**β-Glucosidase Activity in Phytopathogenic Bacteria**

D. C. HILDEBRAND AND MILTON N. SCHROTH

Department of Plant Pathology, University of California, Berkeley, California

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**ABSTRACT**

HILDEBRAND, D. C. (University of California, Berkeley), and MILTON N. SCHROTH. β-Glucosidase activity in phytopathogenic bacteria. Appl. Microbiol. 12: 487-491. 1964.—Most of 58 isolates of phytopathogenic and related bacteria comprising 24 species in the genera Agrobacterium, Erwinia, Corynebacterium, Pseudomonas, and Xanthomonas exhibited β-glucosidase activity, especially the gall-forming pathogenic pseudomonads and soft rots organisms. The gall-forming pseudomonads and P. fluorescens exhibited no β-glucosidase activity, with the exception of one isolate of *P. savastanoi* which showed slight activity on an inorganic nitrogen-arbutin medium. The best medium for demonstrating β-glucosidase activity contained peptone as the nitrogen source and arbutin. β-Glucosidase activity in this medium was indicated by either acid production or browning. *P. syringae*, in contrast to other bacteria tested, produced most β-glucosidase in a medium containing large amounts of glucose. Chromatographic analyses confirmed that splitting of the glucoside occurred at the glucosidic linkage. Reaction of sonically treated bacterial cells with indican or 3-nitrophenyl-β-D-glucoside proved a rapid method for assaying relative amounts of β-glucosidase among bacterial species. Harda’s paper-strip method of assaying f3-glucosidase was also useful in revealing the distribution and relative amounts of β-glucosidase in most bacteria, but did not indicate the relatively greater amount of β-glucosidase in *P. syringae*.

Bacteria have long been known to ferment glucosides. However, reactions independent of fermentation also were observed. Twort (1907) reported that arbutin-containing media frequently turned brown when the cultures were old and had become alkaline. It was later assumed that this resulted from splitting of the glucoside by a β-glucosidase (Pierstorff, 1931), although it seldom was determined whether this actually had occurred. As Hofmann (1934) pointed out, the fermentation of a glucoside substrate by a microorganism does not necessarily show that cleavage had occurred at the glucosidic linkage. Likewise, the browning of arbutin-containing media does not necessarily indicate that the arbutin was split by a β-glucosidase; Hattori and Sato (1963) reported that arbutin may be oxidized in *Pyrus* sp. to brown-pigmented materials without being split by β-glucosidase.

Veibel (1950) stated that β-glucosidases were widespread in animals, higher plants, and fungi, and, in reference to Hofmann’s (1934) work, stated that they also occurred in the sulfatase bacteria. It was further stated that no systematic search for β-glucosidase activity in bacteria had been made. More recent reviews (Baumann and Pigman, 1957; Pardee, 1962) listed microorganisms as sources of β-glucosidase, but cited only work on yeasts and other fungi.

In view of this general lack of information on β-glucosidase activity in bacteria, and since high β-glucosidase activity occurs in isolates of *Pseudomonas syringae* (Schroth and Hildebrand, in press), a brief survey was made to determine the general distribution of β-glucosidase activity in phytopathogenic bacteria. Also, because of possible importance as a character for use in taxonomy, several different methods of detecting β-glucosidase activity in bacteria were tested.

**MATERIALS AND METHODS**

Bacterial isolates. Fifty-eight isolates from 24 species in five genera (*Erwinia, Pseudomonas, Agrobacterium, Corynebacterium*, and *Xanthomonas*) of phytopathogenic and related bacteria were tested for β-glucosidase activity. All isolates were maintained on potato-dextrose-peptone agar (PDPA) slants. The source and dates of isolation are given in Table 1.

**Demonstration of β-glucosidase activity.** A previous study (Schroth and Hildebrand, in press) reported that β-glucosidase activity in *P. syringae* was readily demonstrated in the mineral-yeast extract medium (RR) of Riker and Riker (1936), with a combination of glucose (1%, w/v) and arbutin (0.5%, w/v) as the carbon source. With *E. amylovora*, it was best demonstrated in the mineral-peptone medium (HL) of Hugh and Liefson (1953), with arbutin (0.5%, w/v) as the sole carbohydrate. Both media were used in these tests.

A 10-ml portion of each medium was seeded with a 24-hr-old culture of the test organism, incubated at 28 C for 24 hr, and left at room temperature for the remainder of the test period. β-Glucosidase activity was estimated after 10 days by chromatographic techniques (Hildebrand and Schroth, 1964), which measured the hydrolysis of arbutin and formation of hydroquinone. Cultures in which no arbutin breakdown or hydroquinone formation could be detected were tested again after 30 days. In addition, the color reactions which occurred in the HL medium (acid or alkaline reaction, or browning) were recorded and compared with results of the chromatograms to determine which reactions correlated with β-glucosidase activity.

**RESULTS**

**Distribution of β-glucosidase.** Most of the 60 isolates tested showed β-glucosidase activity in either the RR or...
### Table 1. β-Glucosidase activity in phytopathogenic and related bacteria, as demonstrated by chromatographic determination of arbutin breakdown and hydroquinone formation, and compared with the color reactions obtained in a typical fermentation medium

<table>
<thead>
<tr>
<th>Organism</th>
<th>Culture designationa</th>
<th>Source</th>
<th>Date isolated</th>
<th>Color reaction in HL mediumc</th>
<th>RR mediumd</th>
<th>RR medium and glucose</th>
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*Arbutin disappearance, Hydroquinone appearance.*
HL medium (Table 1). The gall-nonforming phytopathogenic pseudomonads and the soft rot group showed the highest \( \beta \)-glucosidase activity, whereas the gall-forming and soil-inhabiting pseudomonads showed no activity. Other groups of organisms generally showed moderate activity. Neither medium was superior for the determination of \( \beta \)-glucosidase activity; some bacteria produced greater activity on the RR medium, whereas others produced more on the HL medium. However, the greatest relative differences in \( \beta \)-glucosidase activity, as measured by arbutin disappearance and hydroquinone appearance, generally were noted with the RR medium.

Comparison of the developed chromatograms with color reactions in the HL medium indicated that \( \beta \)-glucosidase activity was accompanied by either an acid reaction or a browning of the medium. HL cultures remaining alkaline and showing no trace of browning were those in which no evidence of arbutin breakdown or hydroquinone formation was detected.

**Organic vs. inorganic nitrogen medium.** Since a number of carbon sources, including amino acids and carbohydrates, may repress the formation of a variety of enzymes (Paigen, 1963), including \( \beta \)-glucosidase in yeast (MacQuillan and Halvorson, 1962), the \( \beta \)-glucosidase activity of 21 previously tested isolates was compared in an inorganic nitrogen vs. an organic nitrogen medium. The inorganic medium of Ayers, Rupp, and Johnson (1919) was used, since it is commonly recommended as a basal medium for fermentation tests (Dowson, 1957). The organic medium was the same, except that 2 g of peptone were substituted for \( \text{NH}_4\text{H}_2\text{PO}_4 \). Arbutin was added to both media (0.5%, w/v) to enable the estimation of \( \beta \)-glucosidase activity and to provide a carbon source. The glucosides, amygdalin and salicin, also were tested to determine their suitability as indicators of \( \beta \)-glucosidase activity. Reactions were recorded and chromatograms were made from samples of the arbutin media after 14 days of incubation as previously described.

All isolates which had shown \( \beta \)-glucosidase activity on the HL medium also showed activity on the organic nitrogen-arbutin (ONA) medium (Table 2). No browning occurred when either salicin or amygdalin was substituted.
for arbutin. However, cultures which produced acid in the ONA medium also produced acid in the salicin and amygdalin media, with the exception of the A. rhizogenes culture in the amygdalin medium. Chromatograms made of the medium again confirmed that β-glucosidase activity was accompanied by either an acid or a browning reaction.

In the inorganic nitrogen-arbutin (INA) medium, reactions were either neutral or acid. No browning occurred during the 14 days of incubation; therefore, visual detection of β-glucosidase activity could not be made as with the ONA medium. There were no differences noted in acid production between the INA and ONA media, except for one isolate of P. savastanoi which produced a slight amount of acid on the INA medium. Reactions with amygdalin and salicin were comparable to those found in the ONA medium. Chromatograms of the INA medium generally showed that slightly more arbutin hydrolysis and hydroquinone formation had occurred than in the ONA medium.

Other β-glucosidase tests. Hardy (1962) reported a method of detecting β-glucosidase activity in bacteria by impregnating filter paper strips (5 by 30 mm) with a 0.01 M solution of p-nitrophenyl-β-D-glucoside (PNPG) and placing them on agar plates which previously had been seeded with the test organism. The time of color formation was noted as the measurement of β-glucosidase activity. This method was compared with the results of the fermentation tests previously described, and with a method in which a 5-mm loopful of bacteria from a 24-hr-old culture was placed in 3 ml of 0.01 M phosphate buffer (pH 6.5) and sonically treated for 3 min with a Bronwill-Blackstone Biosonik ultrasonic probe at 20 kc frequency. After sonic treatment, 0.5 ml of a 0.01 M solution of PNPG or indican (indoxyl-β-D-glucoside) was added to the suspension, and the reaction mixture was incubated at 35 C for up to 2 hr. The time and intensity of color formation was used as the indication of β-glucosidase activity. In four tests, the bacteria were grown on PDPA and nutrient agar (NA) for 24 hr.

With two exceptions, the results of Hardy’s (1962) paper-strip method and the sonic-treatment tests agreed with data obtained with the fermentation studies (Table 3). In fermentation studies, E. carotovora showed the greatest β-glucosidase activity of any bacterium tested; yet, little β-glucosidase was revealed by either the paper-strip or the sonic-treatment methods. P. syringae also showed high β-glucosidase activity in fermentation tests; but, in the paper strip test, the activity detected usually was lower relative to other bacteria. In the sonic-treatment tests, however, the activity remained at a high level. Detection of β-glucosidase was apparently influenced by the medium supporting growth, because β-glucosidase activity generally was greater when the organism was grown on NA.

**DISCUSSION**

The use of fermentation tests is a well-known technique used in classification. Basically, this is an enzyme survey. The end products of metabolism in these tests usually are recorded as acid or gas and alcohol. However, as Clarke (1955)

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<th>Isolate</th>
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<th>PDPA</th>
<th>Sonically treated cells Nutrient agar</th>
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</table>

†U = unreadable.
pointed out, this may be sufficient for some purposes, but often it is important to know which acid or which gas. In addition, negative results (a neutral or alkaline reaction) may be misleading. The alkaline or neutral reactions produced by isolates in the Pseudomonas and Xanthomonas groups in media containing glucosides would lead one to postulate that none of these organisms was capable of splitting the glucosides. Yet, a chromatographic analysis of the media revealed that virtually all the organisms in these groups had split arbutin at the glucosidic linkage.

It is particularly difficult to determine whether fermentation has occurred when acid-gas reactions are weak. This probably is a contributing factor leading to conflicting reports which occur on the ability of certain organisms to ferment a substance. For example, it was reported that E. amylolovora ferments (Elliott, 1951) and does not ferment (Waldee, 1945) β-glucosides. A chromatographic examination of the medium to determine whether the glucoside has been split at the glucosidic linkage avoids such difficulties. It also gives a more accurate determination of the amount of β-glucosidase activity. Pirie (1955) previously suggested that information should be obtained on the rates of production as well as on the kinds of acids and gases produced. Our studies indicate that there may be significant differences in the amounts of β-glucosidase among closely related organisms, even within a species.

In most cases, our data indicate that an organic nitrogen-arbutin medium is best for detecting β-glucosidase, since β-glucosidase activity in this medium is reflected by either acid production or browning. The other glucosides tested did not give the browning reaction, even when inorganic nitrogen was used as the nitrogen source. However, one isolate of P. savastanoi which showed no β-glucosidase activity in an organic nitrogen medium did show slight activity in an inorganic nitrogen-arbutin medium. Therefore, isolates which show no activity in an organic medium should be tested additionally in an arbutin medium with inorganic nitrogen.

The paper-strip test of Harda (1962), although generally useful in determining the distribution and relative amounts of β-glucosidase, did not detect the significantly greater amount of β-glucosidase activity occurring in P. syringae. This high β-glucosidase activity in P. syringae, however, was readily detected in the test with sonically treated bacterial cells. This proved a rapid method for detecting and obtaining an estimate of the amount of β-glucosidase activity among bacterial species. The failure of either method to reveal the capacity of E. carotovora to produce large amounts of β-glucosidase may have been due to repression of enzyme synthesis by metabolizable organic carbon sources in the culture media (NA and PDPA). PDPA contains glucose, which is an efficient repressor of β-glucosidase synthesis in yeast (MacQuillan and Halvorson, 1962). Only P. syringae consistently produced more β-glucosidase in the presence of large amounts of glucose.

**Literature Cited**


Baumann, H., and W. Pigan. 1957. Naturally occurring glyco-


