Presence on Sweetpotato Through the Growing Season of *Erwinia chrysanthemi*, Cause of Stem and Root Rot

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ABSTRACT

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Storage roots of sweetpotato (*Ipomoea batatas*) cv. Beauregard were either dipped in a 10^8 cfu/ml suspension of a rifampicin-resistant, virulent strain of *Erwinia chrysanthemi* (2rr) or implanted with a micropipette tip containing 50 μl of the same suspension. The roots were then planted in field beds. At both the first and second harvests of plants, slips (sprouts) were cut above the soil line or pulled from the mother roots and transplanted to the field. Strain 2rr was recovered from inoculated roots 7 days after the roots were bedded and at the first and second harvests of slips. The bacterium also was present on or in symptomless vine cuttings at transplanting and on or in the underground stem and daughter storage roots at harvest. However, little stem rot was observed in the field. Inoculation of stem cuttings at transplanting or whether pulled or cut slips were used for transplants did not affect disease occurrence. Strain 2rr was recovered from 23 and 9% of samples from pulled and cut slips at harvest, respectively. When slips of sweetpotato cv. Jewel were cut with a contaminated knife, strain 2rr was recovered from the cut stub of the sprout, from slips removed at the subsequent cutting, from the surface of the mother root, and from the underground stem of the daughter plants at harvest. Thus, symptomless mother roots, slips, and vines may harbor latent populations of *E. chrysanthemi* that may serve as sources of inoculum for bacterial stem and root rot of sweetpotato.

Bacterial stem and root rot of sweetpotato (*Ipomoea batatas* (L.) Lam.), caused by *Erwinia chrysanthemi* Burkholder, McFadden, and Dimock, was unknown until 1974, when a major outbreak occurred in production areas of Georgia (2,11,16). The outbreak appeared to threaten the economic viability of the sweetpotato industry in that state (16). The disease develops on vines in the field and on storage roots in the field, in storage, and in plant production beds (2).

In Louisiana, bacterial stem rot has not caused serious losses, but bacterial root rot has been found to a limited extent in storage roots in plant beds and at harvest. However, increased use of recently released cultivars may lead to greater incidence and severity of bacterial stem or root rot in the field. Storage roots of these cultivars have shown greater susceptibility than older standard cultivars to *E. chrysanthemi* when artificially inoculated (3,15).

This study was conducted to determine sources of inoculum of *E. chrysanthemi* in sweetpotato production. Because the disease has been observed on storage roots in plant production beds, possible dissemination of the bacterium from contaminated mother roots to daughter plants and storage roots was examined. A preliminary report on this research has been presented (8).

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MATERIALS AND METHODS

Inoculum. Cells of the bacteria were grown in nutrient broth in a rotary shaker for 24 hr at 25 C, concentrated by centrifugation at 10,000 *g* for 10 min, and suspended in sterile distilled water (SDW). Bacterial suspensions were adjusted to an optical density of 0.15 at 620 nm (approximately 10^8 cfu/ml) measured with a spectrophotometer (Spectronic 20, Bausch & Lomb, Rochester, NY).

Rifampicin resistance. A rifampicin-resistant strain of *E. chrysanthemi*, 2rr, was selected from strain Ech-2, originally isolated from sweetpotato and provided by J. W. Moyer, North Carolina State University. Strain 2rr was selected by plating a dense suspension of Ech-2 on plates of yeast extract (10 g), dextrose (20 g), calcium carbonate (20 g) agar (15 g/L) (YDC) amended with 100 μg/ml of rifampicin. Plates were incubated at 32 C, and isolated colonies were streaked three times in succession on rifampicin-amended YDC.

The virulence of 2rr in sweetpotato was compared with that of Ech-2 and other wild-type strains of *E. chrysanthemi* from sweetpotato by previously described inoculation techniques (3). Strains Ech-31, Ech-37, and U-9 were isolated from storage roots obtained from Louisiana, Georgia, and Texas, respectively. Strains A-15, A-17, and A-19 were provided by R. S. Dickey and C. Zumoff, Cornell University, and were originally isolated in Georgia during the study of Schaad and Brenner (16). Stem rot virulence was tested on five plants each of Beauregard and Jewel for each strain. Terminal vine cuttings collected from the field were grown in the greenhouse in 15-cm-diameter clay pots containing sand, soil, and Jiffy mix (1:1:1, v/v) for 1 wk before inoculation. A toothpick that had been dipped in a suspension of 10^8 cfu/ml was implanted in the stem. Stem rot severity was rated 1 wk after inoculation on a 0–5 scale, where 0 = no disease and 5 = plant dead (3,6). Stem inoculations were performed twice.

Virulence in storage roots was compared among strains by infectivity titration on Beauregard storage roots (3,6). Each root was inoculated with a dilution series from 10^8 to 10^3 cfu/ml. Micropipette tips containing 50 μl of the appropriate dilutions were implanted at different locations on the root. Roots were cut open 6 days later, and the depth and diameter of lesions were measured. Regression analysis was performed to determine if there was a significant correlation between concentration and response probit (6). Storage root inoculations were conducted four times.

Bedding. In mid-March of 1988, 1989, and 1990, storage roots (mother roots) of Beauregard sweetpotato were bedded, i.e., placed in a single layer in a field bed and covered with soil and black plastic mulch. Immediately before bedding, uninjured roots were dipped in a suspension of 2rr or a micropipette tip containing 50 μl of the same suspension was implanted about 1 cm deep in the roots (3,10). Beds were arranged in a randomized complete block design with seven replications of 10-root plots per treatment. A separate row with four roots per treatment for each of seven blocks was established for sample taking. After the second harvest of transplants in 1989 and 1990, mother storage roots were dug and the number of sound mother roots was recorded.

Transplanting. At both first and second plant harvests, slips (sprouts) were pulled from beds of each treatment of mother roots and separated into two

groups. The belowground portion was cut off the slips in one group, and both groups were transplanted to the field. The six treatments (pulled or cut slips from control, dipped, or tip-inoculated mother roots) were planted in the field in a randomized complete block design. Each treatment was replicated seven times in 10-plant plots. The slips were planted 30 cm apart with 90 cm between plots and 120 cm between rows. In a second experiment conducted in the field in 1989 and repeated in 1990, sprouts from noninoculated storage roots were pulled or pulled and cut and the basal end of each slip was dipped in a suspension of 2rr; the controls were noninoculated pulled and cut sprouts. Each treatment was replicated five times in 10-plant plots.

Knife transmission. Storage roots of Beauregard were planted in 25-cm-diameter pots in the greenhouse. When sprouts were about 30 cm long, they were cut with a knife previously dipped in a suspension of 2rr. After 2 mo, the presence of 2rr on the surface of mother storage roots and on 2-cm-long pieces from the base of slips was assessed.

In the field, slips of Jewel also were cut with a contaminated knife in 1988 and 1989. Both inoculated and noninoculated treatments were replicated four times in 10-plant plots. At harvest, two underground stems were sampled from each plot and assayed for 2rr.

Survival in storage. In October 1989, four crates of daughter roots harvested from plots planted with slips from roots inoculated with 2rr in March and one crate from plots planted with slips from noninoculated roots were stored at 18 ± 3 C. Also, two crates of Beauregard storage roots harvested in a field separated from the experimental plots were dipped in a 10^8 cfu/ml suspension of 2rr and stored. These samples were assayed for 2rr in March, when they were bedded, and again in May.

Assaying for *E. chrysanthemi*. The population of 2rr on the surface of mother roots was determined at bedding, at 7 days after bedding, and at the first and second harvests of slips in the field or at the end of greenhouse experiments. Storage roots were dug and washed individually in plastic bags containing 100 ml of SDW. Aliquots of 0.01 ml of the serially diluted wash water were plated on circular areas (17 mm in diameter) cut with a metallic tube cap in plates of crystal violet-pectate medium (4,14) amended with rifampicin (100 mg/L) and cycloheximide (25 mg/L) (CVP-RC). Plates were checked for 2rr colonies after incubation for 48 hr at 32 C.

Slips harvested from different treatments were washed individually in plastic bags with 50 ml of SDW. After at least 30 min, the wash water was serially diluted and plated on CVP-RC or a 1-ml aliquot of the suspension was added to 9 ml of crystal violet-pectate broth enrichment medium (CVPB) containing 4.5 g of sodium polypectate, 1 ml of 0.075% aqueous crystal violet, 0.5 g of $NaNO_3$, and 2.25 ml of 1 N NaOH per 500 ml of distilled water (4,14). After 2 and 4 days at 32 C, aliquots of the enrichment culture were plated on CVP-RC and incubated as above.

In 1988, two daughter roots from each field plot were transferred individually to plastic bags containing 100 ml of SDW. After a 7-day incubation at room temperature, serially diluted samples of liquid were plated on CVP-RC and incubated as above. In 1989, an adaptation of a technique used with Irish potatoes to determine bacterial soft rot potential was attempted with sweetpotatoes. Two storage roots from each plot were punctured 10 times at different sites with a flamed needle, immersed in distilled water in polyethylene bags, incubated at room temperature (25 ± 2 C) for 5 days, and examined for rotting (1).

At harvest in each year, two underground stem sections (25 cm long) from each plot were transferred individually

Table 1. Production of slips in beds of sweetpotato (cv. Beauregard) storage roots not inoculated or inoculated with *Erwinia chrysanthemi* by two methods at bedding in each of 3 yr

	1988				1989				1990			
	First[x]		Second[x]		First		Second		First		Second	
Treatment	No.[y]	Wt.[y]	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
Control	23	0.86	19	0.44	60	1.72	62 a[z]	1.37 a	34	1.26	30	0.53
Dipped	25	0.66	25	0.46	63	1.54	45 b	1.06 ab	31	1.29	22	0.48
Tip-inoculated	17	0.60	15	0.20	51	1.28	28 c	0.67 b	38	1.45	24	0.45

[x]First and second harvests of slips.
[y]Mean of seven 10-root plots; no. = number and wt. = total fresh weight (kg) of slips per plot.
[z]Means with the same letter for the second pulling in 1989 were not significantly different according to Duncan's multiple range test ($P = 0.05$); differences for other treatments were not significant ($P = 0.05$).

Table 2. Yield of storage roots from plots planted with sweetpotato (cv. Beauregard) slips cut or pulled from beds with mother roots dipped into a suspension of *Erwinia chrysanthemi* or inoculated by implanting a micropipette tip containing inoculum at bedding

		1988				1989				1990			
		First[x]		Second[x]		First		Second		First		Second	
Treatment	Harvest	No.[y]	Wt.[y]	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
Control	Pulled	79	18.4	24	3.9	51	7.6	50 b[z]	8.3	43	14.0	36	6.7
	Cut	64	16.4	28	5.3	58	9.3	63 a	10.6	47	12.6	30	7.8
Dipped	Pulled	67	16.6	28	4.7	59	8.7	64 a	9.4	51	15.8	32	6.5
	Cut	73	20.3	31	5.8	57	8.8	59 ab	9.9	37	11.4	28	6.5
Tip-inoculated	Pulled	75	17.7	18	2.5	57	8.5	60 ab	8.6	42	13.3	24	5.0
	Cut	65	20.2	24	4.5	61	8.2	51 b	9.1	41	14.7	23	5.4
Source of variation ($P>F$)													
Plant (cut vs. pulled)		0.32	0.59	0.17	0.031	0.47	0.89	0.497	0.09	0.47	0.20	0.36	0.44
Treatment		0.76	0.95	0.11	0.101	0.57	0.34	0.041	0.42	0.57	0.89	0.11	0.07
Plant × treatment		0.32	0.53	0.94	0.697	0.55	0.97	0.002	0.52	0.55	0.12	0.83	0.80

[x]First and second transplantings.
[y]Mean of seven replications; no. = number of marketable-sized and wt. = yield (kg) of storage roots per plot.
[z]Means with the same letter in the same column were not significantly different according to Duncan's multiple range test ($P = 0.05$); differences in other tests were not significant ($P = 0.05$).

to plastic bags containing 100 ml of SDW. The same procedure used to assess for presence of 2rr on storage roots was followed.

In March 1990, roots stored through the winter were peeled, and a 1-g sample of periderm was transferred to tubes with 9 ml of CVPB, then incubated at 32 C. In May, 5-cm segments were cut from the aboveground stems with a flamed scalpel, transferred to tubes of CVPB in the field, and incubated at 32 C. After incubation for 48 and 96 hr in each test, 0.01-ml aliquots from the enrichment cultures were plated on CVP-RC and incubated as above.

Statistical analysis. Crop response parameters (number and weight of storage roots and plants produced) were analyzed with the general linear models procedure of SAS (SAS Institute, Cary, NC). Frequency of bacterial recovery was analyzed by using the chi-square value in the CATMOD procedure of SAS.

RESULTS

Virulence of 2rr. Stem rot indices were not significantly different between 2rr and Ech-2 on Beauregard and Jewel. Stem rot indices on Beauregard were 2.0 and 1.6 for 2rr and Ech-2, respectively, and ranged from 0.4 to 2.0 for the six other sweetpotato strains of *E. chrysanthemi* tested (LSD = 0.57, $P = 0.05$, CV = 52%). Stem rot indices on Jewel were 1.8 and 2.0 for 2rr and Ech-2, respectively, and ranged from 0.4 to 2.0 for the other strains (LSD = 0.45, $P = 0.0001$, CV = 33%). Lesion dimension in Beauregard storage roots was significantly smaller for 2rr (17 mm) than for Ech-2 (31 mm). The other six strains ranged from 4 to 23 mm (LSD = 4.2, $P = 0.0001$, CV = 90%).

Effects of inoculation on crop development. After harvest of slips was completed in 1989, the number of apparently healthy mother roots of the 70 bedded did not differ significantly ($P = 0.05$) between the dipped treatment (39 roots) and the tip-inoculated treatment (23 roots) but was lower than that in the noninoculated treatment (54 roots). In 1990, numbers of surviving mother roots did not differ significantly among these treatments.

The number of slips produced by storage roots was not affected by inoculation, except for the second transplant harvest in 1989, when production was significantly lower in both inoculation treatments than in the control (Table 1). Likewise, sweetpotato yield by weight was not affected, except for the second transplanting in 1989 (Table 2). Little stem rot occurred in the fields during the three seasons; only one or two of the 70 plants in some treatments showed symptoms.

Recovery of *E. chrysanthemi*. In each of the three seasons, the pathogen was recovered from mother storage roots the day they were bedded, 7 days later, and at the first and second harvest of slips in a similar frequency. Strain 2rr was recovered from two noninoculated mother roots but only at the second slip harvest in 1990. Overall, strain 2rr was recovered from 95% of dipped mother roots both at bedding and 7 days later and from 68 and 79% of tip-inoculated mother roots at bedding and 7 days later, respectively. Frequency of recovery was similar (42–53%) from inoculated mother roots at first and second slip harvests regardless of inoculation method. Populations of *E. chrysanthemi* on or in mother roots in plant beds decreased from March to July (Fig. 1), ranging from approximately 10 to 10^6 cfu/cm^2 of root surface. Strain 2rr also was recovered from underground stems at harvest of daughter storage roots in September and October from the first and second transplantings. Frequency of recovery was greater in 1988 (38% of stems from all inoculated treatments) than in 1989 (8%) or 1990 (4%) and was similar for both inoculation methods. Strain 2rr was recovered from 20% of stems from inoculated treatments at the first harvest and from 10% at the second harvest. Strain 2rr was recovered from only one noninoculated plant, at the second harvest in 1990. The pathogen was recovered from 15% of symptomless slips produced by mother roots from both inoculated treatments in 1988. The pathogen was found on or in 71% of dipped and 43% of tip-inoculated slips in 1989 and on or in 29% of dipped and 15% of tip-inoculated slips in 1990. *E. chrysanthemi* was not recovered from slips from noninoculated mother roots.

Frequencies of recovery of 2rr from daughter storage roots at harvest did not differ significantly (Table 3). At the second harvest in 1988, *E. chrysanthemi* was recovered from 0, 15, and 0% of sampled daughter roots produced on plants pulled from noninoculated, dipped, and tip-inoculated mother roots, respectively. The pathogen was recovered from 15, 43, and 29% of daughter roots produced on plants cut from noninoculated, dipped, or tip-inoculated mother roots, respectively. Attempts to assess root rot potential in 1989 by a polybag test failed. The incubation conditions led to a high incidence of souring, a disease with which pectolytic clostridia have been associated (7). Strain 2rr was not recovered from rotting tissue.

Pulling vs. cutting of transplants. Method of harvesting slips had no significant effect on frequency of recovery of 2rr (Table 3). Strain 2rr was recovered from underground stems of daughter plants produced from pulled (23%) or cut (9%) sprouts from mother roots inoculated at bedding. When stems were inoculated at transplanting, the

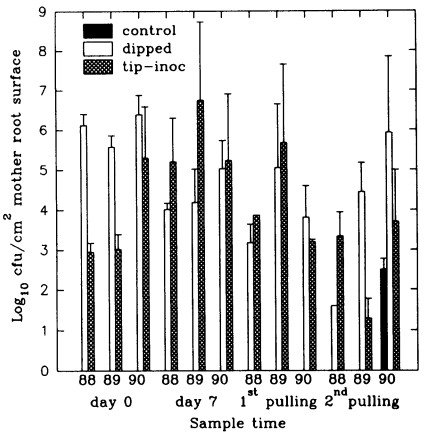

Fig. 1. Populations of a rifampicin-resistant strain of *Erwinia chrysanthemi* (2rr) recovered on the day of bedding, 7 days later, and at the first and second pullings from sweetpotato mother roots. Roots were either dipped at bedding in a cell suspension (10^8 cfu/ml) or implanted with micropipette tips containing 50 µl of the same suspension; controls were noninoculated roots. Data are from tests in 1988, 1989, and 1990. Vertical bars represent standard deviations.

Table 3. Analysis of variance values[t] for data on frequency of recovery of *Erwinia chrysanthemi* strain 2rr

Source	Slips[u]		Mother roots[v]		Stems[w]	
	χ^2	*P*	χ^2	*P*	χ^2	*P*
Intercept	15.48	0.0001	2.77	0.0961	77.00	0.0000
Treatment[x]	4.19	0.1228	46.32	0.0000	3.89	0.1429
Year	2.63	0.2687	2.74	0.2538	11.19	0.0037
Time[y]	...	...	7.27	0.0637	0.60	0.4380
Plant[z]	...	...	...	...	3.44	0.0634
Residual	1.35	0.8523	6.18	0.9861	9.84	0.9997

[t] SAS CATMOD procedure.
[u] Basal segments from symptomless slips pulled from plant beds.
[v] Surface of mother roots from plant beds.
[w] Segments of underground portions of stems, assayed at harvest of daughter roots.
[x] Mother roots were either not inoculated or inoculated by inserting a micropipette tip containing 10^8 cfu/ml of strain 2rr or by dipping the whole root in the same suspension.
[y] Mother roots were sampled at 0 and 7 days after inoculation and at the time of pulling the first and second harvests of slips; underground stems were sampled at the first and second harvests.
[z] Slips were pulled and either cut or not cut above the soil line.

pathogen was recovered in 1989 from 40 and 50% of underground stems of daughter plants produced from pulled or cut transplants, respectively. In 1990, 2rr was recovered from 93% of underground stems from both pulled and cut transplants. Regardless of the time of inoculation with *E. chrysanthemi*, no effect of pulling vs. cutting of transplants on stem rot incidence was observed in either year.

Survival in storage. Strain 2rr was not recovered from daughter roots from sprouts produced by mother roots inoculated with 2rr in March 1989 and stored from October to March 1990. It was not recovered in March (at bedding) or in May 1990 or at harvest from the 5-cm aboveground stems. On storage roots inoculated in October 1989, however, the populations of 2rr were about 10^5 cfu/g of root periderm in March and May 1990; 2rr was not recovered from the 5-cm aboveground stem segments.

Knife transmission. When sweetpotato sprouts were cut with a contaminated knife in the greenhouse, 2rr was recovered from nine of 15 slips from the second cutting 1 mo later and six of 12 slips from the third cutting 2 mo later. The strain was also recovered from the surface of 10 of 12 mother roots at the third cutting. When stems were cut with a contaminated knife in the field, 2rr was recovered from six and four of eight underground stems sampled at harvest in 1988 and 1989, respectively. The strain was not recovered from noninoculated control plants in either year.

DISCUSSION

E. chrysanthemi on or in mother roots in March, at the time of bedding, was transmitted to slips. The pathogen was carried to the field on or in symptomless vines at transplanting in June and July and was recovered from underground stems and daughter roots at harvest in September and October. The bacteria survived the storage period on roots inoculated in October and were recovered at bedding in March and when slips were pulled in May. Thus, three potential sources of inoculum are identified: mother roots, slips, and daughter roots to be used as mother roots the next season.

Unlike transmission of *E. carotovora* in Irish potato, in which contaminated seed tubers planted in the field are the main source of contamination of daughter tubers (12), the transmission of *E. chrysanthemi* from sweetpotato mother roots to daughter roots depends on the presence of the bacterium on or in the slips. Neither Ech-2 nor 2rr could be recovered from infested soil after 30 days at 4, 25, or 37 C (6). Because rifampicin-resistant erwinias were not recovered from noninoculated plants, and because the strains used apparently do not survive in soil, the recovery of rifampicin-resistant erwinias on slips from inoculated mother roots suggests that the pathogen is carried to the field on or in the slips.

The low level of disease incidence in the field could be partly attributed to the low proportions of pulled or cut slips contaminated by 2rr. Although pulled and cut slips also were inoculated at transplanting, the disease incidence still remained negligible. However, the frequency of recovery of *E. chrysanthemi* from underground stems was higher in slips inoculated directly than in those harvested from mother roots inoculated at bedding. Although no data are available on the occurrence of bacterial stem and root rot in commercial sweetpotato production, sporadic, isolated outbreaks occur even on farms with no history of the disease (C. A. Clark, *unpublished*).

The lack of disease in the field over the 3-yr period of this study does not appear related to the virulence of 2rr. This mutant caused as much disease in stems as did other wild-type strains from sweetpotato and the wild-type strain of *E. chrysanthemi* from which it was derived. Although somewhat less virulent than its progenitor in causing root rot, 2rr was similar to the other wild-type sweetpotato strains in this respect. In addition, 2rr has been compared with these strains for virulence on a number of other hosts and in a number of physiological tests and appeared similar to Ech-2 in all the evaluations (6). Ech-2 did not cause significant disease when used in inoculations at the same location in 1989 (C. A. Clark, *unpublished*).

The cultivar Beauregard is one of the most susceptible sweetpotato genotypes to bacterial root rot but is intermediate in susceptibility to bacterial stem rot (3). Consequently, factors other than the presence of the pathogen or relative storage root susceptibility must have been limiting to disease development in the field. This is supported by at least two observations. First, bedded mother roots inoculated with a micropipette tip containing a large number of bacterial cells (10^8/ml) did not always rot completely. Second, the number of apparently intact mother roots remaining after the second pulling was lower in the inoculated than in the noninoculated group only in 1989. Coincidently, heavy rains (950 mm) occurred during May–July of that year. Future studies should examine the role of factors that lead to development of hypoxia, such as excessive soil moisture or heat stress, in triggering development of bacterial stem and root rot (10).

The main advantage in using cut slips or vine cuttings instead of pulled slips is that they are less likely to carry Fusarium wilt, black rot, soil rot, scurf, other soilborne pathogens, or sweetpotato weevils to the field (2,9). Even though the percent recovery of *E. chrysanthemi* at harvest from plants produced from pulled slips was greater than that from cut slips, the importance of survival of *E. chrysanthemi* at low populations should not be underestimated. Only a few cells can function as primary inoculum when conditions are conducive, as shown with *E. carotovora* in Irish potato (5,13). Thus, the importance of type of transplanting in the epidemiology of *E. chrysanthemi* still needs investigation.

Contaminated tools may transmit *E. chrysanthemi* to the first slips transplanted each year. Also, contaminating the cut stubs may result in contamination of mother roots and subsequent transplantings. In addition, the bacteria may be present in or on daughter roots produced from those transplantings. Evidence for this mode of transmission was provided by results of greenhouse and field experiments using knives contaminated with *E. chrysanthemi* (6). There is considerable practical interest in this aspect of epidemiology of the disease, and further investigation is required, particularly into the potential of mechanical plant harvesters in transmitting the bacteria from plant beds to the field.

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