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Biological Relationship of *Meloidogyne hapla* Populations to Alfalfa Cultivars[1]

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Abstract: Greenhouse and growth chamber studies were established to determine if there are pathological and physiological differences among *Meloidogyne hapla* populations from California (CA), Nevada (NV), Utah (UT), and Wyoming (WY) on alfalfa cultivars classified as resistant or susceptible to root-knot nematodes. In the greenhouse, plant survival was not consistent with resistance classifications. While all highly resistant Nevada Synthetic germplasm (Nev Syn XX) plants survived inoculation with all nematode populations, two cultivars classified as moderately resistant ('Chief' and 'Kingstar') survived ($P \leq 0.05$) inoculation with *M. hapla* populations better than did 'Lobo' cultivar, which is classified as resistant. Plant growth of Nev Syn XX was suppressed by only the CA population, whereas growth of the other alfalfa cultivars classified as *M. hapla* resistant or moderately resistant was suppressed by all nematode populations. Excluding Nev Syn XX, all alfalfa cultivars were severely galled and susceptible to all nematode populations. Except for Nev Syn XX, reproduction did not differ among the nematode populations on alfalfa cultivars. Nev Syn XX was not as favorable a host to CA as were the other cultivars; but, it was a good host (reproductive factor [Rf] = 37). Temperature affected plant resistance; the UT and WY populations were more pathogenic at 15–25 C, and CA was more pathogenic at 30 C. Nev Syn XX was susceptible to all nematode populations, except for CA, at only 30 C, and all other alfalfa cultivars were susceptible to all nematode populations at all temperatures.

Key words: Alfalfa, *Medicago sativa, Meloidogyne hapla,* Nematode, northern root-knot, population, race, reproduction, resistance, root growth, shoot growth, susceptibility, temperature.

Meloidogyne hapla Chitwood is the most widespread root-knot nematode species affecting the growth of alfalfa, *Medicago sativa* L., in the western United States (2,6, 20). *Meloidogyne hapla* can significantly suppress the growth, yield, and longevity of susceptible alfalfa cultivars (6,15,19).

Resistance is the only economic method of controlling *Meloidogyne* spp. on alfalfa (1,3,11,17,18). However, the pathological and physiological difference observed in root-knot nematode species (4,8,10,13,17) indicate that plants classified as resistant should be used with caution. For example, highly resistant Nevada Synthetic XX germplasm (Nev Syn XX) (17) is the only alfalfa selection resistant to most *M. hapla* populations (6,13,19) but is susceptible to a race from California (9). Temperature is also known to affect the pathological relationship between root-knot nematodes and alfalfa (5–7,12,16).

Because cultivars classified as resistant are susceptible to a Utah population of *M. hapla* (8), we performed controlled greenhouse and growth chamber studies to i) investigate the pathological and temperature-induced differences between geographically separated *M. hapla* populations in the western United States, and ii) determine if the resistance or susceptibility of alfalfa cultivars differs from that listed under certification (1).

Materials and Methods

Nematode inoculum: Meloidogyne hapla populations used in this study were as follows: CA collected initially from alfalfa at Visalia, California; NV from alfalfa at Reno, Nevada; UT from lettuce, *Lactuca sativa* L., at Ogden, Utah; and WY from alfalfa from alfalfa at Laramie, Wyoming (9,12). For congruity, the CA population, which is a known race, is also referred to as a population. Nematode populations were cultured on tomato, *Lycopersicon esculentum* Mill. cv. Rutgers, in a greenhouse, and

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eggs were collected using sodium hypochlorite (14).

Alfalfa cultivars: Classification of alfalfa resistance to *Meloidogyne* spp. based on a percentage of resistant plants is: highly resistant (HR) = >50% resistance; resistant (R) = 31–50% resistance; moderate resistant (MR) = 15–30% resistance; susceptible (S) = 0–5% resistance (1). The cultivars studied and their resistance classifications in this experiment were *M. sativa* 'Lobo' (R) and 'Chief', 'Kingstar', 'WL 316', and 'Vernal' (MR) (1). Nevada Synthetic germplasm ("Nev Syn XX") (17) (HR) was used as a resistant control. 'Commandor', 'Deseret', and 'Ranger' (S) were used as controls (8). Alfalfa plants were grown from seeds that had been scarified, surface-sterilized with captan (*cis*-N-(trichloromethylthio)-4-cyclohexene-1,2-dicarboximide), and germinated on filter paper (9).

Greenhouse bench experiment: Twenty-eight-day-old alfalfa seedlings were transplanted into individual 6-cm-wide plastic containers containing 540 g steam-sterilized Kidman fine sandy loam soil (coarse-loamy mixed mesic Calcic Haploxerolls [84% sand, 8% silt, 8% clay; 1.0% OM; pH 7.4]). Twenty-eight days after planting, each seedling was inoculated with 0 and 4.0 nematode eggs/cm^3 soil (2.16×10^3 eggs/pot). Eggs in an aqueous suspension of deionized water were poured into four holes 10 cm deep in the soil around the plant hypocotyl base. Uninoculated plants served as controls, to which deionized water was added in a manner similar to that for nematode inocula. Containers were maintained on a greenhouse bench at a soil temperature of 24 ± 4 C. The experiment was a 4 × 9 × 2 factorial (4 nematode species × 9 plant cultivars × 2 inoculum densities) in a randomized complete block design with 25 replications (pots), with one plant per replicate. Plants received 19 hours of light per day supplemented with high-output fluorescent lamps and were watered daily and fertilized monthly with a complete nutrient solution (10 × 10 × 10 NPK). Cultivars were harvested 120 days after inoculation. Plant survival, shoot and root weights, and root galling indices (1 = no galling, 2 = 1–10%, 3 = 11–20%, 4 = 21–50%, 5 = 51–80%, 6 = 81–100% root tissue galled) were determined. Nematode eggs were extracted from each root system by the NaOCl method (14), the nematode reproductive factor (Rf = final nematode population (Pf)/initial nematode population (Pi)), and resistance classification was calculated for each plant. The criterion for classifying as resistant was Rf < 1 (3). The experiment was repeated, and the data are means of the two experiments. Data were analyzed with ANOVA, and means were separated by Duncan's multiple-range test. Plant survival data were arcsine transformed.

Growth chamber experiment: A study similar to the greenhouse experiment was conducted in temperature-controlled growth chambers but was limited to one plant entry per resistance classification. The alfalfa cultivars were Nev Syn XX (HR), Lobo (R), Chief (MR), and Deseret (S). Plants were grown in four chambers maintained at 15, 20, 25, and 30 ± 2 C. When plants were 28 days old, each was inoculated with one of the nematode populations and maintained as in the greenhouse bench experiment. The experiment was a 4 × 4 × 4 × 2 factorial (4 temperatures × 4 plant entries × 4 nematode populations × 2 inoculum densities) in a randomized block design with 10 replications of one plant per replicate. Plants were harvested 120 days after inoculation and data were recorded. The experiment was repeated, and the data are means of the two experiments.

Results

Greenhouse bench experiment: Following inoculation with *Meloidogyne hapla,* survival was generally greater ($P \leq 0.05$) in cultivars classified as resistant than in susceptible cultivars. However, a greater number of Chief plants, classified as moderately resistant, survived CA, UT, and WY populations ($P \leq 0.05$) than did Lobo plants classified as resistant (Table 1). All Nev Syn

TABLE 1. Percentage survival of alfalfa of different resistance classes inoculated with *Meloidogyne hapla* populations from California (CA), Nevada (NV), Utah (UT), and Wyoming (WY).

Cultivar	Fall dormancy†	Resistance class‡	CA	NV	UT	WY	Uninoculated control
Nev Syn XX	4	HR	100 aA	100 aA	100 aA	100 aA	100 aA
Lobo	6	R	92 bB	100 aA	88 bB	88 bB	100 aA
Chief	4	MR	100 aA	100 aA	100 aA	100 aA	100 aA
Kingstar	3	MR	100 aA	100 aA	100 aA	92 bB	100 aA
WL 316	4	MR	92 bB	92 bB	84 bC	92 bB	100 aA
Vernal	2	MR	88 bcB	88 bcB	84 bBC	80 cC	100 aA
Commandor	4	S	88 bcB	88 bcB	80 bcC	76 cdC	100 aA
Deseret	5	S	84 cB	84 cB	76 cC	76 cdC	100 aA
Ranger	3	S	84 cB	84 cB	76 cC	72 dC	100 aA

Values are the means of 25 replications (one plant per replicate), and means followed by the same letter do not differ ($P \leq 0.05$) according to Duncan's multiple-range test (lowercase letters for columns; capital letters for rows). Data were transformed using arcsine transformation. Twenty-eight-day-old plants were inoculated with 4.0 eggs/cm^3 soil and grown in the greenhouse at 24 ± 4 C for an additional 120 days.

† 1 = highly dormant, grown in northern conditions; 9 = nondormant, grown in southern conditions.

‡ HR = >50% resistance; R = 31–50% resistance; MR = 15–30% resistance; S = 0–5% resistance.

XX and Chief plants survived inoculation with all *M. hapla* populations, but survival of plants of the remaining seven alfalfa cultivars differed ($P \leq 0.05$) among nematode populations. The UT and WY populations were generally more virulent than were the CA and NV populations.

Dry-shoot weight of Nev Syn XX was suppressed ($P \leq 0.05$) by only the CA population, whereas dry-shoot weights of the other alfalfa cultivars were suppressed by all nematode populations (Table 2). Except for Nev Syn XX, dry-shoot weights did not differ ($P \geq 0.05$) among nematode

TABLE 2. Plant growth of alfalfa of different resistance classes inoculated with *Meloidogyne hapla* populations from California (CA), Nevada (NV), Utah (UT), and Wyoming (WY).

Cultivar	Fall dormancy†	Resistance class‡	CA	NV	UT	WY	Uninoculated control
					Dry-shoot weight (g)		
Nev Syn XX	4	HR	2.4 aB	3.3 aA	3.0 aA	3.1 aA	3.3 aA
Lobo	6	R	1.8 aB	1.4 bB	1.3 bB	1.4 bB	3.3 aA
Chief	4	MR	1.9 aB	1.3 bB	1.4 bB	1.5 bB	3.3 aA
Kingstar	3	MR	1.8 aB	1.4 bB	1.4 bB	1.3 bB	3.4 aA
WL 316	4	MR	1.7 aB	1.2 bB	1.3 bB	1.2 bB	3.1 aA
Vernal	2	MR	1.7 aB	1.4 bB	1.0 bB	1.1 bB	3.0 aA
Commandor	4	S	1.6 aB	1.2 bB	1.2 bB	1.2 bB	3.1 aA
Deseret	5	S	1.7 aB	1.1 bB	1.0 bB	1.4 bB	3.1 aA
Ranger	3	S	1.6 aB	1.1 bB	1.3 bB	1.2 bB	3.0 aA
					Dry-root weight (g)		
Nev Syn XX	4	HR	3.6 aA	3.7 aA	3.7 aA	3.6 aA	3.8 aA
Lobo	6	R	2.9 bB	2.1 bB	2.2 bB	2.2 bB	3.5 abA
Chief	4	MR	2.7 bB	2.2 bB	2.3 bB	2.3 bB	4.0 aA
Kingstar	3	MR	3.0 bB	2.3 bB	2.4 bB	2.2 bB	3.9 aA
WL 316	4	MR	3.0 bB	2.4 bB	2.3 bB	2.1 bB	3.4 abA
Vernal	2	MR	2.8 bB	2.2 bB	2.3 bB	2.0 bB	3.0 bA
Commandor	4	S	2.7 bB	2.1 bB	2.0 bB	2.1 bB	3.1 bA
Deseret	5	S	2.9 bB	2.3 bB	2.2 bB	2.3 bB	3.0 bA
Ranger	3	S	2.8 bB	2.1 bB	2.1 bB	2.1 bB	3.1 bA

Values are the means of 25 replications (one plant per replicate), and means followed by the same letter do not differ ($P \leq 0.05$) according to Duncan's multiple-range test (lowercase letters for columns; capital letters for rows). Twenty-eight-day-old plants were inoculated with 4.0 eggs/cm^3 soil and grown in the greenhouse at 24 ± 4 C for an additional 120 days.

† 1 = highly dormant, grown in northern conditions; 9 = nondormant, grown in southern conditions.

‡ HR = >50% resistance; R = 31–50% resistance; MR = 15–30% resistance; S = 0–5% resistance.

TABLE 3. Root galling of alfalfa of different resistance classes inoculated with *Meloidogyne hapla* populations from California (CA), Nevada (NV), Utah (UT), and Wyoming (WY).

Cultivar	Fall dormancy†	Resistance class‡	CA	NV	UT	WY
				Root galling indices§		
Nev Syn XX	4	HR	4.1 bA	1.3 bB	1.6 bB	1.7 bB
Lobo	6	R	4.4 bA	4.6 aA	4.6 aA	4.4 aA
Chief	4	MR	4.4 bA	4.6 aA	4.4 aA	4.7 aA
Kingstar	3	MR	4.5 bA	4.5 aA	4.5 aA	4.6 aA
WL 316	4	MR	4.3 bA	4.4 aA	4.4 aA	4.7 aA
Vernal	2	MR	4.6 bA	4.4 aA	4.8 aA	4.9 aA
Commandor	4	S	4.5 bA	4.4 aA	4.7 aA	5.0 aA
Deseret	5	S	4.6 bA	4.4 bA	5.0 aA	4.7 aA
Ranger	3	S	4.7 bA	4.7 ab	5.0 aA	5.1 aA
				Nematode reproductive factor¶		
Nev Syn XX	4	HR	37 bA	<1 bB	<1 bB	< bB
Lobo	6	R	55 aA	54 aA	54 aA	56 aA
Chief	4	MR	59 aA	53 aA	60 aA	60 aA
Kingstar	3	MR	54 aA	58 aA	61 aA	58 aA
WL 316	4	MR	53 aA	51 aA	58 aA	54 aA
Vernal	2	MR	58 aA	54 aA	63 aA	52 aA
Commandor	4	S	55 aA	56 aA	63 aA	64 aA
Deseret	5	S	61 aA	55 aA	62 aA	60 aA
Ranger	3	S	59 aA	56 aA	60 aA	63 aA

Values are the means of 25 replications (one plant per replicate), and means followed by the same letter do not differ ($P \leq 0.05$) according to Duncan's multiple-range test (lowercase letters for columns; capital letters for rows). Twenty-eight-day-old plants were inoculated with 4.0 eggs/cm^3 soil and grown in the greenhouse at 24 ± 4 C for an additional 120 days.

† 1 = highly dormant, grown in northernmost conditions; 9 = nondormant, grown in southernmost conditions (1).

‡ HR = >50% resistance; R = 31–50% resistance; MR = 15–30% resistance; S = 0–5% resistance.

§ 1 = no galling, 2 = 1–10%, 3 = 11–20%, 4 = 21–50%, 5 = 51–80%, 6 = 81–100% root tissue galled.

¶ Nematode reproductive factor = final nematode population per plant/initial nematode population per plant.

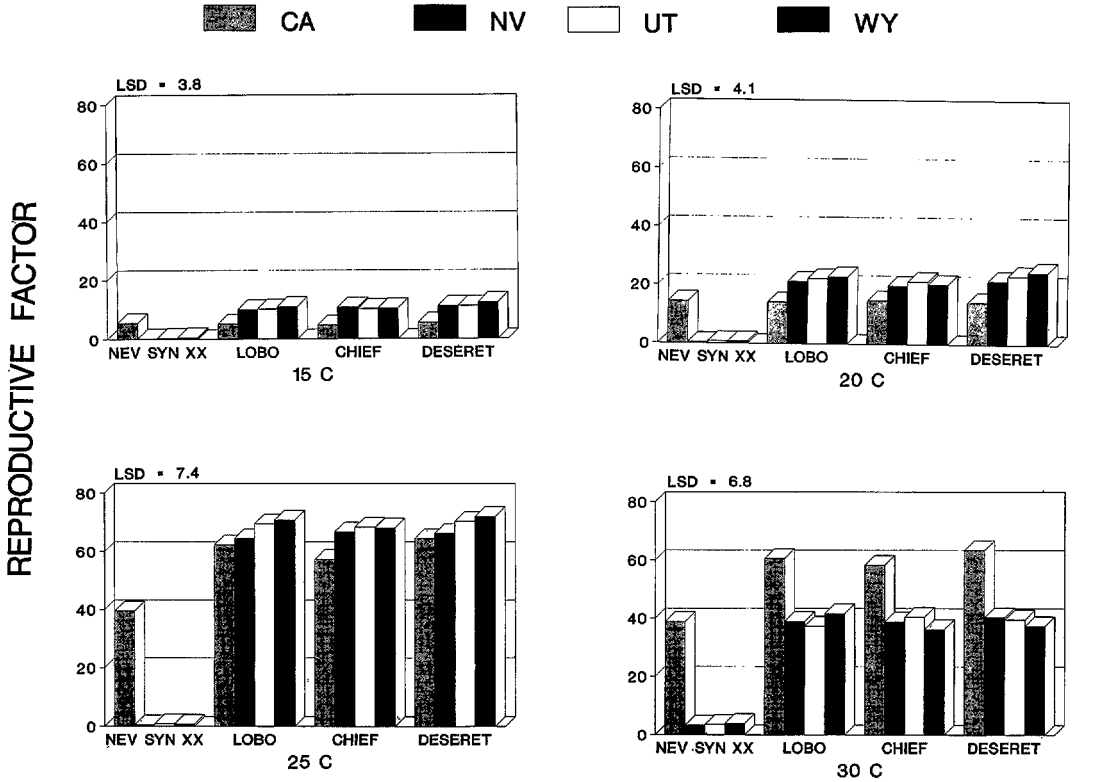

FIG. 1. The influence of *Meloidogyne hapla* populations from California (CA), Nevada (NV), Utah (UT), and Wyoming (WY) on survival of alfalfa cultivars with different resistance classifications grown at four temperatures. Inocula = 4.0 eggs/cm^3 soil per plant. Nev Syn XX is classed as highly resistant, Lobo as resistant, Chief as moderately resistant, and Deseret as susceptible to *M. hapla*.

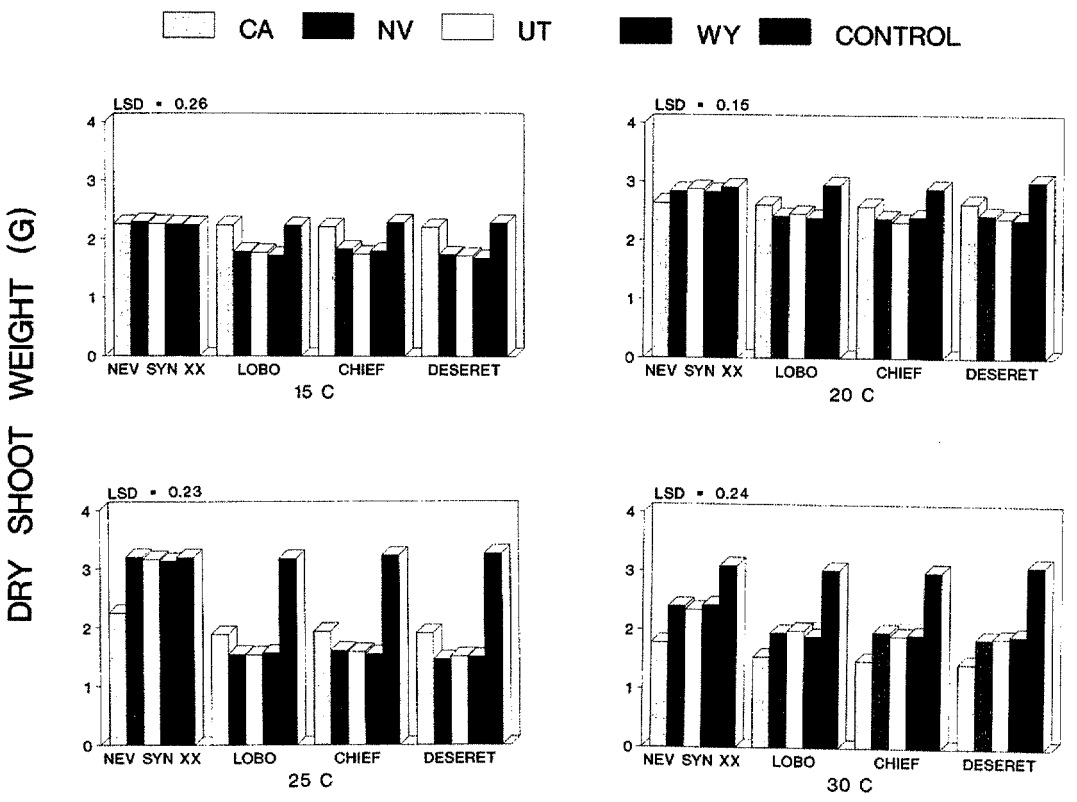

FIG. 2. The influence of *Meloidogyne hapla* populations from California (CA), Nevada (NV), Utah (UT), and Wyoming (WY) on dry shoot weight of alfalfa cultivars with different resistance classifications grown at four temperatures. Inocula = 4.0 eggs/cm^3 soil per plant. LSD is for nematode populations within cultivars. Nev Syn XX is classed as highly resistant, Lobo as resistant, Chief as moderately resistant, and Deseret as susceptible to *M. hapla.*

populations on any cultivar, and there were no differences in suppression among alfalfa cultivars classified as resistant, moderately resistant, and susceptible. Except for Nev Syn XX, all nematode populations suppressed ($P \leq 0.05$) dry-root weights of all cultivars (Table 2).

All *M. hapla* populations induced severe galling on all alfalfa cultivars, except Nev Syn XX, which was severely galled by only the CA population (Table 3). Similarly, the Rf did not differ ($P \leq 0.05$) among the nematode populations and alfalfa cultivars, except for Nev Syn XX, which was susceptible only to CA. However, the Rf of CA on Nev Syn XX was the lowest ($P \leq 0.05$) of any nematode population on any cultivar.

Growth chamber experiment: Survival of alfalfa cultivars was affected by temperature. All Nev Syn XX and Chief plants survived inoculation with all nematode populations at all temperatures; survival was lowest in susceptible Deseret alfalfa (Fig. 1). At 20–30 C, the CA population suppressed ($P \leq 0.05$) dry-shoot weight of all alfalfa cultivars (Fig. 2). At 20–25 C, the reduction in dry-shoot weights was greater ($P \leq 0.05$) on Lobo, Chief, and Deseret with the NV, UT, and WY populations than with the CA population. These populations suppressed dry-shoot weights of Lobo, Chief, and Deseret at all temperatures and of Nev Syn XX at 30 C. Dry-root weight patterns were similar to those of dry-shoot weights. Except for Nev Syn XX, the NV, UT, and WY populations suppressed ($P \leq 0.05$) root weights more at 15–25 C than did the CA population, whereas the CA population suppressed root weights more than the other populations ($P \leq 0.05$) at 30 C (Fig. 3).

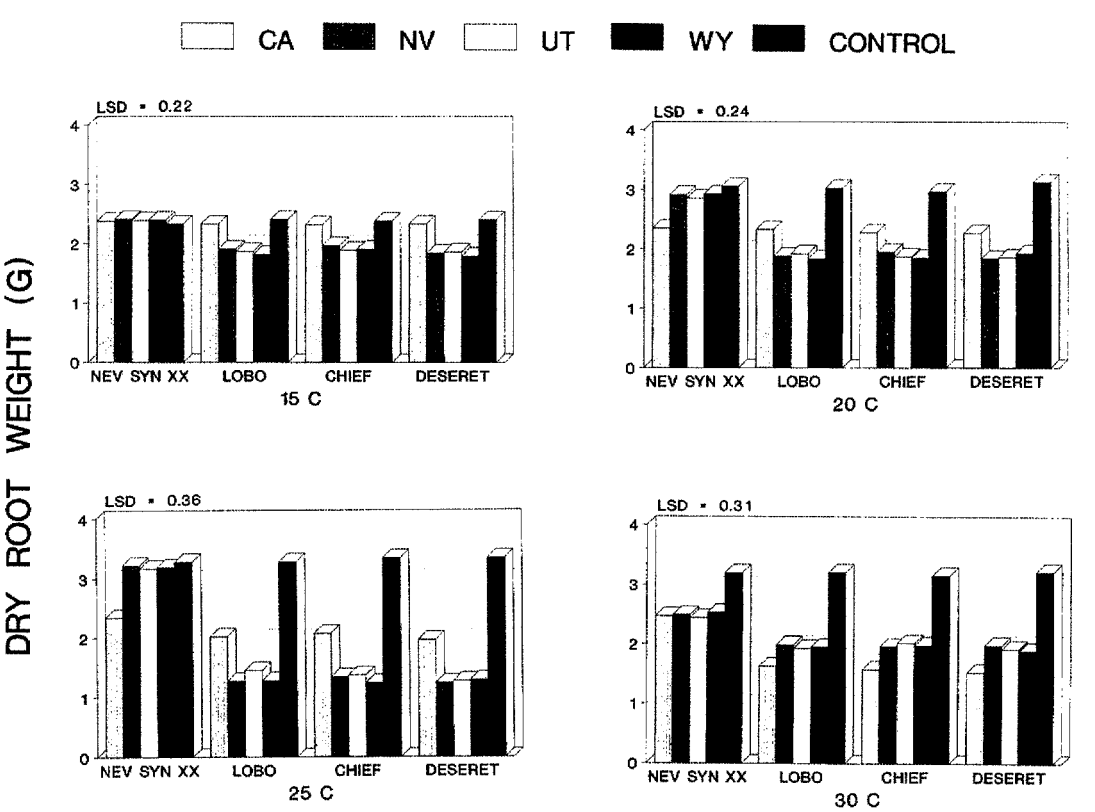

FIG. 3. The influence of *Meloidogyne hapla* populations from California (CA), Nevada (NV), Utah (UT), and Wyoming (WY) on dry root weight of alfalfa cultivars with different resistance classifications grown at four temperatures. Inocula = 4.0 eggs/cm^3 soil per plant. LSD is for nematode populations within cultivars. Nev Syn XX is classed as highly resistant, Lobo as resistant, Chief as moderately resistant, and Deseret as susceptible to *M. hapla*.

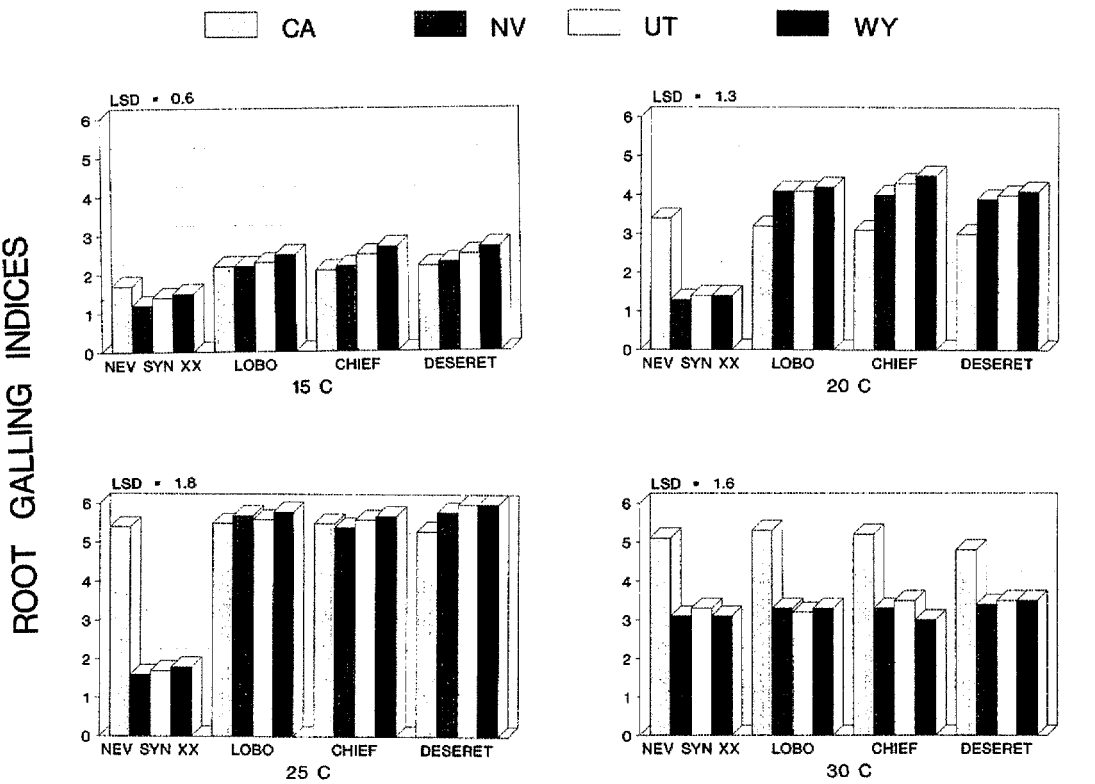

FIG. 4. The influence of *Meloidogyne hapla* populations from California (CA), Nevada (NV), Utah (UT), and Wyoming (WY) on root galling of alfalfa cultivars with different resistance classifications grown at four temperatures. Inocula = 4.0 eggs/cm^3 soil per plant. LSD is for nematode populations within cultivars. Nev Syn XX is classed as highly resistant, Lobo as resistant, Chief as moderately resistant, and Deseret as susceptible to *M. hapla*. Root-gall index is rated on a scale of 1 = no galling to 6 = 81–100% galling.

Galling by the CA population increased with temperature to 25 C. At 30 C, the CA population caused the greatest ($P \leq 0.05$) galling (Fig. 4). Root galling by the NV, UT, and WY populations was minimal on Nev Syn XX at 15–25 C but increased to >3.0 ($P \leq 0.05$) at 30 C. On Lobo, Chief, and Deseret, root galling by NV, UT, and WY populations increased from 15–25 C but decreased at 30 C ($P \leq 0.05$).

Reproduction of the CA population increased on all cultivars as the temperature increased from 15–25 C, and the Rf was similar at 25 and 30 C (Fig. 5). Although there were no differences in the root galling indices (Fig. 4), the Rf of the CA population was less ($P \leq 0.05$) on Nev Syn XX than on the other cultivars at all temperatures. Although the root galling indices were similar for all nematode populations, the Rf for the NV, UT, and WY populations were greater ($P \leq 0.05$) than for the CA population on Lobo, Chief, and Deseret at 15–25 C, but were less ($P \leq 0.05$) at 30 C. The Rf of the NV, UT, and WY populations peaked at 25 C and declined at 30 C, whereas Rf for the CA population peaked at 25 and 30 C.

Discussion

Like Rf, plant survival was not consistent with the resistance classification (1). Of the alfalfa selections studied, only the Nev Syn

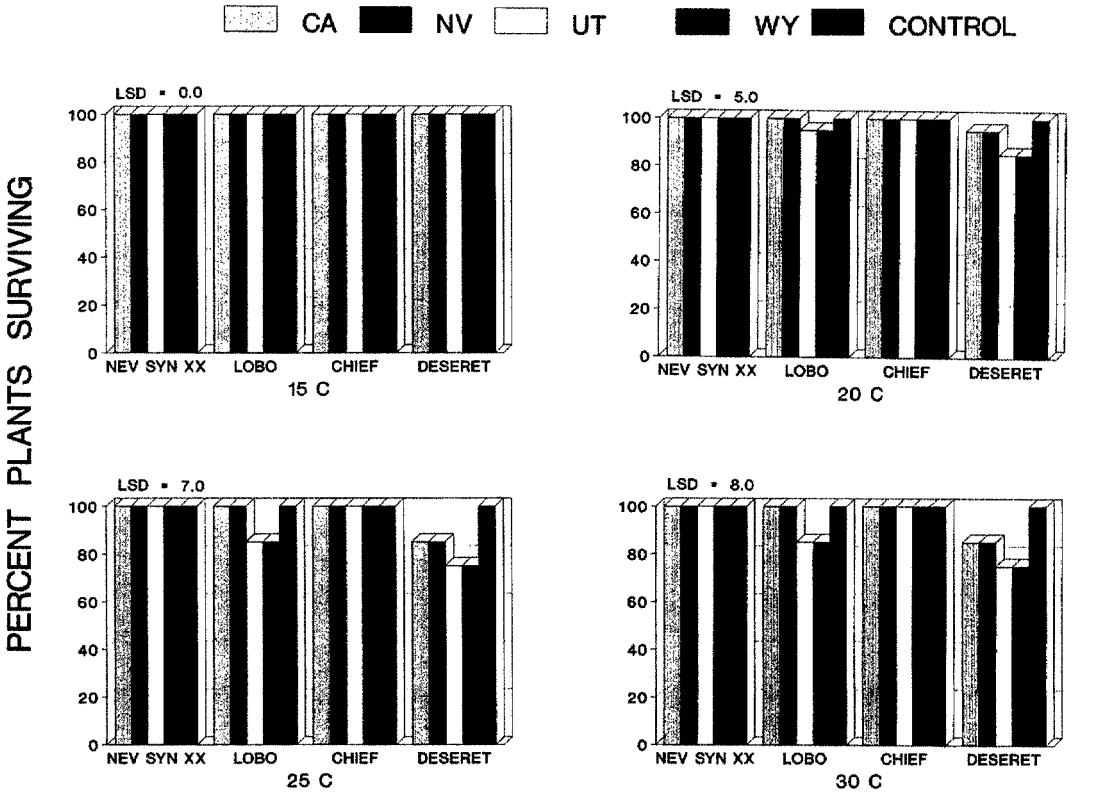

FIG. 5. Reproduction of *Meloidogyne hapla* populations from California (CA), Nevada (NV), Utah (UT), and Wyoming (WY) on alfalfa cultivars with different resistance classifications at four temperatures. Inocula = 4.0 eggs/cm^3 soil per plant. Reproductive factor = final nematode population/initial nematode population. LSD is for nematode populations within cultivars. Nev Syn XX is classed as highly resistant, Lobo as resistant, Chief as moderately resistant, and Deseret as susceptible to *M. hapla*.

XX germplasm was 100% resistant to NV, WY, and UT populations based on the reproductive factor (Rf < 1). All commercial alfalfa cultivars were 100% susceptible to NV, UT, and WY populations. More Chief and Kingstar plants, classified as moderately resistant, survived than did Lobo plants, classified as resistant. If a plant is susceptible but achieves normal or near-normal growth, it is defined as tolerant (3). Based on its survival rate, Chief could be classified as tolerant.

Temperature affected the nematode-host relationships, which agrees with previous findings (5,7,12). In this study, plant survival, root galling indices, and Rf often differed with temperature, with the same nematode population and host.

Because Nev Syn XX germplasm is susceptible to a race of *M. hapla* from California (9) nematode populations from different regions should be considered in screening alfalfa selections for resistance. The concept of population or race differences should be considered in any alfalfa breeding program involving root-knot nematodes as well as other nematodes, particularly *Ditylenchus dipsaci* (Kühn) Filipjev and *Pratylenchus* spp. Filipjev, when race or population may differ in virulence or host specificity. An accurate determination of plant resistance is important, and a total resistance (100%) to root-knot nematodes is desirable. Tolerance, such as observed with Chief, should be considered where resistance is not available. Performance of resistant varieties, however, can be affected by fungal and bacterial pathogens acting in disease complexes with *Meloidogyne* spp. (6,8,15,19). Nematodes, especially *Meloidogyne* spp., can predispose resistant plants to fungal and bacterial pathogens, inducing greater damage than the additive effect of the two pathogens (6,8,15,19).

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