Ecology of *Xanthomonas campestris* pv. *juglandis* on Persian (English) Walnuts

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ABSTRACT

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Isolations made from apparently healthy dormant and developing buds and catkins of seven Persian (English) walnut varieties showed that these structures were frequently infested with the walnut blight bacterium, *Xanthomonas campestris* pv. *juglandis*. Buds were infested significantly more often than catkins, indicating that dormant buds represent the major overwintering site of the pathogen. Epiphytic populations of *X. c.* pv. *juglandis* on buds ranged up to 5.9×10^5 colony-forming units (cfu) per bud, with internal populations up to 1.4×10^6 cfu. Ninety percent of the dormant buds with epiphytic populations of the pathogen were also internally infested. Infected foliage, with epiphytic populations of up to 10^9 cfu per leaf, served as a source of secondary inoculum for late season infection of nuts and infestation of developing buds and catkins. No evidence was obtained to substantiate the role of blighted branch cankers in the overwinter survival of *X. c.* pv. *juglandis*. The number of epiphytically infested buds was reduced by dormant season applications of Kocide 101 and an experimental compound. However, the addition of dormant season sprays to conventional spray programs did not significantly improve walnut blight control.

Bacterial blight of Persian (English) walnuts, *Juglans regia* L., caused by *Xanthomonas campestris* pv. *juglandis*, is the most serious aboveground disease of walnuts in California. Previous studies on the epidemiology of *X. c.* pv. *juglandis* presented conflicting views on how and where the pathogen overwintered. Pierce (15,16), who originally described the disease in California in 1901, reported that the pathogen overwintered in infected branches and nuts. Although R. E. Smith (21) was unable to recover the pathogen from year-old branch cankers, he supported Pierce's assumption that these cankers were the major overwintering site. In Oregon, Miller (11,12) reported that discolored and diseased buds and catkins were the source of inoculum for spring infections, but O. C. Smith (20) demonstrated that in California the pathogen moved from branch cankers to infect buds and catkins. None of these studies clearly established how the pathogen overwintered on walnuts or how epidemics were initiated in the spring.

The development of a brilliant cresyl blue starch (BS) medium, a semiselective medium for the isolation of *X. c.* pv. *juglandis*, facilitated a quantitative study of dormant bud and catkin infestation with two early blooming walnut varieties (14). These studies showed that apparently healthy buds and catkins frequently harbored the pathogen and could be a source of overwintering inoculum.

In the studies reported here, seven walnut varieties, representing early, middle, and late blooming habits, were surveyed for the occurrence of infested buds and catkins. The nature and patterns of bacterial colonization and the distribution of infested buds and catkins were also investigated. A preliminary report has been published (13).

MATERIALS AND METHODS

Sampling and isolation procedure. Trees were sampled by pruning 8–10 cm of terminal growth from branches. Eight to 12 twigs per tree were collected from each of 10–15 trees per orchard. Leaves were removed from twigs collected during the growing season to prevent foliar contamination of buds and catkins while in transit to the laboratory. Terminal and lateral walnut buds and catkins were aseptically excised from twigs with a sterile razor blade in the laboratory. Each bud and catkin was placed in 10 ml of sterile distilled water (SDW) and agitated for 20 min on a gyrotory shaker (New Brunswick Scientific, New Brunswick, NJ 08904). A 0.1-ml aliquot from each suspension was spread with a sterile glass rod onto petri dishes of BS medium (14) and incubated at 28 C for 48–72 hr.

This isolation procedure only recovered surface populations of the pathogen and was used to identify epiphytically infested buds and catkins. On BS medium, *X. c.* pv. *juglandis* was identified on the basis of its colony morphology and the ability to hydrolyze starch (12). Except where specified, this sampling and isolation procedure was used in all experiments involving buds and catkins.

Walnut variety survey. From 1977 to 1979, dormant and developing buds and catkins collected from seven commercial walnut varieties representing early (March 15), middle (April 1), and late (April 15) blooming habits were assayed for the presence of *X. c.* pv. *juglandis*. A total of 29 orchards was surveyed. The early-blooming varieties examined were Eureka, Payne, Ashley and Serr; middle varieties were Hartley and Marchette; and the one late variety studied was Franquette. Isolations were made from 20–40 randomly selected buds, and a similar number of catkins were collected from each orchard. All the orchards studied, except the Hartley and Franquette plantings, had histories of recent walnut blight epidemics. Isolations were made from apparently healthy buds only.

Epiphytic and internal colonization of infested buds and catkins. Isolations were made on BS medium to determine the epiphytic populations of *X. c.* pv. *juglandis* from 45 buds collected from the Payne variety by the methods previously described. To eliminate the epiphytic bacterial populations and assess the internal populations, these buds were then treated for 15 min in 10 ml of 0.525% NaOCl with 0.05 ml of anionic Tergitol 7 (Sigma Chemical Co., St. Louis, MO 63178). Each bud was rinsed twice in SDW, then placed in 10 ml of SDW and agitated for 20 min. After agitation, a 0.1-ml aliquot from each bud suspension was spread onto BS medium to evaluate the effectiveness of the surface treatment. Individual buds were then triturated in a mortar and pestle in 10 ml of SDW, and isolations were made by spreading 0.1 ml of these suspensions on BS medium. Two isolations were made from each of 45 catkins, one to assess the epiphytic population and one to assess the internal population of *X. c.* pv. *juglandis*.

Distribution of infested buds and catkins. The effect of sprinkler irrigation on the vertical distribution of infested buds within seven walnut trees was studied in two Payne orchards. The lower regions of these trees were wetted during sprinkler irrigation, whereas the upper portion remained comparatively dry. Accordingly, the sampled trees were divided into two regions, one from ground level

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to 2.3 m aboveground and one 2.3 m and above. Four trees in one orchard and three trees in another were sampled by collecting 10–15 twigs, 8–10 cm long, from each of the two regions. A random sample of 30–58 buds was assayed for epiphytic populations of *X. c.* pv. *juglandis*, using the isolation procedures described.

Sprinkler irrigation and blight inoculum. Water from sprinkler irrigation was collected from beneath six infected Payne trees in August of the 1975–1976 growing season and examined for the presence of *X. c.* pv. *juglandis*. Although blighted leaves and nuts were present in these trees, no signs of fresh, "active" infections were apparent. Empty 17 × 150-mm test tubes were placed upright in 400-ml beakers at four locations beneath each tree, representing the north, south, east, and west portions of the leaf canopy. Immediately following the irrigation, all 24 samples were capped and returned to the laboratory, where serial dilutions of the collected water were spread onto BS medium. Colony counts were made after 72 hr of incubation at 28 C.

Influence of infected foliage. The influence of infected foliage on the incidence of adjacent bud and catkin infestation was studied in two orchards of the Payne variety. In August, when buds and catkins were almost fully developed, 10 twigs with healthy foliage and 10 with infected foliage were collected from each of five trees. Using the described isolation procedure, 20 buds and 20 catkins from each 10-twig sample were assayed for the presence of *X. c.* pv. *juglandis*. Percentages of epiphytically infested buds and catkins detected on twigs with and without infected foliage were compared.

Dormant season spray trials. The effect of dormant-season copper sprays on reducing *X. c.* pv. *juglandis* inoculum and crop losses was investigated in two field plots. In one plot, of the Marchette variety, Kocide® 101 (Kocide Chemical Corporation, Houston, TX 77015) was applied at 481 g/100 L to evaluate timing and frequency of sprays relative to crop loss and bud infestation. Treated trees were sprayed to runoff. Single-tree treatments were replicated five times in a randomized complete block design. Seven days after each dormant-season spray and again at harvest, 10 buds from each of the treated trees and the untreated controls were assayed on BS medium for the presence of the pathogen. Treatments were compared on the basis of percent blighted nuts and frequency of bud infestation.

In the second plot (Ashley variety), four compounds were applied during dormancy to determine whether these sprays reduced the overwintering population of *X. c.* pv. *juglandis*. Individual limbs were sprayed to runoff with a compressed-air garden sprayer (H. D. Hudson Manufacturing Co., Chicago, IL 60655). Treatments were replicated once in each of seven trees in a randomized complete block design, seven replications per treatment. Sprays were applied March 18, approximately seven days before bud break. Shoots were then collected from each treatment seven days after bud break, when shoots were 3–10 cm long. A shoot was defined as all the new growth that emerged from an individual bud, including leaves, stems, nutlets, and developing buds and catkins.

Isolations were made from five shoots per replication by washing each shoot in 100 ml of SDW for 20 min. Serial dilutions from these suspensions were seeded onto BS medium, and colony counts were made after 72 hr at 28 C.

RESULTS

Walnut variety survey. Buds and catkins infested with *X. c.* pv. *juglandis* were detected in all seven varieties studied (Table 1). Among the early-blooming varieties, bud infestation was greatest in Payne and Ashley. Infestation varied from 5 to 95% of buds in the 18 Payne and Ashley orchards examined, and in eight of these orchards, over 50% of the buds harbored the pathogen. With Serr and Eureka, the other early-blooming varieties, bud infestation ranged from 5 to 30% and 0 to 20%, respectively. The infestation frequencies with Hartley and Franquette (later-blooming varieties) were 0–13% and 0–33%, respectively.

Colonization of buds and catkins by *X. c.* pv. *juglandis*. Two thirds of the 45 Payne buds examined were infested with *X. c.* pv. *juglandis*, of which 90% had both epiphytic and internal populations of the pathogen. Seven percent were epiphytically infested only and 3% had only internal infestation. Combined epiphytic and internal populations of the pathogen from individual buds ranged from 2.3×10^5 to 1.4×10^6 cfu. With buds that were both epiphytically and internally infested, the internal populations were usually 10-fold greater.

Isolations from 45 catkins indicated that 20 (44.4%) were infested. Of these, 45% were both epiphytically and internally infested, 30% were only internally colonized, and 25% were only epiphytically infested. Epiphytic populations ranged from 2.0×10^2 to 2.1×10^5 cfu per catkin. Internal populations were not assessed.

Influence of sprinkler irrigation on bud infestation. Between the months of May and September, commercial California walnut orchards require 26.0–33.5 in. of water per acre (4). Sprinklers are the preferred means of applying water because they facilitate effective water management by preventing orchard flooding, which is conducive to root and crown rot development. On the basis of chi-square analysis, a significantly greater percentage of epiphytically infested buds occurred in the low, sprinkler-sprayed region of the leaf canopy in six of the seven Payne trees (Table 2). In the two orchards, bud infestation averaged 37.6 and 88.8% in the lower region of the canopy compared to 25.6 and 64.4% in the region above the sprinkler-sprayed zones. Irrigation water collected at the base of infected trees after falling through the leaf canopy in August 1976 contained an average *X. c.* pv. *juglandis* population of 8.6×10^3 and 5.4×10^4/ml, respectively, in the two orchards.

Influence of infected foliage. Based on chi-square analysis of the data, buds of the Payne variety that developed on twigs with infected foliage were infested significantly more often than buds developing on twigs with healthy foliage. An average of 26.1% of the buds associated with healthy foliage were infested, compared to 35.9% infestation of buds near infected leaves. The frequency of catkin infestation did not appear to be influenced by adjacent infected foliage. On diseased twigs, 44% of the catkins were infested compared to 46% on healthy twigs.

Fruitful and vegetative bud infestation. Walnut trees produce vegetative and fruitful (nutlet-bearing) buds. Depending on the variety, fruitful buds may occur terminally, laterally, or both. Dormant terminal and lateral buds of six walnut varieties with differing habits of bearing fruitful buds were examined to determine whether one bud type was more susceptible to infestation than the other. Two orchards of each variety were sampled, and buds were assayed on BS.

Within individual orchards, approximately equivalent numbers of terminal and lateral buds were epiphytically infested with *X. c.* pv. *juglandis*, indicating that neither bud type nor bud position influenced infestation frequency. Franquette, a terminal-bearing variety, averaged 13.2% infested lateral buds compared with 14.3% infested terminal buds. Payne, a lateral nut-bearing variety, showed infestation rates of 21.5% in lateral buds and 23.1% in terminals.

Twig cankers. Monitoring 20 twig cankers on the Payne variety for two consecutive growing seasons (1977–1978 and 1978–1979) showed that blight bacteria did not survive over winter in these cankers. During the first season of canker development, the pathogen was recovered from the surface of all 20 cankers, both at midseason (June) and before dormancy (September). However, no macroscopic exudations of bacteria or bacterial strands were observed. Following winter dormancy, *X. c.* pv. *juglandis* could no longer be isolated from twig cankers. These cankers were dry and hardened in appearance; all were colonized by *Alternaria* spp., and 17 of the 20 were colonized by *Rhizopus stolonifer*.

Dormant-season spray trials. The number of buds epiphytically infested by *X. c.* pv. *juglandis* was reduced by applying Kocide when the walnut trees were dormant (Table 3). After the first spray (applied 21 December 1977), bud infestation was reduced from 82 to 70 and 74% in the two treatments applied. These trees were again sprayed on 27 January 1978, and the number of epiphytically infested buds was reduced to 58 and 66%, respectively. In the period between these sprays, the number of buds infested on the untreated trees increased slightly to 84%. Trees receiving one dormant spray

(January only) showed a reduction in bud infestation equivalent to that observed on trees receiving two dormant sprays.

Crop loss assessments made at harvest showed that the four and five Kocide applications (one or two dormant-season and three bloom-period sprays) were not significantly better than the conventional program of three bloom-period sprays for controlling nut blight. However, evaluation of buds after harvest indicated that greater reductions in bud infestation occurred with treatments that included dormant sprays.

In a second field plot, in which single branches were sprayed, one-week-old shoots that developed from treated buds were assayed for *X. c.* pv. *juglandis* (Table 4). With all five treatments, significantly lower populations of the pathogen were detected on the new growth compared to those on untreated checks. However, even with $CuSO_4$-H_2O, the most effective treatment, the mean population per shoot was 1.86×10^5 cfu.

DISCUSSION

These studies indicate that infested buds and catkins are the major overwintering sites for *X. c.* pv. *juglandis* in the seven walnut varieties surveyed. Although Miller (12) reported that diseased and discolored buds were the overwintering sites for the pathogen in Oregon, the infested buds and catkins in our studies were apparently healthy, showing no evidence of necrosis or infection. The ability of *X. c.* pv. *juglandis* to colonize buds epiphytically and internally is advantageous for enhancing survival and promoting rapid dissemination. Internal colonization enables the pathogen to survive periods of environmental stress (eg, drying and ultraviolet light), whereas epiphytic colonization assures a ready source of inoculum when environmental conditions favor disease development.

The presence of a resident population of the pathogen within dormant walnut buds may explain the aggregated nonrandom distribution of infected leaves observed in spring. Early in the season, some buds produce shoots with heavily infected leaves although adjacent buds commonly produce healthy shoots. On the infected shoots, basal leaves, which occupied the outermost position in the dormant buds, were infected more often than apical leaves. Bud infestation apparently begins with epiphytic colonization followed by a centripetal invasion of internal bud parts. Accordingly, leaves forming in the outermost positions in the bud would be the first contaminated during the process of internal bud infestation. Subsequently, these infected leaves are an important source of inoculum for the infection of other leaves, nutlets, and the infestation of developing buds. The location of buds (terminal or lateral) and bud fruitfulness did not appear to affect the incidence of bud infestation. However, a significantly greater percentage of buds associated with infected foliage were infested than were buds associated with healthy foliage.

Twigs infected during spring were a source of inoculum for secondary spread of blight during the growing season. However, the pathogen was not recovered from one-year-old cankers, suggesting that these cankers were not sites where *X. c.* pv. *juglandis* overwintered.

The blooming habits of varieties, rainfall patterns, and orchard design influenced the development and severity of blight and the subsequent infestation of buds and catkins. The incidence of bud

TABLE 1. Recovery of *Xanthomonas campestris* pv. *juglandis* from dormant and developing walnut buds and catkins

Variety	County[a]	Date sampled (month/yr)	Number of buds and catkins[b]	Percent epiphytically infested	
				Buds	Catkins
Early blooming[c]					
Ashley	Butte	6/77	20	90[d,e]	90
	Butte	2/79	20	45	35
	Butte	6/77	20	12.5	25
	Butte	6/77	20	15	15
	Butte	8/77	20	5	0[e]
	Butte	6/77	20	45	...
	Butte	10/78	40	25	10
	Tulare	8/78	30	14	0
	Tulare	8/78	20	5	0
	Glenn	10/78	40	73	20
	Tehama	3/79	60	73	...
Eureka	Contra Costa	9/78	20	0	0
	Contra Costa	10/78	20	10	20
	Tulare	10/78	20	20	0
Payne	Tulare	4/77	20	10	0
	Contra Costa	2/78	40	60[d,e]	70
	Contra Costa	12/77	20	95	95
	Contra Costa	10/77	40	75	55
	Contra Costa	8/77	40	80	70
	Contra Costa	8/77	20	75	45
	Contra Costa	3/77	20	45	55
Serr	Contra Costa	9/77	20	20	0
	Tulare	9/77	20	5	0
	Tulare	10/77	20	30	0
Middle blooming					
Hartley	Butte	4/77	40	0	0
	Contra Costa	4/78	20	13	21
Marchette	Tulare	11/77	40	63	18
Late blooming					
Franquette	Butte	4/77	40	0	0
	Contra Costa	4/78	24	33	16.6

[a] Butte, Contra Costa, Glenn, and Tehama are northern California counties. Tulare County is in the southern San Joaquin Valley.
[b] Number from which isolations were made.
[c] Blooming habits were based on leafing dates: early, March 15; middle, April 1; and late, after April 15.
[d] On the basis of a paired *t*-test, buds were infested significantly more often than catkins.
[e] The limit of sensitivity of the isolation procedure was about 100 cells per sample unit. Populations below 100 cells per sample unit would not be detected.

TABLE 2. Percentage of buds infested with *Xanthomonas campestris* pv. *juglandis* in relation to location in the leaf canopy

Orchard[a]	Tree	Buds infested low[b]		Buds infested high[c]	
		Number[d]	Percent	Number[d]	Percent
I	1	20/36	55.6	8/36	22.2
	2	18/52	34.6	16/38	42.1
	3	24/58	41.4	12/38	31.6
	4	14/56	25.0	4/44	9.1
	Mean		39.2[e]		25.6
II	1	24/30	80.0	12/30	40.0
	2	30/30	100.0	28/30	93.0
	3	26/30	87.0	18/30	60.0
	Mean		88.9[e]		64.4

[a] The orchards sampled were the Payne variety.
[b] Buds were sampled from branches no higher than 2.3 m aboveground.
[c] Buds were sampled from branches above 2.3 m.
[d] Number of infested buds divided by the total number of buds tested.
[e] The two means in this orchard were significantly different based on chi-square analysis.

infestation was greatest (mean = 41.6%) on the early-blooming varieties Payne and Ashley, growing in the northern California counties where spring rainfall occurs more frequently. In the drier southern counties, bud infestation averaged 9.7% on the same varieties. The Serr variety exhibited some field resistance (17) to blight, and crop losses have seldom been serious in spite of its early blooming habit. This field resistance was reflected in low bud and catkin infestation. However, when Serr and its two parent varieties were artificially inoculated with the pathogen, disease readily occurred and spread naturally to uninoculated parts of the trees (Mulrean and Schroth, *unpublished*). These inoculations indicated that neither Serr nor its parents possessed true resistance (17). The middle-blooming Hartley and late-blooming Franquette, which generally bloomed after spring rains had subsided, sustained only minor nut and leaf blight during the season. In these varieties, as with Serr, the incidence of bud and catkin infestation was low. The Marchette orchard, however, was an exception among the later blooming varieties in that blight caused major crop losses and a correspondingly high incidence of bud and catkin infestation occurred. These walnut trees were interplanted with plums, and the resulting dense leaf canopy restricted air movement and increased the frequency and duration of dews. These conditions are conducive to blight development and subsequent bud and catkin infestation.

Bacterial pathogens frequently have been reported to overwinter or survive for protracted periods in apparently healthy buds (1–3, 5–10,18,19,22). This means of survival is especially important for pathogens like *X. c.* pv. *juglandis* that have no known alternate host. The epidemiological importance of bud colonization by pathogens, whether epiphytic or internal, varies somewhat between perennial and annual hosts and is influenced by the climate in which the host plant is growing. The effectiveness of bactericides for controlling bacterial diseases like walnut blight is limited by the inability of these materials to reduce or eliminate internally borne bud inoculum. Topical applications of copper and bactericides still allow survival of ample bacteria within the bud to initiate disease under suitable environmental conditions. Accordingly, with walnut blight, applications of bactericides reduced the number of epiphytically infested buds and significantly reduced populations of the pathogen on new growth. These reductions were not sufficient to have any effect on the overall progress of the blight epidemic or subsequent crop loss. None of the materials tested eradicated *X. c.* pv. *juglandis* from within dormant infested buds. Preventing bud and catkin infestation with protective sprays would be an approach to reducing the amount of overwintering inoculum. However, this is not economically feasible at the present time. Until bactericides with eradicative or systemic activity are developed, bacterial pathogens that overwinter in protected sites on the host plant will continue to be difficult to control.

TABLE 3. Effects of dormant season Kocide® sprays on nut blight and bud infestation on the Marchette walnut variety

Treatments[a]	Percent of buds infested after dormant spray on		Percent of nuts blighted at harvest (1978)[c]	Percent of buds infested after harvest (1978)[d]
	21 December 1977[b]	27 January 1978[b]		
Two dormant	70	58[c]	24.40 a	ND
One dormant and three bloom	ND[e]	56	10.56 b	30.12 a
Two dormant and three bloom	74	66	21.64 b	40.32 a
Three bloom	ND	ND	12.20 b	42.64 b
Unsprayed	82	84	29.0 a	60.04 b

[a] Single-tree treatments were replicated five times in a randomized complete block design. All Kocide treatments were applied at 0.481 kg/100 L using a pull-type orchard sprayer with a handgun. Trees were sprayed to runoff.
[b] Ten buds from each of seven replications of the treated and control trees were assayed for infestation 7 days later.
[c] Harvest was 29 September. Values in the column followed by the same letter are not significantly different ($P = 0.05$), least significant difference = 6.77.
[d] Values in the column followed by the same letter are not significantly different ($P = 0.01$), least significant difference = 18.79.
[e] Not done.

TABLE 4. Populations of *Xanthomonas campestris* pv. *juglandis* on young walnut shoots[a] following dormant season application of four bactericides

Treatments[b]	Mean shoot population ($\times 10^5$)[c]
$CuSO_4$-$5H_2O$ (25% Cu, 10 g/L)	1.86 a
A-16886-b[d]	
100 ppm	4.43 a
200 ppm	9.03 a
Tribasic $CuSO_4$ (53% Cu, 5 g/L)	23.33 a
$MnSO_4$-H_2O (10 g/L)	30.60 a
Untreated	1,110.62 b

[a] All the new growth that emerged from an individual bud, including leaves, stems, nutlets, and development buds and catkins.
[b] All treatments were applied to the Ashley variety on 18 March 1980, using a pressurized garden sprayer.
[c] Means are based on isolations from five shoots per replication with each treatment replicated seven times in randomized complete block design. Values followed by the same letter are not significantly different ($P = 0.05$), least significant difference = 767.05.
[d] A-16886-b is an experimental bactericide provided by Eli Lily, Inc.

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