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INFLUENCE OF DROUGHT STRESS ON SWEETPOTATO RESISTANCE TO SWEETPOTATO WEEVIL, *CYLAS FORMICARIUS* (COLEOPTERA: APOINIDAE), AND STORAGE ROOT CHEMISTRY

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ABSTRACT

The effect of drought stress on the resistance of sweetpotato roots to sweetpotato weevil (SPW), *Cylas formicarius* (Fab.), was studied in 1997 and 1998 in two genotypes ("Beauregard" and "Excel") with different SPW susceptibility. Storage roots produced under drought or normal conditions were tested for adult feeding, oviposition, larval survival and pupal weight in the laboratory under no-choice and free-choice test conditions. The levels of sweetpotato resin glycoside and caffeic acid in the periderm tissue of the roots were also determined. Drought-stressed roots received significantly more SPW eggs under no-choice and free-choice conditions and more feeding punctures under free-choice conditions than non-stressed roots in 1997. Larval survival rate was significantly lower on drought-stressed roots. A significant drought effect on feeding, oviposition and larval survival was absent in 1998. Drought stress had no effect on sweetpotato resin glycosides content in both years, but significantly reduced the content of caffeic acid in 1997. Genotype had a significant effect on SPW feeding in 1997 and on feeding and oviposition in 1998 under free-choice test conditions, where Beauregard was preferred for both feeding and oviposition. Beauregard also supported a significantly higher larval survival rate compared with Excel. Resin glycosides or caffeic acid contents were similar for the two genotypes in 1997, while higher level of resin glycosides was detected in Excel than in Beauregard in 1998. The interaction between drought stress and genotype was significant for adult feeding under free-choice conditions and for larval survival, indicating a different response between the two genotypes.

Key Words: host plant resistance, feeding, oviposition, resin glycosides, caffeic acid.

RESUMEN

El efecto de estres causado por la sequía sobre la resistencia de las raices del camote (= batata) al "gorgojo del camote" *Cylas formicarius* (Fab.), se estudio durante 1997 y 1998 en dos genotipos ("Beauregard" y "Excel") con susceptibilidad diferentes al insecto. Las raices almacenadas producidas bajo condiciones de sequía o condiciones normales fueron evaluadas para la alimentación de adultos, la oviposición, la sobrevivencia de las larvas, y el peso de las pupas en el laboratorio bajo condiciones de pruebas de no-alternativa y de selección libre. Los niveles del glucósido de la resina del camote y el ácido cafeico en el tejido del peridermo de las raices tambien fueron determinados. Las raices con el estrés de la sequía recibieron significativamente más huevos del gorgojo de camote bajo las condiciones de no alternativa y de selección libre y más picaduras de alimentación bajo las condiciones de no-alternativa que en las raices sin estrés en 1997. Un efecto significativo de la sequía sobre la alimentación, oviposición, y sobrevivencia de las larvas no se presentó en 1998. El estrés de la sequía no tenia efecto sobre el contenido de los glucósidos de la resina de camote en ambos años, pero redujó significativamente el contenido del ácido cafeico en 1997. El genotipo tuvo un efecto significativo sobre la alimentación y la oviposición en 1998 bajo condiciones de pruebas de selección libre, donde el Beauregard fue preferido para la alimentación y la oviposición. El genotipo Beauregard tambien suportó una tasa de sobrevivencia de larvas significativemente más alta en comparación con el Excel. El contenido de los glucósidos de la resina o del ácido cafeico fueron similares para los dos genotipos en 1997, mientras que niveles más altos de glucósidos fueron detectados en Excel que en Beauregard en 1998.

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Sweetpotato weevil (SPW) *Cylas formicarius* (Fab.) is a destructive insect pest of sweetpotato *Ipomoea batatas* (L.) Lam. worldwide (Chalfant et al. 1990). It attacks sweetpotato both in the field and during storage. Adults make feeding and oviposition punctures on root surfaces, reducing root quality and market value. Larvae feed internally and induce terpenoid production in storage roots that imparts a bitter taste and renders even slightly damaged roots unfit for human or animal consumption (Uritani et al. 1975). The search for SPW-resistant sweetpotato cultivars has been conducted for decades, but little success has been achieved partly because of the inconsistent expression of the resistance (Collins et al. 1991). Sweetpotato exhibits a wide variation in a number of traits such as yield, dry matter, intercellular space, nutrient content, flavor components, secondary metabolites, and resistance to microorganisms and insects (Ezell & Wilcox 1958; Hammett 1974; Collins et al. 1987; Woolfe 1991; Clark & LaBonte 1992; Thompson et al. 1992; Marti et al. 1993). Identification of environmental factors that affect the expression of resistance and the knowledge of the magnitude of these variations would assist in the development of cultivars with stable SPW resistance. In addition, secondary plant compounds are often associated with host plant resistance. Sweetpotato resin glycosides and caffeic acid are two such compounds found in the sweetpotato storage roots that have shown insecticidal activities (Peterson & Harrison 1992; Peterson et al. 1998; Jackson & Peterson 2000). Any effect of environmental factors on the level of these two compounds may provide insights on sweetpotato weevil resistance.

Drought stress is a common abiotic environmental factor that induces physical and/or chemical changes in plants and consequently influences the associated herbivorous insects (Holtzer et al. 1988). In this study, both field and laboratory experiments were conducted to determine the impact of drought stress on SPW resistance by measuring adult feeding, oviposition, larval survival, and development (pupal weight) on storage roots. Two genotypes with different levels of SPW susceptibility were used. Sweetpotato resin glycosides and caffeic acid contents also were analyzed.

Materials and Methods

Field Experiment

The experiments were conducted at the Sweet Potato Research Station, Louisiana State University Agricultural Center, Chase, Louisiana, in 1997 and 1998. "Beauregard" and "Excel" were used because Beauregard, a major cultivar in the region, is susceptible to SPW and Excel has shown a moderate level of resistance (Story et al. 1996). The treatments were 2×2 factorial combinations of water treatment (drought stressed and irrigated) by genotype arranged in a randomized complete block design with 4 replications. Each plot consisted of four 25-plant rows. Uniform transplants were mechanically transplanted on 30 June, 1997, and 27 June, 1998 in a Gilbert silt loam with a pH of 5.6 at 0.3-m spacing within rows on 1.0-m centered beds. The fields were fumigated with Telone™ C-17 (1,3-dicholropropene) 2 weeks before transplanting. Standard cultural practices were followed throughout the growing season (Boudreaux 1994).

The drought stress treatment was initiated 50 days after transplant (DAT) by constructing moveable rain shelters over the plots to exclude natural precipitation. The shelters were placed over the plots wherever there was more than 30% chance of precipitation in the local weather forecast. Otherwise, the plots were left open. The irrigated plots were watered starting 3 weeks after transplant with drip tubes (3.8 ml/min). Storage roots were harvested at 120 DAT, cured (30°C, 90% RH for 7 d), and stored at 15 ± 2°C for about 30 d before the bioassays and chemical analyses were started.

Insect Rearing

A SPW colony was established in January of 1997 from a field-collected population (about 500 adult insects) and maintained on storage roots of Beauregard in plastic containers (5.6 L) with screen covers at 28 ± 2°C and 85 ± 10% RH in the laboratory located at Louisiana State University Baton Rouge campus. In preparing experimental insects, 5 fresh storage roots (US #1) were exposed to about 1000 unsexed adults for 5 d and then removed and kept under the conditions described above. Emerging adults were collected weekly and held with fresh storage roots. Female adults 3-4 wk old were used in the bioassays to ensure adequate egg-laying capability (Wilson et al. 1988).

Adult Feeding and Oviposition Bioassay

The bioassay technique was an adaptation of one previously described by Mullen et al. (1980) that has been used in several SPW feeding and oviposition studies (Wilson et al. 1988). The apparatus consisted of a 24-well tissue culture plate ($12.5 \times 8.5 \times 2.0$ cm, Falcon® Model 3047, Becton Dickenson & Co., Lincoln Park, NJ) placed in a rectangular clear plastic container ($17 \times 12 \times 6$ cm, Tri-State Plastic, Dixon, KY). Cores were cut from storage roots with a cork borer (1.6 cm diameter) and were inserted into the wells so that only the periderm was exposed. The diameters of the cores and the wells were the same, providing a close fit. Female adults were kept without food for 3 h before being introduced into the arena at a density of 2 weevils per root core. A moist cotton

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ball was placed in the container to prevent desiccation of the cores. After 24 h the number of feeding punctures on each root core was counted, and after 48 h the number of eggs was counted. No-choice tests were conducted by presenting a single root core in the arena. Free-choice tests were conducted by presenting 4 root cores in the arena which were cut from one root (U.S. #1) randomly selected from each treatment combination. Before testing, the roots were gently washed with tap water and allowed to dry. All tests were conducted at 28 ± 5°C, 85 ± 10% RH under total darkness to eliminate light as a variable. For each treatment, the tests were repeated 4 times with 4 roots (sampling units). Roots from four field blocks were tested in 4 consecutive weeks.

Larval Survival and Development Bioassay

SPW were reared individually in Petri dishes by transferring a single egg into a root section (about 1.5 × 1.5 × 1.5 cm) in a cavity (1-2 mm deep, 4.0 mm diameter) cut with a cork borer. Eggs were obtained by exposing Beauregard storage roots to a large number of females for 24 h. A pair of needle-nosed forceps was used to transfer eggs. At 12 d after the eggs were deposited, root sections were examined to determine if eggs had hatched. Nonviable eggs or rotten root sections were discarded. At about 25 d after oviposition, root sections were dissected for pupae. Larval survival and pupal weight were recorded. Two replications of each treatment combination were conducted with sample sizes ranging from 18 to 32 pupae each. The bioassays were conducted under conditions of 28 ± 5°C and 85 ± 10% RH in total darkness.

Chemical Analysis

The chemical analysis was conducted in the USDA-ARS Vegetable Laboratory, Charleston, South Carolina. Storage roots were carefully washed under flowing water and allowed to dry. Periderm tissue was gently scraped off with a scalpel, dried at 50°C, and ground to a fine powder in liquid nitrogen with a mortar and pestle. Subsequently the powder was re-dried at 40°C and stored in vials under nitrogen at -20°C until analysis. Powder samples were weighed (200 mg) into Teflon-lined, screw-capped test tubes, and 2.0 ml of methanol were added containing 0.08 mg of chrysin (recrystallized from amyl alcohol) as an internal standard. Test tubes were ultrasonicated for 20 min while the surrounding water was ice-cooled. The tubes were centrifuged and the supernatant was filtered through Nylon-66 membrane filters (0.20 µm, Pierce Chemical Company, Rockville, IL) into auto injector vials. Resin glycosides and caffeic acid concentrations were analyzed by reverse-phase HPLC with 20 µl of the solution. For resin glycosides, a H_2O/MeOH linear gradient from 60% to 100% MeOH in 15 min was used and held at 100% MeOH for 25 min; flow rate was 1 ml min^{-1} and detection was at 230 nm. For caffeic acid, a second injection of 20 µl was made, with the same sample as was used for the resin glycosides analysis. A H_2O/MeOH linear gradient from 10% to 100% MeOH in 35 min was used and held at 100% MeOH for 25 min; flow rate was 1 ml min^{-1} and detection was at 340 nm. Each solvent contained 0.1% H_3PO_4. The column used was a Beckman Ultrasphere C_{18}, 5 µm (4.6 × 250 mm, Beckman and Coulter, Fullerton, CA). Purified reference substances were used as external standards to determine response factor versus chrysin for quantification. Reference glycoside material was purified by Sephadex column chromatography followed by semi-preparative HPLC as described previously (Peterson et al. 1998). Reference caffeic acid was purchased from Aldrich Chemical Company (Milwaukee, WI).

Data Analysis

The data were analyzed by year using two-way analysis of variance (PROC GLM, SAS 1990). A square-root transformation was used for larval survival data. Year effect was evaluated by analyzing the data by one-way analysis of variance. The significance level was $\alpha = 0.05$.

Results

Adult Feeding and Oviposition

Drought stress significantly increased adult SPW feeding and oviposition in free-choice tests and oviposition in no-choice tests in 1997 (Table 1). In 1998, drought stress had no significant effect on oviposition or on feeding (Table 1). Year effect was significant on feeding (no-choice test: $F = 23.08$, $df = 1,24$, $P < 0.0001$; free-choice test: $F = 10.09$, $df = 1,24$, $P = 0.0041$) and on oviposition under both testing conditions (no-choice test: $F = 50.51$, $df = 1,24$, $P < 0.0001$; free-choice test: $F = 17.50$, $df = 1,24$, $P = 0.0003$). Beauregard received more feeding punctures than Excel in free-choice tests, but not in no-choice tests in 1997. No significant cultivar effect was found on oviposition in 1997. In 1998, cultivar had a significant effect on both feeding and oviposition in free-choice tests where Beauregard was the preferred cultivar, but there was no cultivar effect in no-choice tests (Table 1). The interaction of drought stress and cultivar was significant for feeding in free-choice tests in 1997, but not in 1998 (Table 1).

Larval Survival and Development

Drought stress significantly reduced larval survival rate in 1997, but not in 1998 (Table 2). No significant drought effect was found on pupal

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TABLE 1. THE EFFECT OF DROUGHT STRESS AND CULTIVAR ON SWEETPOTATO WEEVIL ADULT FEEDING AND OVIPOSITION UNDER NO-CHOICE AND CHOICE TEST CONDITIONS IN 1997 AND 1998.

		1997				1998			
		No-choice test		Choice test		No-choice test		Choice test	
Cultivar	Water treatment	Feeding punctures[a]	Eggs[b]	Feeding punctures[c]	Eggs[d]	Feeding punctures[e]	Eggs[f]	Feeding punctures[g]	Eggs[h]
Beauregard	Drought	31.0 ± 4.3	9.3 ± 1.1	51.6 ± 5.5	9.6 ± 1.5	38.4 ± 4.1	12.4 ± 0.9	46.6 ± 5.9	12.1 ± 1.1
Beauregard	Irrigated	27.9 ± 2.3	7.1 ± 0.4	30.8 ± 1.4	8.3 ± 0.7	43.7 ± 5.7	13.2 ± 1.3	50.3 ± 1.6	11.9 ± 0.6
Excel	Drought	24.4 ± 1.1	8.8 ± 0.5	26.8 ± 1.9	9.6 ± 1.6	36.3 ± 2.0	12.6 ± 1.2	35.2 ± 4.3	10.6 ± 1.1
Excel	Irrigated	25.3 ± 2.7	6.3 ± 0.5	23.1 ± 1.1	6.1 ± 0.6	32.3 ± 5.2	9.31 ± 0.7	36.4 ± 4.9	8.4 ± 0.9

Mean ± SEM.
[a]Water treatment: $F = 0.15$; $df = 1,9$; $P = 0.7055$. Cultivar: $F = 2.76$; $df = 1,9$; $P = 0.1311$. Interaction: $F = 0.49$; $df = 1,9$; $P = 0.5002$.
[b]Water treatment: $F = 13.32$; $df = 1,9$; $P = 0.0053$. Cultivar: $F = 1.04$; $df = 1,9$; $P = 0.3335$. Interaction: $F = 0.06$; $df = 1,9$; $P = 0.8132$.
[c]Water treatment: $F = 25.83$; $df = 1,9$; $P = 0.0007$. Cultivar: $F = 45.86$; $df = 1,9$; $P < 0.0001$. Interaction: $F = 12.59$; $df = 1,9$; $P = 0.0062$.
[d]Water treatment: $F = 5.90$; $df = 1,9$; $P = 0.0380$. Cultivar: $F = 1.18$; $df = 1,9$; $P = 0.3052$. Interaction: $F = 1.18$; $df = 1,9$; $P = 0.3054$.
[e]Water treatment: $F = 0.03$; $df = 1,9$; $P = 0.8574$. Cultivar: $F = 3.99$; $df = 1,9$; $P = 0.0768$. Interaction: $F = 1.92$; $df = 1,9$; $P = 0.1987$.
[f]Water treatment: $F = 2.90$; $df = 1,9$; $P = 0.1225$. Cultivar: $F = 2.71$; $df = 1,9$; $P = 0.1341$. Interaction: $F = 1.10$; $df = 1,9$; $P = 0.3168$.
[g]Water treatment: $F = 0.75$; $df = 1,9$; $P = 0.4084$. Cultivar: $F = 20.38$; $df = 1,9$; $P = 0.0015$. Interaction: $F = 0.20$; $df = 1,9$; $P = 0.6670$.
[h]Water treatment: $F = 2.72$; $df = 1,9$; $P = 0.1332$. Cultivar: $F = 11.18$; $df = 1,9$; $P = 0.0086$. Interaction: $F = 1.72$; $df = 1,9$; $P = 0.2220$.

weight in both years. Higher larval survival rate was found on Beauregard than on Excel in 1997 and in 1998 (Table 2). Weevils reared on Beauregard had lower pupal weight than that of Excel in 1997, but not in 1998. Drought and cultivar interaction effect was significant for larval survival in 1997, but not in 1998. No significant interaction effect was found with pupal weight (Table 2). The test for year effect was not significant for larval survival ($F = 1.18$; $df = 1,16$; $P = 0.2936$) and pupal weight ($F = 1.34$; $df = 1,16$; $P = 0.2642$).

Resin Glycosides and Caffeic Acid Contents

Drought stress did not have a significant effect on the level of resin glycosides in either year (Table 3). Drought stress significantly reduced the level of caffeic acid in 1997, but not in 1998. Excel tended to have a higher level of resin glycosides than Beauregard, but this difference was statistically significant only in 1998. Both genotypes contained similar levels of caffeic acid (Table 3). No significant interaction effect was found. Year effect was significant for caffeic acid ($F = 88.45$; $df = 1,21$; $P < 0.0001$), but not for resin glycosides ($F = 0.01$; $df = 1,21$; $P = 0.9283$).

Discussion

The impact of drought stress on plants and its consequences on herbivorous insects has drawn much attention. Numerous studies have been reported on the subject with often conflicting results obtained in different insect-host plant systems (Holtzer et al. 1988; Koricheva et al. 1998). Drought is often associated with heavy insect damage (Kelly 1917; White 1969). Several explanations for this ecological consequence have been proposed, including higher plant nutritional quality, more favorable micro-environment, and diminishment of plant defense systems (White 1974; Mattson & Haack 1987). More recent studies regarding the effect of drought stress on insects have focused on evaluating host suitability, and found that drought-stressed plants often have reduced suitability. Many insect species, such as *Pseudoplusia includens* (Lambert & Heatherly 1991), *Epilachna varivestis* (McQuate & Conner 1990), and *Empoasca fabae* (Hoffman et al. 1990, 1991), exhibited a lower feeding and/or oviposition level, longer development time, higher mortalities, and lower fecundities when fed on drought-stressed plants. Our study showed that drought stress seemed to favor SPW feeding and oviposition but reduced larval survival rate. The magnitude of the response of the two genotypes appeared to differ.

Drought stress may alter the production of secondary plant compounds (Gershenzon 1984; Holtzer et al. 1988). Sweetpotato contains numerous secondary compounds, which are produced either constitutively or upon induction by external agents (Kays 1992). Boehmeryl acetate found in the periderm tissue of storage roots was identified as a SPW oviposition stimulant (Son 1989). The results of this study suggest that drought stress may increase the activity of this oviposition stimulant because weevils deposited more eggs on drought-stressed plants. Jackson and Peterson (2000) reported sublethal effects of sweetpotato resin glycosides on *Plutella xylostella*. Caffeic acid showed adverse effects on a generalist herbivore, *Helicoverpa zea* (Summers & Felton 1994) and sweetpotato pathogenic fungi (Harrison et al. 2003a). Recent analyses showed that the levels of resin glycosides and caffeic acid vary between sweetpotato genotypes and within genotypes among years or areas of production (Harrison et al. 2003a, b). This may indicate a relationship between the quantity of these two compounds and the antibiosis of sweetpotato. It also may indicate that the production of these compounds is subject to environmental influence. The results in this study show that drought stress significantly re-

Table 2. The effect of drought stress and cultivar on sweetpotato weevil larval survival and pupal weight reared on storage roots in 1997 and 1998.

		1997		1998	
Cultivar	Water treatment	Larval survival (%)[a]	Pupal weight (mg)[b]	Larval survival (%)[c]	Pupal weight (mg)[d]
Beauregard	Drought	95.4 ± 2.5	7.20 ± 0.1	94.5 ± 1.6	7.44 ± 0.3
Beauregard	Irrigated	97.4 ± 0.8	7.22 ± 0.1	100.0 ± 0.0	7.68 ± 0.2
Excel	Drought	79.4 ± 1.1	7.57 ± 0.2	88.3 ± 4.3	7.61 ± 0.0
Excel	Irrigated	91.4 ± 0.1	7.84 ± 0.6	88.9 ± 4.2	8.06 ± 0.1

Mean ± SEM.
[a]Water treatment: F=12.02; df =1,9; P=0.0071. Cultivar: F=29.04; df =1,9; P=0.0004. Interaction: F=6.26; df =1,9; P=0.0338.
[b]Water treatment: F=1.03; df =1,9; P=0.3363. Cultivar: F=12.05; df=1,9; P=0.0070. Interaction: F=0.80; df =1,9; P=0.3956.
[c]Water treatment: F=1.90; df=1,9; P=0.2014. Cultivar: F=16.27; df=1,9; P=0.0030. Interaction: F=1.23; df =1,9; P=0.2962.
[d]Water treatment: F=1.73; df =1,9; P=0.2209. Cultivar: F=1.06; df=1,9; P=0.3301. Interaction: F=0.15; df =1,9; P=0.7075.

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TABLE 3. THE EFFECTS OF DROUGHT STRESS AND CULTIVAR ON RESIN GLYCOSIDE AND CAFFEIC ACID LEVELS IN PERIDERM TISSUE OF SWEETPOTATO STORAGE ROOTS IN 1997 AND 1998.

		1997		1998	
Cultivar	Water treatment	Resin glycoside[a] (% DW)	Caffeic acid[b] (% DW)	Resin glycoside[c] (% DW)	Caffeic acid[d] (% DW)
Beauregard	Drought	0.84 ± 0.150 (3)	0.17 ± 0.071 (3)	0.86 ± 0.100 (3)	0.44 ± 0.021 (3)
Beauregard	Irrigated	0.74 ± 0.212 (4)	0.31 ± 0.025 (4)	0.75 ± 0.081 (4)	0.44 ± 0.037 (4)
Excel	Drought	2.16 ± 1.052 (4)	0.18 ± 0.001 (4)	1.54 ± 0.151 (3)	0.46 ± 0.009 (3)
Excel	Irrigated	1.10 ± 0.125 (4)	0.22 ± 0.015 (4)	1.73 ± 0.155 (4)	0.44 ± 0.019 (4)

Mean ± SEM (sample size); DW = dry weight.
[a]Water treatment: $F = 2.56$; $df = 1,8$; $P = 0.1481$. Cultivar: $F = 1.55$; $df = 1,8$; $P = 0.2483$. Interaction: $F = 0.28$; $df = 1,8$; $P = 0.6133$.
[b]Water treatment: $F = 8.24$; $df = 1,8$; $P = 0.0198$. Cultivar: $F = 1.62$; $df = 1,8$; $P = 0.2389$. Interaction: $F = 2.59$; $df = 1,9$; $P = 0.1464$.
[c]Water treatment: $F = 1.20$; $df = 1,7$; $P = 0.3100$. Cultivar: $F = 62.37$; $df = 1,7$; $P < 0.0001$. Interaction: $F = 2.10$; $df = 1,7$; $P = 0.1908$.
[d]Water treatment: $F = 1.86$; $df = 1,7$; $P = 0.2150$. Cultivar: $F = 0.69$; $df = 1,7$; $P = 0.4342$. Interaction: $F = 0.44$; $df = 1,7$; $P = 0.5290$.

duced the level of caffeic acid but had no effect on the level of resin glycosides, suggesting that the lower larval survival rate observed on drought stressed plants was not due to higher caffeic acid or resin glycoside content. It appears that there is no relationship between the level of these two compounds and sweetpotato weevil resistance. This is possibly because of the feeding behavior of the weevil, in which weevils chew through the periderm and feed primarily on the tissue beneath it, thereby avoiding the periderm layer.

In addition, the effect of drought stress on SPW resistance and on the storage root chemistry was not consistent between years. Significant drought effects in 1997 diminished in 1998. This may be due to the unusual hot and dry conditions in the area in 1998, in which all plots perhaps were stressed.

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