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Susceptibility of Bacillus anthracis to Gamma and Cherry bacteriophage

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SUSCEPTIBILITY OF \textit{Bacillus anthracis} TO GAMMA AND CHERRY BACTERIOPHAGE

A Thesis
Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in Partial Fulfillment of the Requirements for the Degree of Master of Science
in
Veterinary Medical Science
Through the The Department of Pathobiological Sciences

By
Preston A. Fulmer
B.S., University of Arkansas, 2000
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ABSTRACT

*Bacillus anthracis* is a bacterium that causes severe disease mainly in ruminants, but can affect any mammal, including humans. A popular method for the detection of this organism is susceptibility of the bacterial isolate to $\gamma$ bacteriophage. However, to date no study on the resistance of a wide variety of *B. anthracis* isolates has been conducted. The following study examines the rate of resistance of a wide range of *B. anthracis* isolates to $\gamma$ phage as well as another phage specific for *B. anthracis* known as Cherry phage. We also compared susceptibility to phage with another detection method, susceptibility to penicillin, to determine any association between the two. The origin of the resistant isolates was examined to determine associations between resistance and isolate origin. Finally, the gross structure and resistant rates of the two phages were compared to determine any relation between the two viruses. We found that *B. anthracis* showed 20% resistance to $\gamma$ phage, which we propose is too high to continue its use as a reliable diagnostic tool. No association was found between resistance to penicillin and resistance to phage. No association was found between isolate origin and resistance. No conclusions could be drawn as to the relationship between the two phages.
CHAPTER 1
INTRODUCTION

*Bacillus anthracis* is a bacterium that causes severe disease mainly in ruminants, but can affect any mammal, including humans. A popular method for the detection of this organism is susceptibility of the bacterial isolate to Gamma bacteriophage. Currently there are two bacteriophages specific for *B. anthracis* at Louisiana State University: Gamma phage and Cherry phage. Susceptibility to Gamma phage is a recommended identification method for *B. anthracis*. There are many *B. anthracis* isolates available for testing. These isolates have been grouped into 89 genotypes. This thesis examines the rate of resistance of a wide range of *B. anthracis* isolates to Gamma phage as well as another phage specific for *B. anthracis* known as Cherry phage. We also compared susceptibility to phage with another detection method, susceptibility to penicillin, to determine any association between resistance to bacteriophage and resistance to penicillin. The origin of the resistant isolates was examined to determine association between resistance and isolate origin. Finally, the gross structure and resistant rates of the two phages were compared to determine any relation between the two viruses. The hypotheses of this thesis are: there will be resistance among the tested *B. anthracis* isolates to bacteriophage, there will be an association between resistance to bacteriophage and resistance to penicillin, and there will be an association between isolate origin and resistance to bacteriophage.
CHAPTER 2
GENOTYPE RESULTS

INTRODUCTION

*Bacillus anthracis* is a bacterium that causes severe disease mainly in ruminants, but can affect any mammal, including humans. A popular method for the detection of this organism is susceptibility of the bacterial isolate to Gamma bacteriophage. This study examines the rate of resistance of a wide range of *B. anthracis* isolates to Gamma phage as well as another phage specific for *B. anthracis* known as Cherry phage. We also compared susceptibility to phage with another detection method, susceptibility to penicillin, to determine any association between the two. The origin of the resistant isolates was examined to determine any association between bacteriophage resistance and isolate origin. Finally, the gross structure and number of isolates differentially resistant to the two phages were compared to determine any relation between the two viruses. 89 genetically diverse isolates were used as determined by multiple locus variable number tandem repeat analysis (MLVA). We suggest that when the phage is tested over isolates from all 89 genotypes, there will be resistant isolates, and that the number of resistant isolates will be too high to continue the use of bacteriophage as a reliable diagnostic tool. We also hypothesize that Gamma phage is a separate and distinct virus from Cherry phage. This will be determined by comparing the resistance rates of the two viruses as well as transmission electron micrographs of the two viruses.

LITERATURE REVIEW

*Bacillus anthracis* is a Gram-positive rod-shaped bacterium. It possesses a polysaccharide capsule in its vegetative state, which is necessary for virulence. The bacterium is capable of forming an endospore in conditions that are unfavorable for its growth. This spore form is very resistant to a variety of environmental conditions, including extreme temperature,
extreme pH, desiccation, and UV radiation\textsuperscript{19}. If conditions once again become favorable for
growth of the vegetative form of the bacteria, the spore will germinate and begin to grow and
divide normally\textsuperscript{19}.

\textit{B. anthracis} causes a disease commonly referred to as anthrax. Due to the resilience of
the endospore form of the organism, it is most commonly the form that is the initial cause of
disease\textsuperscript{19}. \textit{B. anthracis} can cause three types of infections: cutaneous, gastrointestinal, and
inhalational. The most common and least dangerous type is cutaneous infection. This occurs
when the organism invades the skin, usually via a cut or abrasion. With treatment, this form has
a mortality rate of less than 1\%\textsuperscript{19}. The second form is the gastrointestinal form. This form is
often seen in carnivores as it is contacted through eating infected meat or drinking contaminated
water. The third and most dangerous form of the disease is inhalation anthrax. This form of the
disease is contracted through the inhalation of \textit{B. anthracis} spores. In this form the spores
germinate and the bacteria subsequently colonize the mediastinal lymph nodes of the animal\textsuperscript{19}. It
may then spread to the meninges or other organ systems. This form is almost invariably fatal,
with a near 100\% mortality rate if not treated within 24-48 hours of contact\textsuperscript{19}. Anthrax is most
often seen in ruminants; however, the bacteria can infect many other species, including humans.
Nearly all human infections occur through direct or indirect contact with infected animals\textsuperscript{19}.
While it is true that most human infections are due to contact with infected animals, there are
other means by which humans may become infected, the most notable of which, especially
recently, is bioterrorism. The endospore form of \textit{B. anthracis} has been developed as a biological
weapon for many years\textsuperscript{19}. This form of the organism makes an ideal weapon for several reasons:
its resilience and longevity in the environment, the ease by which it is spread through the air, and
the high mortality rate that occurs as a result of contact with the organism. Its ease of use as a
biological weapon was recently demonstrated during the anthrax attacks which occurred in
September and October of 2001 in which anthrax spores were sent in envelopes through the mail. These attacks led to 22 infections and five deaths from inhalation anthrax.

The pathogenesis of \textit{B. anthracis} is regulated by two plasmids found in the organism: pXO1 and pXO2. pXO1 encodes three toxins that are responsible for the majority of pathology caused by \textit{B. anthracis}, designated Protective Antigen (PA), Lethal Factor (LF), and Edema Factor (EF)\textsuperscript{19}. Protective Antigen derives its name from the fact that it is the major, and thus “protective” component of the human anthrax vaccine. In the disease process, PA binds to a receptor on the cell surface and then is cleaved by a host protease. This cleavage exposes a receptor on the PA, which causes a competition between LF and EF for the receptor. Once bound, the PA-LF/EF complex is internalized and the LF/EF is released into the cytosol of the cell. EF causes the production of abnormal amounts of cyclic-AMP (cAMP), which in turn causes the leakage of water and ions from the affected cell\textsuperscript{19}. This causes edema and is the source for the factor’s name. LF is an aminopeptidase that cleaves a protein kinase involved in a pathway responsible for regulating cell growth, thereby causing a disruption of the pathway. However, the exact mechanism of the pathway disruption is not fully understood at this time. This leads to the death of the cell, thus the name “lethal factor”. It is known, at least in tissue culture models, that a major target for LF is macrophages. When LF affects macrophages, they release large amounts of the pro-inflammatory cytokines tumor necrosis factor alpha (TNF-\(\alpha\)) and interleukin-1 (IL-1)\textsuperscript{19}. A major cause of death due to \textit{B. anthracis} infection is thought to be a shock-type mechanism due to the release of large amounts of these cytokines\textsuperscript{19}. The pXO2 plasmid contributes to pathogenicity by encoding for a poly-D-glutamic acid capsule necessary for the organism’s pathogenesis. The capsule’s role is primarily to serve as protection from phagocytosis by the host immune system\textsuperscript{19}. 
*B. anthracis* is an extremely genetically homogenous pathogen. This makes distinguishing between separate strains extremely difficult. Recently, a technique was developed to aid in this process. Multiple-Locus Variable-Number Tandem Repeat analysis (MLVA) uses 8 different loci (6 genomic loci and one on each of the plasmids pXO1 and pXO2) to differentiate between isolates\(^7\). This process determines the number of tandem repeats at each of these loci and uses that information to separate isolates into distinct genotypes. The original study used 426 isolates and separated them into 89 distinct genotypes\(^7\).

Several bacteriophages that are known to lyse *B. anthracis* have been described. W phage was known as early as 1955\(^1,2,11\). A phage known as AP-50 was isolated from *B. cereus* and found to lyse *B. anthracis*\(^14,13,15\). There is little detailed information regarding AP-50 and W phage. Most of the work was done in the 1950’s and 1960’s and thus there was little molecular work done. The phages are similar in shape having an icosahedral head and long tail\(^14\). Another bacteriophage that lysed *B. anthracis*, known as Gamma phage, was first described in 1955\(^1\). The phage was tested against 41 isolates of *B. anthracis* acquired from health labs from various states. It was also tested against 223 isolates from several other members of the *Bacillus* family, including *B. cereus, B. subtilis,* and *B. megatarium*. In the study, Gamma phage was found to lyse all 41 of the *B. anthracis* isolates. However, the phage lysed none of the isolates belonging to the other *Bacillus* species. Due to these results, susceptibility to Gamma phage was proposed as a method to identify *B. anthracis*\(^1\). Gamma phage, along with W phage, was also shown to induce motility and capsule production in non-motile unencapsulated *B. anthracis* strains\(^2\). However, the mechanism for this induction is not known.

No further work was done with Gamma phage until the mid to late seventies when a group of researchers at Mie University School of Medicine in Japan published a series of papers that further described the molecular structure of the bacteriophage\(^21,22\). In 1975, the structure of
the virion was determined by negative staining and electron microscopy. The phage was found to have an icosahedral head and a long, non-sheathed tail. The head was 52 nm wide, and the tail was 185 nm long with a width of 9.5 nm\textsuperscript{22}. At this time, the phage particle was found to consist of 10 separate proteins, four of which were found to be structural proteins from the icosahedral head\textsuperscript{22}. Another study by the same group found that the receptor site for Gamma phage attachment to the cell was a combination of D-glucosamine and L-diaminopimelic acid. This was done by incubating Gamma phage with various cell wall fractionations and determining which inhibited cell wall attachment. The exact components of these fractionations were determined by paper chromatography, and the components were each incubated separately with Gamma phage\textsuperscript{21}.

Due to the ability of Gamma phage to lyse \textit{B. anthracis}, recent studies have attempted to determine whether or not the phage contains a protein which could be of some therapeutic use in \textit{B. anthracis} infections. One such study focused on a protein known as Phage lysine Gamma, or Ply G. The gene that encodes this protein contains a 702 base pair open reading frame (ORF) that is homologous to \textit{N}-acetyl\textit{L}

These lysins are known to hydrolyze the covalently bound cross-links present between the subunits of peptidoglycan, which are necessary to maintain the structural stability of the cell wall. Purified Ply G was shown to lyse \textit{B. anthracis in vitro}. To determine the presence of any therapeutic effect, Ply G was given to mice that were given a lethal dose of \textit{B. anthracis} intraperitoneally. The Ply G was administered 15 minutes after the \textit{B. anthracis}. Control animals died within 5 hours. However, of the mice given Ply G, 68\% fully recovered, with the remainder surviving for 6-21 hours\textsuperscript{16}. Mutagenesis studies were then conducted to determine the likelihood that resistance to Ply G would develop. This was done by exposing \textit{B. anthracis} to methanesulphonic acid ethyl ester (EMS). This approach provided no Ply G resistant mutants.
However, by comparison, exposure to EMS resulted in a 1000-fold increase in novobiocin resistance and a 10,000-fold increase in streptomycin resistance. It was also shown that strains of \textit{B. anthracis} that were resistant to lysis by Gamma phage were indeed sensitive to Ply G\textsuperscript{16}.

Despite previous studies, there is still much to be learned about this phage. Very little is known about the genome, other than the fact that it is dsDNA. Its size, number and location of ORFs, and sequence remain to be determined. Also, very little is known about the number and function of structural and non-structural proteins. While the number of proteins present in the mature virion has been previously determined, the structure and function of these proteins is not known\textsuperscript{22}.

Several different phages have been proposed as diagnostic tools\textsuperscript{1,8,18}. Due to its ability to lyse \textit{B. anthracis}, Gamma phage is suggested as a diagnostic tool for the identification of \textit{B. anthracis} as outlined by the World Health Organization (WHO)\textsuperscript{19}. The complete identification process is outlined in the WHO \textit{Guidelines for the Surveillance and Control of Anthrax in Humans and Animals}\textsuperscript{19}. While the use of Gamma phage as a sole means of identification and detection is not suggested, it is often used as a definitive diagnostic tool due to its ease of use.

Another commonly used diagnostic tool for the detection of \textit{B. anthracis} is sensitivity to penicillin\textsuperscript{19}. Several studies have been conducted regarding the antimicrobial susceptibility of \textit{B. anthracis} \textsuperscript{5,6,9,12}. However, none of these studies examined the susceptibility of such a wide range of genetically diverse isolates as presented in this thesis. Penicillin acts on the cell wall of \textit{B. anthracis} and other bacteria by inhibiting the cross-liking of the peptidoglycan amino-acid side chains\textsuperscript{17}. This causes the formation of an unstable cell wall, and eventual lysis of the bacterium. Resistance of \textit{B. anthracis} to penicillin is likely due to the production of Beta-lactamases\textsuperscript{4}. 
Lysogeny is a process by which a bacteriophage may form a prophage and go “latent” in a bacterium\textsuperscript{10}. Lysogeny studies have been conducted on W and AP50 phage, and lysogeny is known to occur with some of the phages\textsuperscript{3,6,20}. However, no lysogeny studies have been conducted on Gamma phage.

Cherry phage was obtained from Brooks Air Force Base (San Antonio, Texas). A literature search regarding Cherry phage was performed, but no publications could be found. It is possible that the phage was first isolated at the base, or perhaps it is simply Gamma phage that received the name Cherry at some point due to one of Gamma phages original co-discoverers.

**MATERIALS AND METHODS**

**Phage Propagation**

The phages were propagated using *B. anthracis* strain Vollum. A “lawn” of bacteria was prepared on TSA Sheep Blood agar (Remel, Kansas) by swabbing an entire plate. Add 25 µL of bacteriophage to the plate. Spread the virus on the plate using a plate spreader and incubate the plate at 37°C for 24 hours. Add 5 mL nutrient broth to the plate, and scrape the plate to loosen the bacterial growth from the plate. Remove the nutrient broth and bacterial growth from the plate using a pipettor, and add to a 50 mL polyethylene centrifuge tube containing another 5 mL of broth. Incubate the tube at 37°C for 24 hours. After incubation, remove the tube from the incubator and add 2% by volume of 24:1 chloroform:isoamyl alcohol in a fume hood and shake tube for 15 minutes. This lyses any remaining bacteria in the tube. Remove the tube from the shaker, and filter the liquid through a .22 µm filter by vacuum filtration. Serial dilution and plaque counts were used to determine the viral titer produced. Using this method, each plate produces 10mL of bacteriophage with a titer of $10^6 - 10^8$ pfu/mL. This procedure was repeated and multiplied producing 50 mL of Gamma phage at a titer of $1.04 \times 10^8$ pfu/mL and 50mL of cherry phage at a titer of $2.080 \times 10^7$ pfu/mL. The phages were diluted out to a 1:10 dilution of
Gamma phage and a 1:2 dilution of cherry phage so that the titers of the phages would be approximately the same titer at $1 \times 10^7$ pfu/mL.

**Phage DNA Isolation**

The DNA extraction procedure was modified from a Qiagen© $\lambda$ DNA extraction kit (Qiagen, Germany). The kit was originally used to attempt DNA extraction from both phages. The $\lambda$ kit was chosen because Gamma and cherry phages were thought to have a large genome, around 40kb, which is similar in size to that of $\lambda$ phage which is ~46kb. However, the Gamma and cherry phage DNA failed to bind to the column provided with the kit. Therefore, the procedure that was used was modified from the Qiagen procedure. To 50 mL of $10^6$ pfu/mL as prepared above, add 100 $\mu$L of 6 mg/mL DNase I and 20 mg/mL RNase A and incubate the mixture at 37ºC for 30 minutes. This step digests any free cellular DNA and RNA that is present. Add 10 mL of ice-cold 30% polyethylene glycol (PEG 6000) in 3 M NaCl and incubate on ice for one hour. Centrifuge (Beckman Avanti J-25) at 4ºC and 11,000 x g for 10 minutes to pellet the phage. Discard supernatant. Resuspend the phage pellet in 3 mL of buffer (10 mM NaCl; 100 mM Tris-Cl, ph 7.5; 25 mM EDTA). Add 3 mL of 4% sodium dodecyl sulfate (SDS) and incubate at 70ºC for 20 minutes. Add 3 mL of 3 M potassium acetate was added, and the mixture was centrifuged at 4ºC for 30 minutes at 16,000 x g. Transfer the supernatant to a fresh tube, centrifuge again for 10 minutes at 16,000 x g and transfer the supernatant again to a fresh tube. Add 9 mL each 5 M NaCl and 100% isopropyl alcohol and place in a -20ºC freezer overnight. A cloudy precipitate is apparent at this point. Centrifuge the tube at 4ºC for 10 minutes at 5000 x g, and pour off the supernatant. Wash the DNA pellet twice by adding 500 $\mu$L of 90% ethanol and centrifuging for 5 minutes at 3000 x g. Resuspend the pellet in 100 $\mu$L 1X
TE buffer. Extracted DNA was sent to The Institute for Genomic Research (TIGR) (Rockville, Maryland) for sequencing.

**Isolate Testing**

**Phage Susceptibility**

The procedure for testing the 89 genotypes is as follows: To a lawn of the isolate to be tested place 5 µL (~5.2 x 10⁴ pfu) of Gamma phage in the upper right quadrant of the plate, and place 5 µL of cherry phage in the lower right quadrant of the plate. Place the penicillin G E-Test strip over the left half of the plate (Figure 1).

![Figure 1: Plate Setup for testing of the 89 genotypes.](image)

Incubate the plates for 18 hours at 37°C and read. Phage susceptibility is determined by the presence or absence of a clear zone at the spot of application of phage. Nine controls were run to test for specificity of Gamma and cherry phage to *B. anthracis*. All controls were other...
members of the *Bacillus* genus. Two *B. cereus*, 4 *B. megatarium*, 1 *B. subtilus*, and 2 *B. thuringensis* were used.

**Penicillin Susceptibility**

The penicillin G MIC of each isolate is determined per the manufacturer’s instructions (ellipse of growth.) Susceptibility to penicillin is defined using the Staphlococcal breakpoint as described previously⁵. Susceptibility is defined as an MIC of ≤0.12 µg/mL, and resistance is defined as an MIC of ≥0.25 µg/mL.

**Electron Microscopy**

100 µL of Gamma and Cherry phage were provided to the Electron Microscopy Laboratory at LSU School of Veterinary Medicine. The phage was negatively stained and viewed by Zeiss EM-10C transmission electron microscope.

**RESULTS**

**Phage Susceptibility of the Set of 89 Genotypes**

Table 1 gives a summary of results for the 89 genotypes. Complete results are presented in Appendix A.

<table>
<thead>
<tr>
<th>Cherry Phage</th>
<th>Susceptible (S)</th>
<th>Gamma phage Resistant (R)</th>
<th>Total (T)</th>
</tr>
</thead>
<tbody>
<tr>
<td>T</td>
<td>71 (80%)</td>
<td>1</td>
<td>72</td>
</tr>
<tr>
<td>R</td>
<td>1</td>
<td>16 (18%)</td>
<td>17</td>
</tr>
<tr>
<td>S</td>
<td>72</td>
<td>17</td>
<td>89</td>
</tr>
</tbody>
</table>

Of the 89 genotypes, 18 (20%) showed resistance to either Gamma or Cherry phage. 16 of these were resistant to both, while one genotype (GT 34) was resistant to Gamma phage only and
one (GT 61) was resistant to Cherry phage only. All control isolates (*B. cereus, B. megatarium, B. subtilis, and B. thuringensis*) were resistant to both phages.

**Penicillin Susceptibility of the Set of 89 Genotypes**

Penicillin susceptibility is another diagnostic tool used for the detection of *B. anthracis*.\(^{19}\)

Susceptibility to penicillin was determined to compare two separate methods of *B. anthracis* detection. Table 2 gives a summary of the penicillin resistance. MIC is given as µg/mL.

Table 2: Summary of penicillin resistance for the 89 genotypes. MIC is given as µg/mL. Resistance is as follows:  A susceptible to both phages, B Resistant to both phages, C resistant to Gamma phage only, D resistant to Cherry phage only, T is total.

<table>
<thead>
<tr>
<th>MIC</th>
<th>0.19</th>
<th>0.25 ≤1</th>
<th>1</th>
<th>1.5</th>
<th>≥2</th>
</tr>
</thead>
<tbody>
<tr>
<td>40</td>
<td>20</td>
<td>5</td>
<td>1</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>55</td>
<td>21</td>
<td>7</td>
<td>1</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>

21 of 89 (23.6%) genotypes were resistant (MIC ≥0.25) to penicillin. 4 of 89 (4.5%) genotypes were resistant to penicillin and phage. Neither of the differentially resistant genotypes was resistant to penicillin. There was no significant difference between the mean MIC of the resistant and susceptible isolates.

**Isolate Origin**

The origin of the phage resistant isolates was examined to determine any association between isolate origin and resistance to bacteriophage. This is summarized in Table 3 and Figure 2.
Table 3: Origin of resistant genotypes.

<table>
<thead>
<tr>
<th>Country of Origin</th>
<th>Genotypes</th>
<th>Number of Resistant Isolates</th>
</tr>
</thead>
<tbody>
<tr>
<td>China</td>
<td>14, 57, 59</td>
<td>3</td>
</tr>
<tr>
<td>Germany</td>
<td>60, 61</td>
<td>2</td>
</tr>
<tr>
<td>Indonesia</td>
<td>31, 63</td>
<td>2</td>
</tr>
<tr>
<td>Namibia</td>
<td>39, 56</td>
<td>2</td>
</tr>
<tr>
<td>Pakistan</td>
<td>29, 74</td>
<td>2</td>
</tr>
<tr>
<td>Turkey</td>
<td>11, 33</td>
<td>2</td>
</tr>
<tr>
<td>South Korea</td>
<td>34</td>
<td>1</td>
</tr>
<tr>
<td>Switzerland</td>
<td>75</td>
<td>1</td>
</tr>
<tr>
<td>United Kingdom</td>
<td>22</td>
<td>1</td>
</tr>
<tr>
<td>United States</td>
<td>25</td>
<td>1</td>
</tr>
<tr>
<td>Zimbabwe</td>
<td>32</td>
<td>1</td>
</tr>
</tbody>
</table>

Figure 2: Worldwide distribution of resistant genotype origin.
The resistant genotypes show a worldwide distribution, but no association between origin and resistance.

**Comparison of Phages**

The morphology and number of isolates resistant of Gamma and Cherry phage were examined to determine if there were differences between the viruses. Transmission electron micrographs of Gamma phage (Fig 3a) and cherry phage (Fig 3b) showed similar morphology—an icosahedral head with a long tail. Table 4 gives the differentially resistant genotypes.

![Figure 3a: EM of Gamma phage](image1.png)

![Figure 3b: EM of Cherry phage](image2.png)

Table 4: Differentially resistant genotypes.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Gamma phage</th>
<th>Cherry phage</th>
<th>Country of Origin</th>
</tr>
</thead>
<tbody>
<tr>
<td>61</td>
<td>S</td>
<td>R</td>
<td>Germany</td>
</tr>
<tr>
<td>34</td>
<td>R</td>
<td>S</td>
<td>South Korea</td>
</tr>
</tbody>
</table>
Only 2 of 89 (2.2%) genotypes were differentially resistant to Gamma and Cherry phage. This almost negligible difference in the number of resistant isolates seems to indicate very little difference between the two phages. However, it is not conclusive.

**DISCUSSION**

Resistance to bacteriophage is probably to be receptor mediated. Resistant genotypes probably have a mutation in one or both of the two molecules that make up the receptor for the phage. 18 of 89 (20%) genotypes were found to be resistant to bacteriophage. This is a high rate of resistance for use as a definitive diagnostic tool. Diagnostic labs commonly discard isolates that are found to be resistant to bacteriophage, believing that resistant isolates are not *B. anthracis*. The fact that resistant isolates are commonly discarded leads one to believe that perhaps the population is biased in that many isolates which are indeed *B. anthracis* were discarded due to the fact that they were resistant to bacteriophage. If this is so, then the rate of resistance reported here is lower than the true rate of resistance to bacteriophage. Whether this is the case or not, the resistance rate is at least 20%, which is a significant number due to the fact that no resistance has previously been reported. This high rate of resistance precludes the use of bacteriophage as a sole diagnostic tool, and its use should be restricted to use in conjunction with more reliable diagnostic tests, such as PCR.

Upon examination, there was no association found between penicillin resistance and bacteriophage resistance. 21 of 89 (23.6%) genotypes were resistant (MIC ≥0.25) to penicillin. 4 of 89 (4.5%) genotypes were resistant to penicillin and phage. There was no significant difference observed in the mean MIC of resistant vs. susceptible isolates.

There was no association between the origin of a genotype and its resistance to bacteriophage. The resistant isolates showed a worldwide distribution, but no association between origin and resistance was seen.
This study did not give definitive evidence as to whether or not Gamma and Cherry phage are the same virus or not. The electron micrographs showed no gross differences between the viruses, however there was a very slight difference in the resistance rates of \textit{B. anthracis} to the two phages. It is possible that the two phages are actually slightly different strains of the same virus. The sequencing data may clarify this situation.
CHAPTER 3
SET RESULTS

INTRODUCTION

The results for the entire set of isolates tested are reported in this chapter. Unlike the 89 genotypes presented in the previous chapter, the results presented in this chapter do not reflect a genetically diverse population. Due to the isolate collection procedure, many isolates from a single outbreak may be collected. This results in many isolates that are presumed to be identical because they came from the same outbreak.

MATERIALS AND METHODS

The materials and methods used to generate the data reported in this chapter are the same as those used in the previous chapter with one exception. The entire set of isolates was not screened for susceptibility to penicillin G. All other methods were performed exactly as described above.

PHAGE RESISTANCE

Table 5 gives a summary of results for the entire of the set of tested isolates. Complete results for the entire set of isolates is given in Appendix B.

Table 5: Summary of resistance results for the entire set. S is sensitive, R is resistant, T is total.

<table>
<thead>
<tr>
<th>Gamma Phage</th>
<th>Sensitive (S)</th>
<th>Resistant (R)</th>
<th>Total (T)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cherry Phage</td>
<td>908 (90.4%)</td>
<td>6 (0.6%)</td>
<td>914</td>
</tr>
<tr>
<td>T</td>
<td>2 (0.2%)</td>
<td>88 (8.8%)</td>
<td>90</td>
</tr>
<tr>
<td>R</td>
<td>910</td>
<td>94</td>
<td>1004</td>
</tr>
</tbody>
</table>
96 of 1004 (9.6%) of isolates were resistant to at least one phage. 6 of 1004 (0.6%) were resistant to Gamma phage only and 2 of 1004 (0.2%) were resistant to Cherry phage only.

**ISOLATE ORIGIN**

The origin of the resistant isolates was examined. The data for the entire set of tested isolates is presented in Table 6. The worldwide distribution of the resistant isolates is represented in Figure 4.

Table 6: Origin of resistant isolates for the entire set of tested isolates.

<table>
<thead>
<tr>
<th>Country of Origin</th>
<th>Total Isolates</th>
<th>Genotypes</th>
<th>Number of Resistant Isolates</th>
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<tr>
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<td>14, 57, 59</td>
<td>16</td>
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<td>42</td>
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<td>Canada</td>
<td>139</td>
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<td>Italy</td>
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<td>7</td>
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<td>Australia</td>
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<td>5</td>
</tr>
<tr>
<td>Argentina</td>
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<td>4</td>
</tr>
<tr>
<td>Namibia</td>
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<td>39, 56</td>
<td>4</td>
</tr>
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<td>Zimbabwe</td>
<td>13</td>
<td>32</td>
<td>4</td>
</tr>
<tr>
<td>Albania</td>
<td>7</td>
<td></td>
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</tr>
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<td>11, 33</td>
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</tr>
<tr>
<td>Germany</td>
<td>16</td>
<td>60, 61</td>
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</tr>
<tr>
<td>Poland</td>
<td>11</td>
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</tr>
<tr>
<td>South Africa</td>
<td>70</td>
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Table Con’d
<table>
<thead>
<tr>
<th>Country</th>
<th>Count</th>
<th>Total</th>
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<td>1</td>
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<td>Mozambique</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>Nepal</td>
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</tr>
<tr>
<td>Portugal</td>
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<td>1</td>
</tr>
<tr>
<td>Republic of Congo</td>
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<td>Saudi Arabia</td>
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<td>Spain</td>
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<td>South Korea</td>
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<tr>
<td>Switzerland</td>
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<td>75</td>
</tr>
<tr>
<td>Thailand</td>
<td>6</td>
<td>1</td>
</tr>
</tbody>
</table>
The distribution of the resistant isolates is worldwide, as is the genotype distribution. There is no association between resistance and isolate origin. Next the regionality of the isolates was examined to determine if certain regions contained a higher percentage of resistant isolates. This data is presented in table 7.

Table 7: Regional resistance to Gamma and Cherry bacteriophage.

<table>
<thead>
<tr>
<th>Country of Origin</th>
<th>Isolates Tested</th>
<th>Resistant to Phage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Africa</td>
<td>165</td>
<td>16 (9.7%)</td>
</tr>
<tr>
<td>Asia</td>
<td>301</td>
<td>30 (9.9%)</td>
</tr>
<tr>
<td>Australia</td>
<td>41</td>
<td>6 (14.6%)</td>
</tr>
<tr>
<td>Europe</td>
<td>217</td>
<td>28 (12.9%)</td>
</tr>
<tr>
<td>North America</td>
<td>308</td>
<td>12 (3.9%)</td>
</tr>
<tr>
<td>South America</td>
<td>38</td>
<td>4 (10.5%)</td>
</tr>
</tbody>
</table>
For the most part, the regional resistance rates are comparable to the worldwide resistance rates. However there is one notable exception in North America. The resistance rate in North America is less than half that of the rest of the world, suggesting that North American isolates are less likely to be resistant to bacteriophage than isolates from the rest of the world. The North American resistance rate (3.9%) is significantly different than that of the entire world (9.4%) by binomial comparison with p<.01. No other regional resistance rates were significantly different from that of the entire world.

**DISCUSSION**

96 of 1004 (9.6%) of isolates were resistant to at least one phage. 6 of 1004 (0.6%) were resistant to Gamma phage only and 2 of 1004 (0.2%) were resistant to Cherry phage only. This is approximately half the resistance rate found among the genotypes. One theory as to the reason that there is a higher percentage of resistant isolates in the genotype group is the method of isolate collection. The 89 genotypes represent a genetically diverse population, with one representative from each genetic group. The full test set is not genetically diverse. This is due to the manner in which isolates are collected. The full set can contain many isolates from the same outbreak. This means that all of these isolates are presumably the identical.
CHAPTER 4

CONCLUSIONS AND FURTHER STUDY

Many conclusions can be drawn from the information gathered in this study. First, the resistance rate of *B. anthracis* to bacteriophage is 10-20%. We propose that this is too high a rate of resistance to be too high for use as a sole diagnostic method. Second, there is no association between the two common diagnostic tools studied here: susceptibility to penicillin and susceptibility to bacteriophage. Third, there is no association between resistance to bacteriophage and isolate origin. However, no definitive conclusion can be drawn as to whether or not Gamma and Cherry phage are the same virus.

Areas of further study include further elucidation of the bacteriophage resistance mechanism employed by *B. anthracis*. Resistance may be due to mutations in the cell wall receptor that the phage uses to gain entry into the bacteria, however there is no data to support this. Also, further study on the differences and similarities between the two phages should be conducted. The sequencing data, which is currently being analyzed, may give further information as to whether the phages are indeed different, different strains of the same virus, or simply the same virus. There are many possibilities regarding whether or not Gamma and Cherry phage are different viruses. The origin of Cherry virus remains somewhat of a mystery. If the viruses are found to be the same virus, it is possible that Gamma phage became Cherry phage at some point due to the name of it’s co-discoverer.
REFERENCES


20. Vera T. Lysogeny and virulence in *Bacillus anthracis*. Texas Agricultural and Mechanical University, thesis. 1966.


Complete Results for 89 genotypes. S= susceptible, R=resistant. Penicillin G is reported in µg/mL.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Gamma phage</th>
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<th>Penicillin G</th>
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<td>1</td>
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<td>S</td>
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<tr>
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</tr>
</tbody>
</table>
APPENDIX B

ENTIRE SET RESULTS

Complete Results for the entire set of tested isolates.  S=susceptible, R=resistant, NA=not available for testing, GT=genotype (given in appendix A.)

<table>
<thead>
<tr>
<th>Isolate Number</th>
<th>Gamma Phage</th>
<th>Cherry Phage</th>
</tr>
</thead>
<tbody>
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<td>GT</td>
<td>GT</td>
</tr>
<tr>
<td>2</td>
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VITA

Preston Fulmer was born in Little Rock, Arkansas, on June 27, 1979, to Wayne and Paula Fulmer. He has a younger brother, Paul. Preston grew up in the small rural town of Des Arc and graduated as Valedictorian of Des Arc High School in 1997. That fall he enrolled at the University of Arkansas. Preston graduated with a Bachelor of Science Degree in microbiology from the University of Arkansas in December 2000. Later that same month he married Amanda Beck, who was a second year veterinary medicine student at Louisiana State University at the time. Preston moved to Baton Rouge and became employed as a laboratory technician at Kleinpeter Farms Dairy, Inc. where he worked for nine months. In August 2001, Preston enrolled in graduate school at Louisiana State University. He began working with Dr. Pamala R. Coker and Dr. Martin Hugh-Jones in the Special Pathogens Laboratory, and it was there that he conducted the research reported in this thesis. Preston graduated from Louisiana State University in May 2003 with a Master of Science Degree from the School of Veterinary Medical Sciences.