CANE GALL OF BRAMBLES CAUSED BY PHYTOMONAS RUBI N. SP.[1]

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INTRODUCTION

Because of a similarity in gross symptoms, cane gall has often been confused with crown gall caused by *Phytomonas tumefaciens* (Sm. and Town.) Bergey *et al.*, although its identity was apparently established by Banfield (*2, 4, 18*).[2] Pinckard (*13*), in a comparative study of the physiology of cell-stimulating bacteria, demonstrated rather conclusively specific differences between these two organisms and provided a basis for describing the cane gall organism. The present paper summarizes the results of observations made on this disease and its causal organism in New York State during the past 7 years and brings together other pertinent facts from the literature to assist in describing the causal organism.

Cane gall is undoubtedly an old disease since over 40 years ago Bailey (*1*) reported in New York a so-called cane-knot disease of blackberries and illustrated typical cane gall symptoms. He states: "It is apparently not common, but it must be widespread for I have had specimens from as far west as Wisconsin." Shortly thereafter a similar disease was reported from Europe (*17, p. 606, 19, 20*). That cane gall now occurs widely in the raspberry-growing sections of the United States (Ohio, Indiana, Michigan, Illinois, and Oregon) has been indicated by Banfield (*4, 18*). The writer found it in New York in 1932 and Zundel (*21*) has noted its presence in Pennsylvania.

SYMPTOMS

Symptoms appear on the fruiting canes of *Rubus* spp. in late May or June as small spherical protuberances or elongate ridges of white granular gall tissue (fig. 1). The small whitish eruptions rapidly increase in size and number and may completely cover sections of the cane surface, being most abundant on the lower part of the cane but appearing also on the upper part and even on the small terminal branches. After several weeks the whitish gall tissue turns brown and begins to disintegrate near the soil surface (fig. 2). The enlargement of the galls frequently causes the stems to split open and the canes to dry out. These injured canes produce only small seedy berries. Growers refer to the condition as "beading," "coraling," or "knotting."

Under severe disease conditions one New York grower wrote Bailey (*1*), that the disease "progresses rapidly, as the fruit grows, and when the fruit is about two-thirds grown the leaves begin to wither,

[1] Received for publication March 20, 1940.

[2] Italic numbers in parentheses refer to Literature Cited, p. 695.

the cane dries up, and the berries ripen. On very badly diseased canes the berries wither and dry up." The course of the disease as outlined above was very similar to that observed on the Sodus variety of purple raspberry in the writer's garden in 1939.

FIGURE 1.—Stages in cane gall development on black raspberry. The first symptoms appear (*A*) on the fruiting canes in May as spheres or ridges of white granular tissue. The galls increase in number and size and during June they may appear singly or in rows (*B*) or in more or less elongate ridges (*C*). (Photographs furnished by W. M. Banfield).

According to Banfield, cane galls are seldom found on the roots of black raspberry, the plant principally used in his studies, or on the roots or canes of red raspberry, and rarely, if ever, on black raspberry canes during the first year of their growth. Bailey (*1*) states that the disease, "probably attacks the growing shoots, although it is

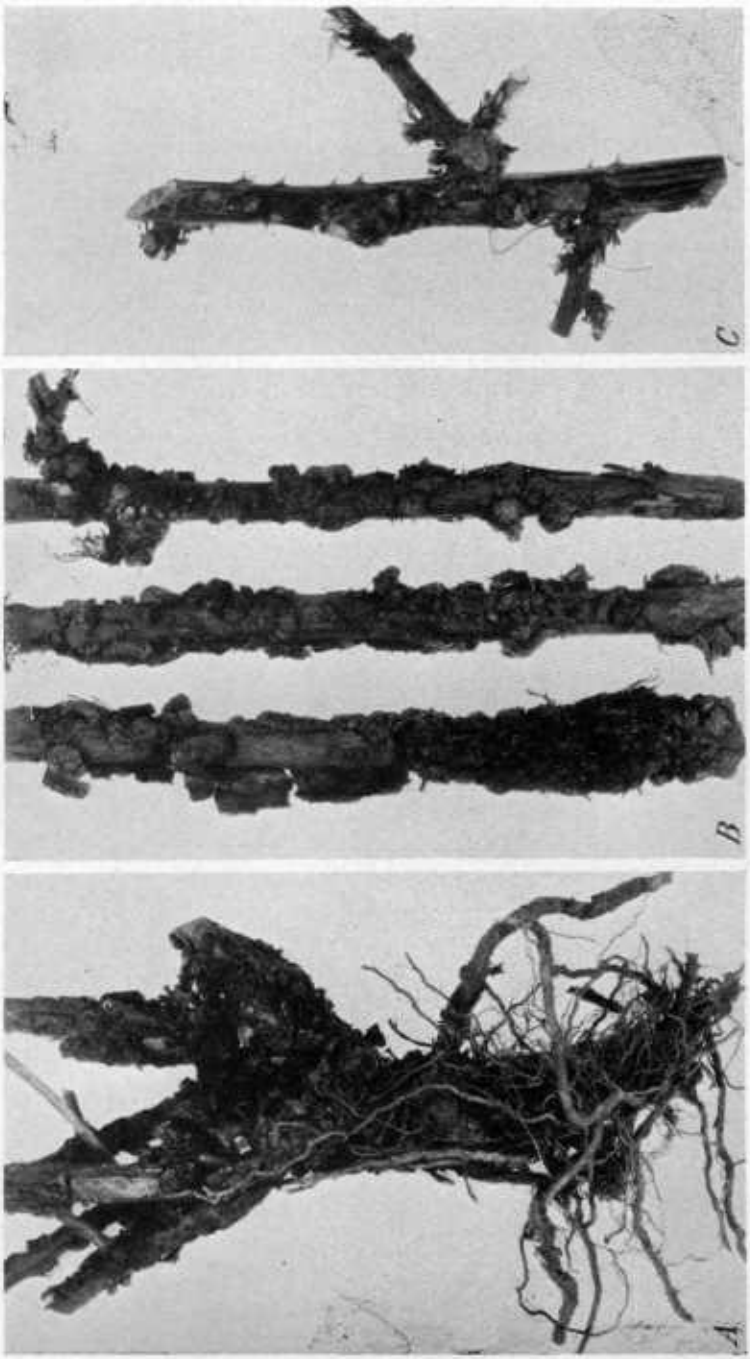

FIGURE 2.—Advanced stage of cane gall on a Plum Farmer black raspberry plant collected in the field in July. Practically all of the galls are discolored and in an advanced stage of deterioration and there is little new cane growth: *A*, Plant showing disintegration of the crown region and sparseness of current season cane growth therefrom; *B*, abundance of galls along the fruiting canes (sometimes these appear in rows and sometimes in indiscriminate order); *C*, galls that have developed on the side branches well up on the plant.

not apparent until the following year, when the grower, noticing that the leaves are yellow and the fruit not filling, examines the canes and finds these knots upon them."

ISOLATION STUDIES

The cane gall organism was readily isolated from fresh young galls by using poured plates of such media as potato-dextrose or potato-mannitol agar.[3] Banfield (*4*) induced cane galls on black raspberry under aseptic conditions, and when isolations were attempted 3 weeks later only cane gall bacteria appeared on the plates. Numerous isolations by the writer from young galls of about the same age, but produced under exposed conditions, generally gave cultures relatively free from contaminants. However, when isolations were attempted from older galls and from soil, serious difficulty was encountered with contaminants, even in the former case, although the greatest care was exercised in removing the outer gall tissue before taking samples.

To discover a more suitable isolation medium, a comparative study was made involving, in addition to the common laboratory media, several selective media (*7*, *11*, *12*) of which the aniline blue medium of Hendrickson et al. proved fairly satisfactory. The bacterial colonies resulting from tissue and soil isolations came up in aniline blue agar plates largely free from contaminants.

Whenever discoloration became pronounced in the cane galls, which was a rather common occurrence in the field in July, it was no longer possible to recover cane gall bacteria from them by any method tried.

Before pathogenicity tests were carried out, the parent cultures were purified by making single-cell isolations (*10*). Five single cells were isolated from each of the original parent cultures obtained from two black and one purple raspberry planting in New York. Growth resulted from two cells isolated from culture 1, five from culture 2, and three from culture 3. These 13 isolates (counting both parents and progeny) appeared identical in culture and were employed in making subsequent studies.

PATHOGENICITY

Galls were readily induced by inoculation of the organism into fruiting canes, current season cane growth and petioles, and roots. Figure 3, *A*, illustrates an early gall development on a current season cane and petiole stimulated by needle-puncture inoculation. A later stage produced in the same manner is shown in figure 3, *B*. A high incidence of infection ranging from 80 to 100 percent usually resulted from needle-puncture inoculations into current-season canes. Figure 3, *C*, illustrates an advanced stage of gall development on new growth, the radial extension of the gall being over 1 inch. Brown patches over the surface indicate that decomposition is taking place.

Small galls were produced on the roots of plants when the bacteria were introduced into the soil either directly or by means of water washing the bacteria off galls above ground. Wounds for infection courts

[3] The ingredients for 1 liter of potato-dextrose agar consisted of 200 gm. of potato (skins removed), 17 gm. of agar, 10 or 20 gm. of dextrose, and distilled water. The same ingredients were used in potato-mannitol agar except for the substitution of 5 gm. of mannitol for the dextrose and the addition of a small pinch of finely powdered calcium carbonate.

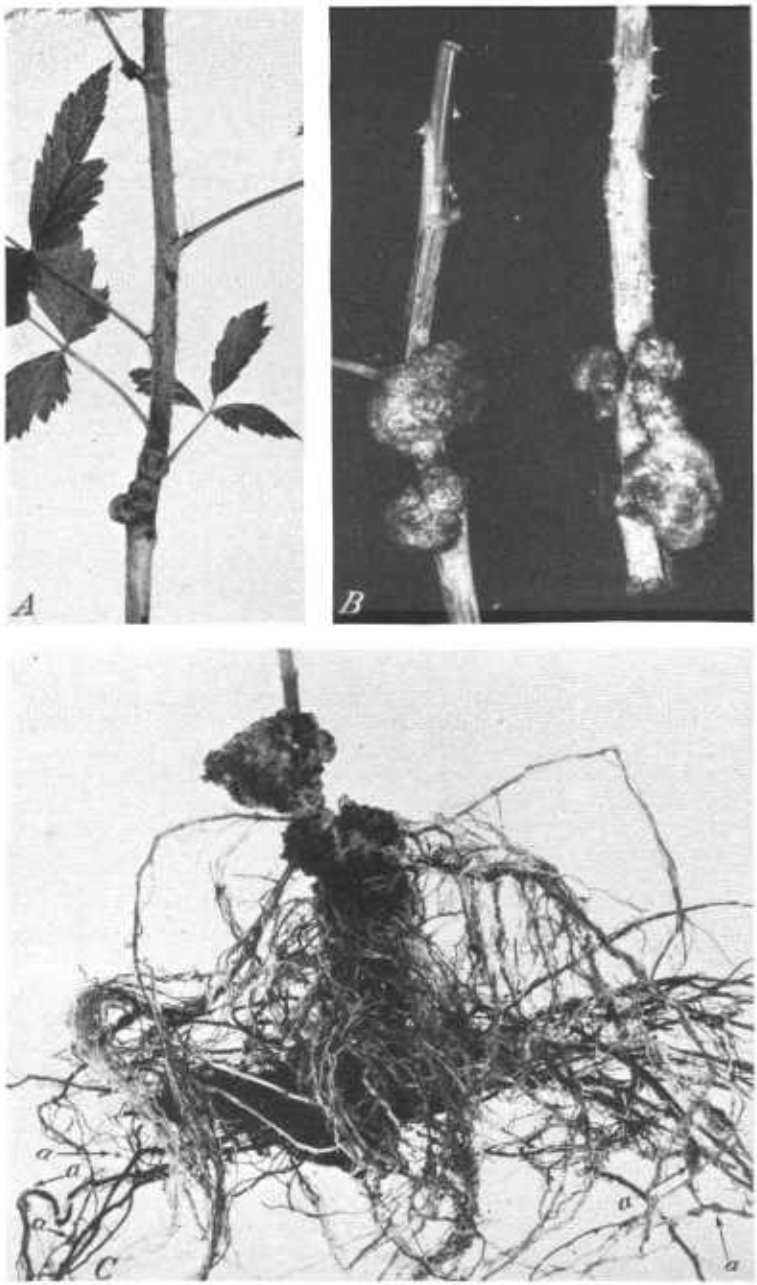

FIGURE 3.—Results of needle-puncture inoculations with the cane gall organism on Plum Farmer black raspberry plants: *A*, Gall symptoms on a petiole and stem of new cane growth 4 weeks after inolcuation; *B*, cane galls on current season stems 2 months after inoculation, with discoloration beginning to set in; *C*, cane galls on current-season growth about 11 weeks after inoculation. These galls measure over 1 inch in radial extension and the surface discoloration indicates a rapid state of deterioration. Small root galls (*a*) are also present.

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were produced by probing among the roots with a sharp tool. Several small galls of this character may be seen in figure 3, *C*, *a*.

When inoculations were made early in the season into fruiting canes, the incidence of infection was lower than when they were made into current-season growth. The reason for this was not ascertained. However, when infections were obtained there was a tendency for the galls to form ridges upward on the stem, the phenomenon so characteristic of infections occurring in the field.

HOST RANGE

Cane gall has been found in New York commercial plantings on black raspberries, purple raspberries, and blackberries, and when inoculated with the cane gall organism these plants and red raspberries also have been found susceptible to infection. On black raspberry canes 25 inoculations induced 25 galls with an average radial extension of 22 mm. after 6 weeks. Similarly on purple raspberry, red raspberry, and blackberry canes, 25 inoculations induced 25, 18, and 25 galls, respectively, with average radial extensions of 20, 4, and 18 mm. These results confirm a report (*18*) from Wisconsin for black raspberries. Although studies on host range are incomplete, it probably deserves mention that none of the plants thus far tested except the brambles have been found susceptible to infection. Pinckard (*13*) also failed to secure infection on tomato, beet, oleander, and olive.

LIFE HISTORY

The life history of the cane gall organism in relation to pathogenesis has received considerable attention especially from Banfield (*4*), but several details still remain to be determined.

The organism seems to enter the plant only through wounds or other injuries, for applications of bacteria to the surfaces of uninjured petioles, stems, and roots have always given negative results. The exact mode of entry in the field is unknown; however, root-feeding insects (*3*) or other insects that injure the plants, pruning wounds, and injuries to the underground parts produced in cultural operations, all would seem to afford adequate opportunity for bacterial invasion.

Banfield (*3*), in studying crown gall on red raspberry, observed that infections occurred only through injuries. A further significant fact observed was that injured tissue on the underground parts of red raspberry remain infection courts for as long as 7 weeks after injury. This slowness of wounds to heal favors the likelihood of invasion by all forms of wound pathogens, including the cane gall organism. Of perhaps equal significance is the delayed incubation period. This has been established for crown gall (*5*), but undoubtedly plays as significant a role in cane gall.

The incubation period (latent period of infection) based on inoculations during the summer months (June to September) was never less than about 2½ weeks and averaged nearer 3 weeks. This interval is somewhat longer than for the crown gall organism on raspberry as reported by Banfield (*3*). From two to four plants were inoculated at monthly intervals by needle punctures, each plant receiving an average of five inoculations into the growing canes. By judicious pruning, new growth was available each month. Inoculations were not attempted later than September, but for April and May the incubation periods averaged approximately 6 and 4 weeks.

The location of the casual organism in cane galls on black raspberry was thoroughly studied by Banfield (*4*), who found the bacteria principally between the cell walls but ramifying throughout all regions of the gall in the form of zoogloeal strands which dissolved away the middle lamella of the cell walls for channels. The gall initials found beneath the phelloderm of fruiting canes in early spring appear to be induced by hyperplasia [4] of the pericycle and phloem ray cells. From the time of the first microscopic appearance of the gall to its maturity, bacterial pockets are of common occurrence in the meristematic areas. Apparently they result from successive lysis and collapse of cells in contact with the bacterial strands; the cells just beyond the bacterial strands divide and those farther removed are not stimulated. As the galls near maturity, cell division becomes progressively more feeble and tissue degeneration more general. It is an interesting fact that the cell walls which are composed largely of cellulose appear not to be dissolved by the bacteria.

The bacteria may be discharged (*4*) from the cavities or pockets in the gall before disintegration sets in. Discharge takes place by way of intercellular channels to the surface which are presumed to have been occupied by bacterial strands.

The cane gall organism was found only in gall tissue when current season stems were inoculated at two widely separated points. Galls 2½ months old produced near the apex or the base of current season canes when they were about 12 inches long were employed. In one case isolations were attempted from the fresh galls and from the apparently healthy stem between these galls cut into four 3-inch pieces. Bacteria were obtained only from the gall tissue. In another case, the galls and stem pieces were immersed in calcium hypochlorite solution [5] for 20 minutes to reduce surface contaminants. Subsequently the galls were passed through sterile distilled water seven times, changing at hourly intervals. Platings were made from the washings, employing potato-mannitol agar and aniline blue selective medium. The results indicate that the bacteria were limited to the immediate gall region, that they had not migrated in current season canes, and that they were freely given off at the gall surface when immersed in water. Only one washing, that immediately following immersion in calcium hypochlorite solution, failed to yield bacteria in abundance from the uninjured galls, and this was undoubtedly due to the residual effects of the disinfectant.

In a similar experiment on fruiting canes the bacteria were obtained from the galls and also from the stem tissue for a short distance (up to 10 mm.) immediately above the galls, a fact which suggests that the fruiting canes must differ in some respects from current-season canes since they afford passage for the bacteria.

Longevity experiments seem to indicate that the period of survival of the cane gall bacterium in soil is much shorter than the periods of a year or more found earlier for the hairy root (*8*) and crown gall (*3*) organisms. Steamed and unsteamed soil were artificially infested with cane gall bacteria and stored either out of doors or in the greenhouse in early October. Isolations were attempted at monthly intervals, the isolation technique of Hildebrand (*8*) being used. The soil samples

[4] Butler (*6*), who examined histologically cane galls on black raspberry received from Wisconsin, mentions the presence of both hypertrophy and "hyperplasy" in the older gall tissue.

[5] Consists of 10 gm. of calcium hypochlorite mixed with 140 cc. of distilled water, filtered, and used fresh at full strength.

consisted of duplicate ½-cubic-foot lots of moderately rich clay loam placed in wooden containers. The steaming treatment was carried on for 1 hour at 15 pounds pressure. The inoculum consisted of a 3-day-old growth of the bacteria on potato-mannitol agar. The maximum survival period found in these experiments approximated 6 months in soil stored outdoors and 4 months in soil stored in the greenhouse, and in each instance the length of survival was about 1 month longer in steamed than in unsteamed soil. The relatively short period of survival of the cane gall bacteria in soil would seem to point to some other mode of overwintering, such as in the plant itself, ut the solution of this problem remains for the future.

THE CAUSAL ORGANISM

The methods given in Pure Culture Study of Bacteria as of 1933–36 were followed except as noted (*15*, *16*). In the studies on physiology, the chief reliance was placed on results given by Pinckard (*13*), whose work on this organism was generally repeated and confirmed.

GROWTH IN CULTURE

When isolations were made from young 3-week-old galls, minute white colonies were visible on the surface of potato-mannitol, potato-dextrose, or yeast-extract-dextrose agar after 3 to 5 days, and after 2 to 3 days when isolations were made from the organism in culture. At the end of 10 days at 24° C. the colonies were circular, smooth, entire, and raised, with the largest not much more than 4 mm. in diameter when the number of colonies to the plate approximated 100. Submerged colonies were disk-shaped (double convex) and approached half the size of surface colonies.

When aniline-blue agar was employed, it was not uncommon for many of the colonies to take up the dye, but tbis did not prove to be of positive diagnostic value.[6] The aniline-blue medium did serve to distinguish the cane gall from the crown gall and hairy root organisms. When streaks were made on the surface of this agar, the cane gall organism, like the crown gall organism, took up the dye, but the hairy root organism did not. Although both absorbed the dye, the cane gall organism made much less growth than the crown gall organism and produced a narrow, thin, almost flat streak in contrast to the broad raised streaks produced by the other two organisms.

In nutrient-broth cultures of the cane gall organism a uniform moderate turbidity was produced in about 2 days, but no pellicle was formed. On potato-mannitol-agar slants a moderate, filiform, glistening white growth developed along the streak in 48 hours. The edges were entire and the consistency of the growth was at first watery to butyrous. Upon aging the growth became a dull creamy white, spread irregularly, flattened, and changed to a tough leather consistency.

The cane gall organism grows slowly as compared with other plant pathogens, an observation also made by Pinckard (*13*). In a study of growth rates (*9*), it was demonstrated that this organism grew more

[6] Because both crown gall and cane gall bacteria take up aniline-blue dye readily when streaked on aniline-blue agar, it was thought that these bacteria might possibly take up the dye when isolations were attempted with poured plates. However, after repeated experiment, it was found that when dilution plates were poured, from none to many colonies took up the dye and the organisms from dyed as well as from undyed colonies were pathogenic. Hendrickson et al. (*7*) also noted that crown gall bacteria have strains which do not absorb dye. This phase of the work deserves further study.

slowly than any of 11 species of plant pathogens, having a minimum generation time of 155 minutes.

MORPHOLOGY

When grown in culture media, the cane-gall organism is a rod with rounded ends usually appearing singly or in pairs but sometimes occurring as short chains. Banfield (*4*), however, observed that when present in host tissue these bacteria are always grouped in chains or in masses and do not occur singly. After having grown on potato-mannitol-agar slants for 48 hours at 24° C. the cells were found to have a mean size of 1.72 μ by 0.64 μ when mounted with congo red negative stain. A repetition of the measurements of 6 of the 13 cultures taken at random from the collection gave a mean size of 1.72 μ by 0.63 μ. For each culture, 100 individual cells were measured.

The organism was motile in several liquid and solid media. Presumptive evidence for motility was obtained when turbidity was observed at considerable distances from the center in tubes of soft potato-mannitol agar (0.3 percent agar) which had been seeded by stab puncture. Following the isolation of single cells in potato-mannitol agar and nutrient broth, the appearance and progress of motility of the progeny cultures was more pronounced in broth than on agar, and on the fourth, fifth, and sixth days after isolation into microculture than earlier.

Polar flagella were demonstrated by means of Gray's and Casares-Gil's flagella stains. The former proved better but still not entirely satisfactory because of difficulty in getting the flagella to take up the dye. Several long flagella were commonly observed near one of the poles in a subpolar position. Only rather rarely were they observed at both poles and in these cases it is possible that the cells were nearing the fission point. Some of the flagella were 10 times as long as the individual cells.

PHYSIOLOGY

The work of Pinckard (*13*) on the utilization of various sources of carbon and nitrogen [7] was repeated and verified by the use of his mineral salt yeast-extract basal medium. Attempts to use the Society of American Bacteriologists' basal medium or to substitute simpler substances, such as *d*-glutamic acid, asparagine, inositol, ascorbic acid, and thiamin for yeast extract, were unsuccessful. All tests were made in quadruplicate. Acid was produced from arabinose, xylose, rhamnose, fructose, mannose, galactose, glucose, lactose, and erythritol. An alkaline reaction appeared with melezitose, starch, inulin, pectin, lactositol, calcium gluconate, formic acid, acetic acid, propionic acid, glycollic acid, malonic acid, succinic acid, tartaric acid, malic acid, and yeast extract only. Cellulose was not fermented.

The cane gall organism appears to be able to use most readily the more complex nitrogen compounds such as ferric ammonium citrate, uric acid, oxamide, succinimide, *l*-asparagune, *l*-tyrosine, *l*-cystine, *d*-glutamic acid, and yeast extract.

Gelatin was not liquefied. On litmus milk a slight serum zone, pink color, acid and curd were produced. Nitrates were not utilized

[7] The writer retested all of Pinckard's carbon sources except aesculin, phloridzin, and calcium gluconate but did not make any determinations on titratable acidity.

and nitrites not produced in the synthetic nitrate medium listed in the Manual of Methods of the Society of American Bacteriologists (*14*). When grown in Bacto-nutrient broth there was a slight test for ammonia (Hansen's method *16, p. 12*). In Bacto-tryptone broth negative tests were obtained for hydrogen sulphide production with ZoBell's method (*15, p. 11*) and for indole with Gnezda's technique (*15, p. 10*). Starch was not hydrolyzed and casein not digested. In agar shake cultures, only slight turbidity developed below the surface, placing the organism somewhere between an aerobe and a facultative anaerobe as to oxygen requirements. No apparent gas was produced. The organism when grown in nutrient broth had a thermal death point of about 56° C.

TAXONOMY

The cane gall organism is considered to be a member of the genus *Phytomonas* and the name *Phytomonas rubi* n. sp. is proposed for it. Synonyms (according to the classifications used by plant pathologists) would be *Bacterium rubi* n. sp. and *Pseudomonas rubi* n. sp.

TECHNICAL DESCRIPTION

Phytomonas rubi n. sp.

Small, Gram-negative, non-acid-fast rod (1.72 μ by 0.64 μ) with rounded ends, chiefly occurring singly and in pairs, occasionally in short chains in culture and in chains and masses but not singly in host tissue. Weak facultative anaerobe with optimum growth at 27° C.; thermal death point about 56° C.; motile by subpolar flagella; spores not formed.

On potato-mannitol-agar slants growth slow, moderate, filiform, white to creamy-white, with butyrous consistency later becoming leathery. Uniform clouding of bouillon cultures in 36 to 48 hours. Gelatin not liquefied; starch not hydrolyzed; nitrates not reduced but slight ammonia produced in nutrient broth; hydrogen sulfide and indole not formed. Acid produced in milk. Acid but no apparent gas from arabinose, xylose, rhamnose, fructose, mannose, galactose, glucose, lactose, erythritol. Alkali but no apparent gas from melezitose, starch, inulin, pectin, lactositol, calcium gluconate, formic acid, acetic acid, propionic acid, glycollic acid, malonic acid, succinic acid, tartaric acid, malic acid, and yeast extract.

Although it also adsorbs dye, it is readily distinguished from crown gall organism when streaked on aniline-blue agar; slow-growing with minimum generation time of about 155 minutes.

Pathogenic on black and purple raspberries, blackberries, and, to much lesser extent, on red raspberry.

DISCUSSION

Cane gall has some things in common with crown gall, especially in gross symptomatalogy and in certain phases of the life history of the causal organisms. *Phytomonas rubi* is distinctly different from *P. tumefaciens* in its physiology and pathogenicity, including growth character on artificial media, a preference for complex nitrogen sources in its metabolism, and a restricted host range. These and other characteristics summarized in table 1 constitute a basis for giving it specific rank. The characteristic of motility by subpolar flagella may have significance in determining its taxonomic position, but for the present it is placed in the genus *Phytomonas*.

At present, cane gall is of minor importance in New York, thanks largely to the efficiency of the inspection service and extension work. Control measures that are adequate for crown gall are easily adequate for cane gall. One reason may be that cane gall generally occurs upon

the visible parts of the canes, which facilitates eradication; another that the cane gall organism apparently is less able than the crown gall organism to survive in soil. Obviously this latter observation needs further study. Prof. L. M. Cooley, formerly at the Geneva (N. Y.) Experiment Station, who cooperated with the writer in the field in the course of these observations on raspberry diseases, noted a progressive decline in cane gall in western New York plantings, and at the present time his successor, Dr. R. F. Suit, has infrequently encountered it in commercial plantings in areas where it was formerly present.

TABLE 1.—*Differential characteristics of the cane gall organism (Phytomonas rubi n. sp.), and the crown gall organism (P. tumefaciens)*

Differential characters	Cane gall organism	Crown gall organism
Symptoms on naturally infected plants.	Galls found at and above soil level	Galls found at and below soil level.
	Galls discolor and decompose rapidly; ordinarily unable to isolate organism after July 1.	Galls, while subject to decomposition, may persist throughout season.
	Long gall ridges or galls distributed indiscriminately on canes.	Galls generally occur individually.
	Bacteria migrate up through outer tissue of cane.	Bacteria unable to migrate up the cane in same manner.
Symptoms on artificially infected plants.	Very small galls on roots	Large galls on roots.
	Small galls below soil level on canes	Large galls at and below soil level on canes.
	Large galls above ground	Small galls above ground.
Longevity of organism in soil	Few months	1 to 3 years.
Host range	Limited genus *Rubus*	Very wide; includes many plant families.
Minimal incubation period	2½ to 3 weeks	10 days to 2 weeks.
Motility of bacteria	Motile	Doubtful motility in many cases.
Stability of bacteria in culture.	Unstable; pathogenicity frequently lost within a year.	Very stable; pathogencity retained for 10 years and longer.
Minimal generation time of bacteria.	155 minutes	78 minutes.
Growth in:		
Nutrient-dextrose broth	Weak growth, slight or no pellicle	Strong growth, heavy pellicle.
Potato-mannitol agar	Thin leathery growth with time	Abundant growth, watery to butyrous.
Nitrogen metabolism	Unable to use potassium nitrate, ammonium nitrate, ammonium sulfate, potassium nitrite, urea, dicyandiamide and acetamide.	Ammonium nitrate, ammonium sulfate, potassium nitrite, urea, dicyandiamide, and acetamide support excellent growth.
Reaction on litmus milk	Slight serum zone	Heavy serum zone.
	Pink color	Grayish brown.
	Acid	Neutral.

SUMMARY

Cane gall, a rather widely distributed but economically relatively unimportant disease of *Rubus* spp., has been investigated and a description given of its symptoms. The characteristic beading and elongate gall ridges on the above-ground canes are in marked contrast to crown gall which ordinarily occurs at or below ground level. The causal organism was readily isolated from young galls, its pathogenicity was proved, and it was studied in detail. The name proposed for the pathogen is *Phytomonas rubi* n. sp. The organism was found to be pathogenic on black raspberry, purple raspberry, blackberry, and red raspberry, but only weakly so on the last-named species upon which it rarely occurs in the field.

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