduction occurred at 10° and 15°C and six months at 35°C was lethal to most plant feeders. Reproduction is but one measure of nematode activity and it is possible that some feeding occurred at 10° and 15°C. Then, too, constant temperatures are highly artificial and it is possible that alternating temperatures might have stimulated reproduction (7). However, in this study it appears that plant feeding forms indigenous to the Cottonwood Site are not appreciably active below 15°C or above 30°C. On the basis of 1970 (4) and 1971 (2) Cottonwood abiotic studies, plant feeders apparently are

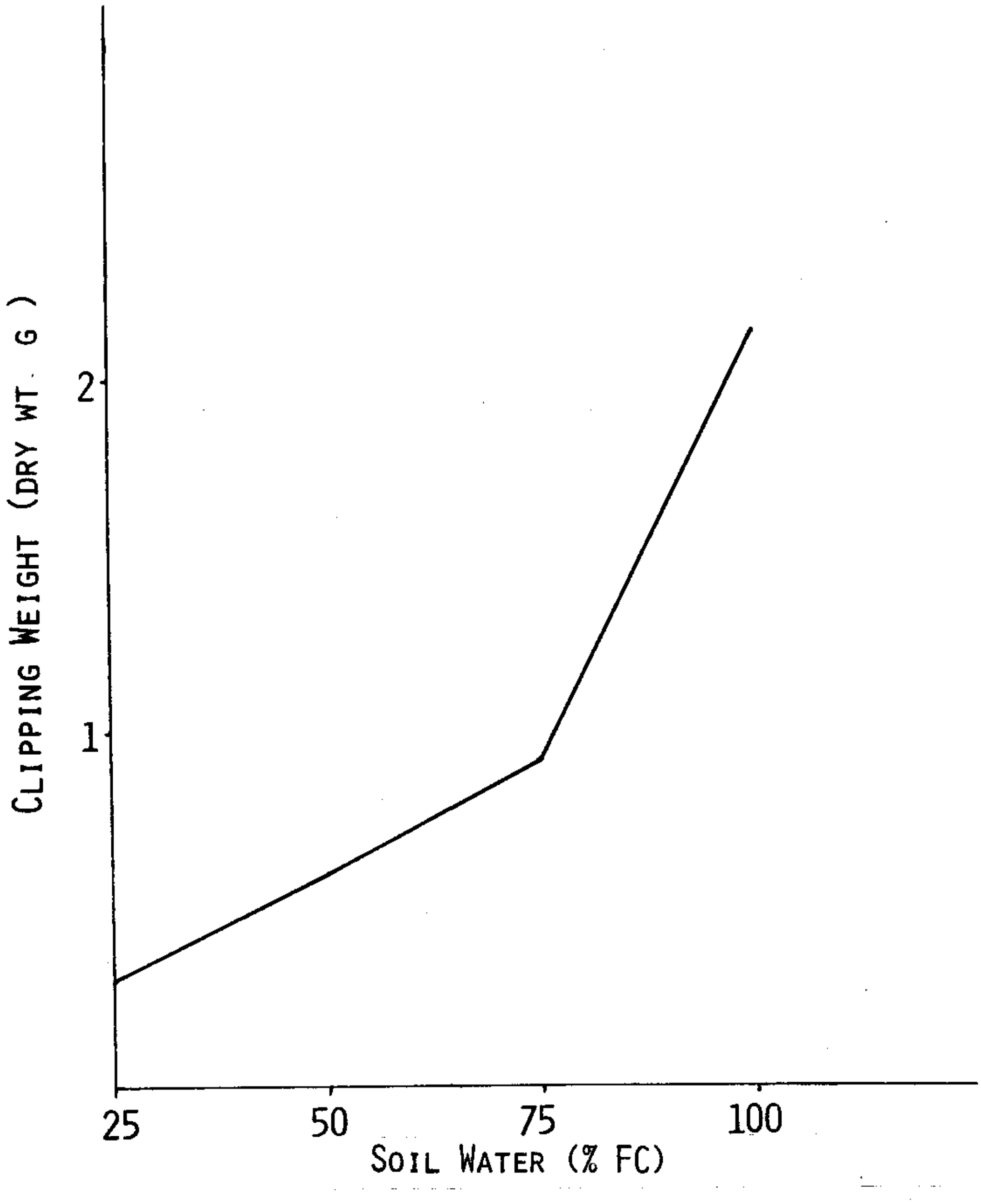

Fig. 12. Effect of soil water on growth of grasses in soil blocks removed from grazed range at the Cottonwood Site.

active only from June through September. This in turn will necessitate a recalculation of nematode intake in an earlier study (6) since it was then assumed that nematodes were active from April through October. As previously mentioned, however, nematode respiration is quite low at low temperatures and thus a recalculation will probably not greatly reduce intake.

Highest reproduction of predaceous forms occurred at 30°C, although numbers of predators did not substantially exceed the initial population levels at any of the temperatures tested. Interestingly, temperature appeared to have little influence on reproduction of saprophagous forms. Perhaps the taxonomically diverse as well as the opportunistic nature of members of this trophic level accounted for lack of temperature response.

Soil water levels tested appeared to be of less importance than temperature. Significant reproduction of most taxa occurred at all soil water levels except 25% field capacity. Optimal reproduction for most taxa occurred at 75% and, with the exception of *Tylenchorhynchus* spp., 100% field capacity inhibited reproduction, possibly because of inadequate aeration at this soil water level. Interpretation of results of the soil water study in terms of the Cottonwood abiotic studies (2, 4) is difficult due to a lack of data points on nematode reproduction between 25 and 50% field capacity. If it is assumed that the increase in nematode numbers from 25 to 50% field capacity was linear and that an increase above the initial population level indicates the nemas were active, it then appears that about 35% field capacity would limit nematode activity. Under this assumption soil water was not limiting to nematodes at the Cottonwood Site in 1970 or 1971. Further support for the above assumption is the highly hygrophilic nature of the nematode cuticle as well as their intimate association with plant roots. All three years of the previous study (6) were above normal in precipitation and thus it is possible that in a dry or even normal year periods could exist that would limit nematode activity.

It is concluded on the basis of both the temperature and soil water studies that plant feeding nematodes were active in 1970 and 1971 during the period of June through September. The absence of response of saprophagous forms to temperature indicates they possess a much wider range of limits to activity than either plant feeders or predators.

ACKNOWLEDGMENTS

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