THE HOSTS OF GYMNOSPORANGIUM GLOBOSUM FARL. AND THEIR RELATIVE SUSCEPTIBILITY

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With plates 125 to 128 and four text-figures

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I. INTRODUCTION

GYMNOSPORANGIUM GLOBOSUM Farl., a heteroecious rust, is restricted in its telial phase to a limited number of species and varieties of *Juniperus*. To the aecial phase, however, representatives of at least ten genera within the Pomoideae may serve as hosts; and certain of these genera, especially *Crataegus*, include a large number of species and varieties.

In spite of the number of hosts hitherto reported for G. globosum, very little information is available regarding the relative susceptibility of the hosts. This is a question of considerable importance because of the great damage done by the rust. A determination of the immune species and the comparative resistance of susceptible species within the various relevant host genera constitute the major part of this paper.

Concurrently with the investigations which led to a determination of the relative susceptibility of the hosts, the writer was enabled to compile a more nearly complete list of the known hosts, from which it appears that, instead of the approximately one hundred hosts hitherto reported, the number of hosts should be conservatively estimated at more than six hundred. This list constitutes the latter portion of the paper.

The work on the problems outlined above has been carried on at the Arnold Arboretum of Harvard University, where may be found one of the finest collections in the world of living representatives of species and varieties of *Juniperus* and of the Pomoideae.

II. RELATIVE SUSCEPTIBILITY OF HOSTS WITHIN GENERA OF THE POMOIDEAE

HISTORY

The earliest successful attempt to determine pomaceous hosts of G. globosum Farl. by means of cultures may be credited to Farlow (1880) who, in 1876-7, using teliospores from Juniperus virginiana, obtained spermogonia on Crataegus tomentosa. Farlow (1885) also made successful cultures on leaves of Crataegus Douglasii, Crataegus Oxyacantha

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and apple seedlings; but he obtained spermogonia only, because his experimental leaves molded before the aecial stage could develop. Thaxter (1887) obtained spermogonia on *Crataegus coccinea, Malus pumila, Sorbus americana*, and *Amelanchier canadensis;* and in 1887–8 (Thaxter, 1889) obtained spermogonia on *Sorbus americana* and *Cydonia oblonga* (= *Cydonia vulgaris*), and both spermogonia and aecia on *Crataegus coccinea* and *Malus pumila*. In a later report Thaxter (1891) confirmed the previous results on *Malus pumila* and records successful infections of *Crataegus crus-galli* and *Sorbus americana*, both resulting in aecial development. In 1906, cultures were made by Arthur (1907) on *Crataegus Pringlei* and *Sorbus americana* resulting in spermogonia and aecia, and on *Malus coronaria* giving spermogonia only. In 1908 Arthur (1909) confirmed his results on *Crataegus Pringlei*, and in 1909 (Arthur, 1910) those of Farlow on *Crataegus coccinea*.

Since Arthur's work more than one hundred suscepts have been added to the host list, mostly by observations made in the field. Authors who have contributed or made significant reference to this list include Clinton (1904 and 1934), Stewart (1910), Kern (1911), Stevens and Hall (1910), Arthur (1921, 1924, 1926 and 1927), Burnham and Latham (1917), Hesler and Whetzel (1917), Jackson (1921), Hunt (1926), Anonymous (1930), Thomas and Mills (1930), Sherbakoff (1932), and others. Bliss (1931), by culture, obtained abundant spermogonia and aecia on *Crataegus mollis*, but obtained only flecking on nine varieties of commercial apples.

These previous reports, together with the investigations made by the writer, warrant the conclusion that the genera involved as suscepts for the aecial phase of *G. globosum* are confined to the sub-family Pomoideae, and include *Amelanchier*, *Crataegus*, *Cydonia*, *Malus*, *Mespilus*, *Pyrus*, *Sorbus*, and the hybrid genera *Crataegomespilus*, *Sorbaronia* and *Sorbopyrus*.

METHODS USED TO DETERMINE SUSCEPTIBILITY

Two methods of approach were utilized in the determination of the various hosts and their relative susceptibility within each genus, namely, (1) quantitative observations on natural infection, and (2) serial artificial inoculations during the progressive development of the foliage to determine both the degree and the duration of the period of susceptibility. These methods of approach were especially applicable to *Crataegus* which is by far the largest genus susceptible to *G. globosum*. All cultures and observations were made on trees in the Arnold Arboretum.

CULTURAL TECHNIQUE

The cultural technique adopted was similar to that described by Crowell (1934). The inoculum was collected either the previous evening, or in the morning prior to inoculating, from Juniperus virginiana. Galls bearing abundant telial flanges were soaked in water until maximum swelling had taken place; then the gelatinous mass was crushed to form a thick aqueous suspension of teliospores. Fresh inoculum was prepared every two hours during inoculation in order to eliminate any possibility of crushing the promycelia emerging from the germinating teliospores, since microscopic examination revealed that the latter would germinate within that time. All inoculations were carried out in duplicate. For each test six to ten leaves on a twig were inoculated; the remainder of the tree served as a control. The spore suspension was painted on both sides of the leaves with a camel's hair brush; then a celluloid cylinder was slipped over the twig and the ends of the cylinder were plugged with moist sphagnum. Care was taken that the inoculation should not be exposed to direct rays of the sun; otherwise burning of the leaves within the cylinder might occur. The sphagnum-plugged cylinder formed an excellent moist chamber; on removal of the tube two days later the sphagnum was always found to be still wet, and both the inside of the tube and the surfaces of the leaves were moist. Thus, with a heavy sowing of spores, a moist atmosphere in the inoculation tube, and a temperature below 25°C. the conditions for optimum spore germination and infection exceeded any that might occur in nature. Plate 127 fig. 5 illustrates a type set-up.

RECORDING OF DATA OBTAINED FROM INOCULATIONS

In recording data the inoculated plants were classified according to four categories or degrees of susceptibility, based on the number of sori, their relative size, and the pathogenic effect on an average-sized leaf. They are designated and defined as follows:

0-IMMUNE; no visible infection obtained.

- 1—RESISTANT; one to five lesions which are relatively small, which cause very little leaf killing and no leaf drop; with or without aecia. This is a type of infection which causes no material harm to the host.
- 2—MODERATELY SUSCEPTIBLE; five to twenty-five lesions per leaf with an intermediate pathogenic effect between categories 1 and 3; aecia always produced. This is a type of infection which, while reducing the photosynthetic leaf area and causing some leaf killing, does not result in defoliation.

3—VERY SUSCEPTIBLE; twenty-five or more lesions which are usually large or fuse to form large masses and which cause severe leaf killing and leaf drop; abundant aecial horns produced in each lesion. This is a type of infection which ruins the foliage.

While these definitions are, in general, applicable in allotting a suscept to any one category, they can not be considered as absolute criteria. Within the genus Crataegus, for example, as will be shown later in this paper, variation in susceptibility is for the most part not physiological but is dependent primarily upon a natural barrier, the cuticle; the probability that the basidiospore can produce infection varies inversely with the thickness of the foliar cuticle. Again, the amount of leaf killing is dependent upon whether infection takes place on main veins or elsewhere on the leaf. Consequently, for Crataegus at least, the actual number of lesions per average-sized leaf was given major significance. In other genera, the type of infection was accorded major consideration. In the genus *Pyrus*, for example, certain species exhibited very small lesions which died shortly after spermogonia appeared, while other species of this genus showed larger lesions producing aecia. In general, however, the foregoing definitions were employed as the bases for placing the various species within the different categories of susceptibility.

INVESTIGATIONS AND CONCLUSIONS WITH RESPECT TO THE VARIOUS GENERA CONSIDERED

For the sake of convenience the various host genera will be considered individually with respect to their relative susceptibility. All the known hosts within each genus will be listed at the end of the paper.

Crataegus

The Arnold Arboretum with almost one thousand trees comprising about five hundred and fifty named species and varieties, spread over twenty-four groups, afforded an excellent opportunity to study the relative susceptibility of the *Crataegi*. But, since the species of this genus hybridize so freely, and since the specific classification is still in an unstable condition, the time and labor involved in making inoculations for each of those species and varieties (especially in the large very susceptible groups where an abundance of natural infection was observed) would not justify the results that might be obtained; consequently typical representatives of each of the twenty-four groups were selected and the results were used as a basis of comparison by groups rather than by species. Likewise the data obtained on all the species and varieties by observations on natural infection were treated by groups rather than by species.

A. PRESENTATION OF DATA OBTAINED BY OBSERVATIONS ON NATURAL INFECTION

In July, 1932, a general spread of G. globosum was observed throughout the entire plantation of *Crataegi* in the Arnold Arboretum.¹ Detailed observations were warranted by the fact that, within each group, the degree of infection was consistently uniform regardless of where the tree happened to be situated; likewise a sharp line of demarcation could be seen between the number of foliar lesions per tree in a relatively resistant group, such as the CRUS-GALLI, and the number per tree in a more susceptible group, such as the COCCINEAE or ANOMALAE.

The amount of infection on any one tree while uniform was slight enough to allow fairly accurate counts to be made of the number of lesions per tree. While these data would hardly be adequate to permit comparison among species within any one group of *Crataegus*, they were sufficient for comparing the relative degree of susceptibility of the various groups represented in the Arboretum. As stated above, about one thousand trees were available for examination.

Observations were made at the spermogonial stage, and again at the aecial stage of the rust. In order that the amount of infection per tree might be fairly compared the trees were graded as to size, five size-classes being used.¹ Counts were made of the number of foliar lesions per tree at both stages of the rust; where the counts exceeded one hundred per tree, the degree of infection was termed "100 +".² A collection of herbarium material was assembled for permanent reference.

In correlating the data obtained a method had to be devised by means of which a tree, for example size I, could be fairly compared with a tree, for example size V. The COCCINEAE, a group containing 46 species represented by 82 trees, exhibited the highest percentage of infection lesions per unit-sized tree. This group was classed as having severe infection, and the values obtained for this group were selected as a basis of com-

¹The five size-classes were arbitrary gradings involving the relative amount of foliage as well as the actual tree size.

 ^{2}A tree with "100+" lesions was considered as having 150 lesions. However, with the exception of those trees that were obviously very susceptible, such occurrences were so rare that deviation from this estimation would make no significant differences in the correlations.

¹This plantation is a pure, open stand situated on an exposed hillside; furthermore, the groups within the genus are arranged in contiguous blocks. Rust-infected cedars were so remote that there was undoubtedly a uniform distribution of inoculum over the *Crataegus* trees.

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parison for all the other groups. It was found that for the CoccineAE: Size I (9 trees) averaged 24.3 lesions per tree. Size II (33 trees) averaged 51.7 lesions per tree. Size III (35 trees) averaged 75.7 lesions per tree.

Size IV (5 trees) averaged 120.0 lesions per tree.

Size V (0 trees).¹

If, for the sake of convenience, the ratio of the number of lesions per tree be changed from 24.3: 51.7: 75.7: 120.0: — to 25: 50: 75: 125: 200, for the respective tree sizes, and these values be considered as units for classifying a tree as having severe infection, then by taking arbitrary averages for the number of lesions required to class a tree as having moderate infection, mild infection, or no infection, the scheme as presented in Fig. 1 for classifying the trees of all the groups may be formulated.

		Number of lesions per tree within the respective tree sizes										
			Ι	II	III	IV	V					
Severe	infection		25	50	75	125	200					
			20	40	60	100	160					
Moderate	infection		15	30	45	75	120					
			10	20	30	50	80					
Mild	infection		5	10	15	25	40					
No	infection		0	0	0	0	0					

FIG. 1. AN ARBITRARY SCHEME TO DETERMINE THE RELATIVE DEGREE OF INFECTION ON TREES OF DIFFERENT SIZES.

From this scheme any tree of any size with any number of lesions may be classified according to the relative amount of infection present. On a tree size I, for example, one to ten lesions would be classed as mild infection, ten to twenty as moderate infection, and more than twenty as severe infection. As may be noted in Fig. 1, the ratio of the average number of lesions for any sized tree for the four degrees of infection is 5: 3: 1: 0. If, then, we multiply the number of trees classed as having severe infection by 5, moderate infection by 3, mild infection by 1, and no infection by 0, take the total of these products and divide by the number of trees considered, a unit is obtained by which the relative susceptibility of any group may be fairly and quite accurately compared

¹The COCCINEAE did not include any trees of size V; as a matter of fact there are only six trees of this size in the plantation. From actual measurements of the various tree sizes and from the table given above, it was estimated that a tree of size V must necessarily have at least 200 lesions to be classed as having severe infection.

with a similarly derived unit for any other group. To illustrate this, let us consider a moderately susceptible group, the MACRACANTHAE, and a resistant group, the CRUS-GALLI:

MACRACANTHAE (see Table II): Severe infection ... 7 trees \times 5 = 35 Moderate infection ... 10 trees \times 3 = 30 Mild infection ... 78 trees \times 1 = 78 No infection ... 4 trees $\times 0 = 0$ Total .. 99 trees 143 Susceptibility unit of comparison 143 = 1.4499 CRUS-GALLI (see Table II): Severe infection ... 0 trees \times 5 = 0 Moderate infection ... 2 trees \times 3 = 6 Mild infection ... 46 trees $\times 1 = 46$ No infection ... 80 trees \times 0 = 0 Total ... 128 trees 52 Susceptibility unit of comparison 52 = 0.41128

The groups of *Crataegus* examined, the number of species examined in each group and the number of trees representing these species, the numbers of trees classed according to the different degrees of infection, and finally the units of comparison, which may now be considered as the relative degrees of susceptibility as indicated by natural infection, are presented in Table II. These values for the degrees of susceptibility have been plotted in Fig. 4.

B. PRESENTATION OF DATA OBTAINED BY SERIAL INOCULATIONS

Serial artificial inoculations were made at the following stages in the foliar development: (a) on April 23 and 24, 1934, at which time very little foliage was evident, a few buds had begun to unfurl, the majority were just breaking through the winter scales, while in many instances it was necessary to part the winter scales and insert the inoculum; (b) on May 7 and 8, 1932 and 1934, respectively, at which times (the foliar conditions being approximately the same in both years) the leaves in practically all cases were in an advanced stage of expansion but were still tender, exhibiting relatively little cuticular development; (c) on May 22 and 23, 1933 and 1934, respectively, at which times the leaf

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cuticle was fairly well developed and most of the trees were in an advanced stage of blossom;¹ (d) on June 28, 1934, when the foliage was, for all practical purposes, fully mature and certain of the groups exhibited a very heavy cuticle on the leaves.²

The number of species inoculated in each group and the percentage of these falling into the different classes of susceptibility for each of the four serial inoculations are presented in Table III. The correlation of these data will be found under sub-section D.



FIG. 2. DISTRIBUTION OF THE GENUS CRATAEGUS IN NORTH AMERICA.

¹In certain groups, for example the CRUS-GALLI, differences could be observed in the type of foliage exhibited by two trees of the same species, in which case both were inoculated to determine if variation in susceptibility existed within a single species. Except in such instances totally different representatives were used in the respective years for inoculations (b) and (c).

²The inoculum for inoculations (c) and (d) had been kept in a refrigerator at 0° C., where, as will be shown in a subsequent publication, the teliospores will retain their viability to more than ninety percent germination for at least a year.

C. FACTORS INFLUENCING THE RELATIVE SUSCEPTIBILITY OF CRATAEGUS

1. The geographical distribution of Crataegus

Of the twenty-nine groups as given by Rehder (1927), twenty-three are of American origin; the remainder have been introduced from Eurasia. With the exception of the MACRACANTHAE, which extend into the middle west, and the DOUGLASIANAE, which are typically western, the American groups, as indicated by the dotted area in Fig. 2, are confined to the eastern part of North America. While certain of these groups are typically more northern than others they overlap to such an extent that no correlation could be made between the distribution and the relative susceptibility of the respective American groups. Although none of the Eurasian groups proved to be very susceptible, no differences from the type of infection produced on American groups could be observed. Consequently, the distribution of the genus gave no information that proved of value in determining the relative susceptibility of the various Crataegus groups.

2. The rôle of the foliar cuticle

By using herbarium material collected in the Arnold Arboretum from natural infection in 1932 a detailed comparison was made between one of the largest and most resistant groups, CRUS-GALLI, and one of the largest and very susceptible groups, TENUIFOLIAE, in an attempt to correlate the susceptibility of the host plant with the mechanical structure of the leaf. As a check on the results obtained, the CoccineAE, another very susceptible group, was examined in a similar manner. The following observations were made:

- (a) Distribution of lesions on the leaf.
 - i. Number of lesions primarily associated with mid and main lateral veins of the leaf.
 - ii. Number of lesions on the chlorenchyma which, for present purposes, may be defined as the leaf area other than that occupied by the mid and main lateral veins.
- (b) Spermogonial stage.
 - i. Number of spermogonia per lesion.
 - ii. Diameter of lesion.
- (c) Aecial stage.
 - i. Number of aecial horns per lesion.
 - ii. Diameter of lesion producing aecia.
 - iii. Length of mature aecial horns.
 - iv. Number of lesions actually producing aecia.
- (d) Detailed notes on thickness of foliar cuticle, degree of hypertrophy and amount of leaf-killing.

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In addition to the above data separate measurements and counts were made for chlorenchyma and vein infections in the COCCINEAE. Table I gives the results obtained for these three groups.

TABLE I PRESENTING DATA ON BIOMETRICS AS OBTAINED FROM HERBARIUM MATERIAL FOR THREE GROUPS OF THE CRATAEGI

Сгочр	- No. species	No. trees	No. leaves	No. lesions	\$ trees infected	<pre>% vein infections</pre>	- Av. no. spermogonia per lesion	Av. diam. of lesion covered by spermogonia	Av. no. aecia per lesion	Av. diam.of lesion covered by aecia	Av. length of aecial horns	% of lesions bearing aecia
Crus-galli	76	121	2216	216	37	83	43	3.0	31	3.7	3.2	66
Tenuifoliae	83	183	1283	1361	96	47	25	2.0	21	3.0	2.5	90
Coccineae	42	75	638	717	97	31	16;33 25	1.7;2.7 2.2	18;32 25	2.2;3.8 3.0	2.3;2.5	100

Crus-galli - thick, coriaceous, waxy leaves. Tenuifoliae and Coccineae - thin, non-waxy leaves.

Within the COCCINEAE the pairs of values (separated by a semi-colon) refer to chlorenchyma and vein infections respectively; the averages are given below the pairs. All measurements were made to the nearest millimeter.

A comparison of these data brings out three significant facts:

(1) Practically all the CRUS-GALLI have thick coriaceous leaves with a very heavy cuticle. The TENUIFOLIAE and COCCINEAE, on the other hand, have thin leaves with little cuticle. This condition was checked for all the other groups, and while the thickness of the leaf itself did not show consistent correlation with the relative susceptibility of the respective groups, there was a surprisingly consistent correlation on the part of cuticular thickness. Groups that finally fell into the moderately susceptible class exhibited an intermediate deposition of cuticle, the degree of which varied somewhat in different species within the respective groups. All the species within the groups which were classed as resistant had consistently heavy cuticle and those classed as very susceptible had consistently little cuticle.

(2) The CRUS-GALLI leaves have more than eighty percent of the infections on veins, the TENUIFOLIAE approximately fifty percent and the COCCINEAE about thirty percent. By correlating these data with the relative susceptibility of the three groups, it appears that the degree of

susceptibility varies inversely as the percentage of infections primarily associated with the main veins.

(3) Although the CRUS-GALLI exhibit the lowest percentage of trees infected, and thus would seem the most resistant, the individual lesions on the leaves of this group have the greatest diameter, and the largest number of spermogonia and aecia per lesion.

When these facts are fitted into the picture of the relative susceptibility of any host tree to the rust, they definitely indicate that the difference in susceptibility is purely mechanical, the cuticle being the deciding factor. The basidiospores of G. globosum, while able to produce infection from the lower surface of the leaf, germinate and gain entrance primarily through the upper side. Thus, spores carried by the wind and alighting on the smooth waxy surface of the CRUS-GALLI leaf are not so liable to adhere, and if they do remain and germinate, a large percentage of the germ-tubes die before they can penetrate the heavy cuticle. Many instances illustrating this phenomenon occurred during investigations of the waxy-leaf types. Within the CRUS-GALLI, for example, a much higher degree of susceptibility relative to the groups with non-waxy leaves was indicated by artificial inoculation where conditions were optimum for the infection process, than by natural infection where the basidiospores must necessarily withstand a certain amount of desiccation before infection can take place. Again, in many cases waxy leaves infected by natural inoculation were found on very low branches only, that is, branches almost touching the ground. Here the leaves were kept cool and moist for longer periods of time by the tall grass that happened to be growing around these trees; such an environment afforded a better opportunity for spore germination and germ-tube penetration.

The distribution of lesions on the leaves gives further evidence of the cuticle acting as a natural barrier. In the CRUS-GALLI eighty-three percent of the lesions were primarily associated with the main veins. The little grooves over these veins afford lodging places for the basidio-spores; moisture tends to remain longer along these areas, rendering a more favorable environment for the infection process. When making artificial inoculation by painting the leaves with an aqueous suspension of basidiospores, it was very difficult to get a film of the suspension to lie uniformly over waxy leaves. The water would form into droplets, and either roll off the leaf entirely or else remain in the little grooves over the veins. One can readily picture the same thing happening when the basidiospores are brought naturally. Inoculation usually takes place during wet weather, as it is then that the telial flanges on the galls swell and the teliospores germinate to produce basidiospores. The latter are

then carried aerially, either directly to the Crataegus leaf by the wind, or else washed out of the air by falling rain onto the host leaf. Here, as in the case of artificial inoculation, the moisture necessary for spore germination accumulates in droplets and these either roll off the waxy leaf or remain in the grooves over the veins, carrying the basidiospores with them.

With a non-waxy leaf we have an altogether different picture. A film of water readily spreads over the surface of the leaf in a uniform layer, in which case the basidiospores are more apt to remain where they happen to alight on the leaf. Here the germinating basidiospores have no heavy cuticle with which to contend and can successfully penetrate the leaf surface almost as easily at any place over the chlorenchyma as over the veins. Since the area occupied by chlorenchyma far exceeds that occupied by the main veins, one can readily see why only thirty-one percent of the lesions on the Coccineae leaves were vein infections as compared with eighty-three percent on the CRUS-GALLI leaves.

The fact that within the CRUS-GALLI group the rust flourished even better than within the more susceptible groups, producing larger lesions with a larger number of spermogonia and aecia per lesion, can also be attributed to the relatively high percentage of vein infections. Regardless of leaf type the very large lesions, some seven to ten millimeters long, with more than one hundred spermogonia and fifty to one hundred aecia per lesion, were vein infections. In the COCCINEAE measurements of vein and chlorenchyma infections were kept separate, in order to obtain quantitative data on the relative size of the lesions and the number of spermogonia and aecia per lesion in the two types of infection. As may be seen from the foregoing table, the lesions are much larger in vein infections, producing almost twice as many spermogonia and aecia. All evidences indicate that G, globosum is capable of establishing a much more efficient nutritional regime when in direct contact with one of the veins. In the early spermogonial stage of even chlorenchyma infections one can see yellowish lines of fungal hyphae, radiating out along the vascular bundles from the centre of the lesion, as shown in Plate 125, Fig. 2. Again, in Plate 125, Fig. 1, the infection appears systemic, extending the entire length of a lateral vein. Plate 125, Fig. 3 shows a main lateral vein infection branching out along one of the sub-lateral veins. In fact, in every vein infection observed (eight hundred and eighteen), as may be seen in Plate 125, Fig. 4, the lesion was typically long and narrow, the long axis corresponding with that of the vein.

Vein infections appeared to produce aecia later in the season than chlorenchyma infections. Many cases were found among the former where

the aecial horns were just emerging or else were very short when the leaves were collected, while nearly all the chlorenchyma lesions had fully developed aecia, with peridial cells ruptured and aeciospores emerging. It would seem, then, that the time of spore production is correlated with the availability of food supply. An infection not primarily associated with a main vein utilizes all the available nutrient and then produces spores. Vein infections, on the other hand, have a greater and more lasting nutrient supply from the host, develop more mycelium and, when they finally do sporulate, have a greater supply of reserve food to produce aecia. Thus chlorenchyma infections produce relatively smaller and fewer aecia over a smaller lesion and at an earlier date than vein infections. This fact would account for the higher percentage of the lesions within the TENUIFOLIAE and COCCINEAE actually producing aecia at the time the herbarium material was collected.

Severe leaf killing, where relatively few lesions per leaf were involved, was due in practically all cases to infections primarily associated with the main veins, the amount of leaf killing depending on how far back from the edge of the leaf the vein was attacked. Plate 126, Fig. 2 shows one lesion on the mid-vein resulting in the death of over half of the leaf. On the other hand, in Plate 126, Fig. 1, may be seen a chlorenchyma infection where leaf killing extends from the point of infection to the margin of the leaf but does not extend beyond the enclosing lateral veins. A purely chlorenchyma infection nearer the center of the leaf rarely causes killing beyond the area of actual infection.

If the degree of susceptibility is in any way physiological, one would necessarily expect that within the resistant groups the rust would have greater difficulty in establishing a satisfactory nutritional regime, and if once established would produce small lesions with relatively few fruiting bodies due to some antagonistic physiological reaction on the part of the host. Crowell (1934) found such to be the case when he determined the relative susceptibility of the genus Malus to Gymnosporangium Juniperi-virginianae Schw. In European species of Malus the lesions were very small, in some cases producing a few spermogonia but no aecia. Somewhat similar instances were found by the writer in determining the relative susceptibility of species of Pyrus to G. globosum. In the Crataegi a few rare instances were found that might suggest differential physiological antagonism on the part of the host. In Plate 126, Fig. 5 is shown a lesion that produced abundant spermogonia but died before any hypertrophy or production of aecia took place; the host tissue may have been hypersensitive to the rust mycelium, the latter taking such a heavy toll on the nutrient content of the leaf that the host tissue

was killed and as a result the fungus died. Plate 126, Fig. 4 illustrates a case of leaf killing extending below the area of infection; this suggests the existence of a toxic agent secreted by the rust. In a few of the collections very small lesions not more than a millimeter in diameter that never produced even spermogonia were found. In Plate 126, Fig. 3 may be seen a small lesion that exhibits no hypertrophy and produced only one aecial horn. However, such instances as the foregoing were rare and not consistent even on a single host, and may be considered as insignificant factors in determining the relative susceptibility of the genus Crataegus. Indeed, from examination of the herbarium material the writer found the exact opposite to any physiological antagonism on the part of the host to be true; G. globosum is apparently able to establish itself more satisfactorily in the most resistant groups, due to the relatively high percentage of vein infections. This condition would indicate that the basis for differences in susceptibility is for the most part mechanical, involving primarily the cuticle as the deciding factor. The CRUS-GALLI is a difficult group for the rust to invade, except for a very short period in the spring before the foliar cuticle has developed to any extent. However, once the rust has successfully penetrated this cuticle it is just as much at home and can do just as much damage or even more in the CRUS-GALLI than it can in the TENUIFOLIAE, COCCINEAE or any other very susceptible group.

3. The degree and the duration of the period of susceptibility

The rôle of the cuticle also explains the significant phase in the duration of the susceptibility of any host. There is a definite duration to this period of susceptibility for all the groups, the degree of which rises rapidly during the unfurling of the leaves and reaches a maximum during and immediately after the period of leaf expansion, then falls off gradually at a rate depending, in part at least, on the rapidity of deposition of foliar cuticle.

In PLATE 127, FIGS. 1–4 are shown the results obtained from the four respective serial inoculations on *Crataegus Pringlei*. At the time of initial inoculation, April 25, 1934, the leaves, approximately one quarter of an inch long, had just begun to unfurl and a very small amount of infection at the tip of one leaf resulted (Fig. 1). The inoculation on May 9, after the leaves had fairly well expanded, produced severe infection (Fig. 2). Inoculation two weeks later resulted in scattered lesions (Fig. 3), while the inoculation on June 28 gave negative results (Fig. 4).

The same phenomenon but from a different approach is evident in Plate 128, Figs. 1 and 2, which demonstrate the results obtained from inoculations on *Crataegus Jonesae* on May 7 and June 4 respectively.

All the leaves in both inoculations received approximately the same amount of inoculum per unit area of leaf. At the time of the first inoculation the five basal leaves were well expanded, while the two upper leaves were just beginning to expand. As may be noted in Fig. 1, much heavier infection occurred on the older leaves. (The large irregular white areas on the younger leaves are holes caused by insects.) In Fig. 2, showing the results of the later inoculation, the reverse situation is seen; on the younger leaves at the end of the twig abundant infection was obtained, while the older leaves exhibited only scattered lesions.

It is quite evident, therefore, that the cuticle cannot be the sole determining factor for variation in susceptibility throughout the entire life of the foliage; certain physiological factors may also be involved. For example, the leaves apparently are not so susceptible during the period of emergence from the winter scales until they are in a moderately advanced stage of expansion, a period prior to any heavy deposition of cuticle. It is possible that the rust is unable to establish itself in the very young leaf. However, since this rust is not primarily of a systemic nature, probably the dilution effect on the number of lesions resulting from the intussusceptional type of foliar growth and consequent expansion, as well as the relatively small leaf area exposed at the time of inoculation, will account for the major part of this phenomenon. Again, even the most susceptible groups, for example, ANOMALAE or COCCI-NEAE, are apparently quite resistant to the rust by the latter part of June, at which time the leaves have by no means the amount of cuticle that is formed on the CRUS-GALLI even in the early part of May. It is possible that the rust is unable to establish a nutritional regime in the mature leaf as exhibited in the latter part of June, a point in favor of assuming a physiological antagonism on the part of the host. The relatively high temperature may also be a factor, by inhibiting spore germination.

Nevertheless these two periods play an insignificant part in any determination of the amount of infection that may accumulate on a host, regardless of the group. In the former case the period is relatively short and the leaf area exposed to the basidiospores by the unfurling buds would be small in comparison with that exposed after the leaves have expanded. As for the latter case practically all the teliospores on the red cedar have germinated by May 25, and the degree of susceptibility of any pomaceous host after the last of May would have no significance in determining the amount of infection that might occur. Thus, for practical purposes in the field the significant period within which infection might take place is between the time the leaves are fairly well expanded and the end of basidiospore dispersal. During this time the thickness and rapidity of deposition of the cuticle are the deciding factors. For this reason the inoculations in April and June, respectively, are not considered in determining the relative susceptibility of the various groups.



FIG. 3. Illustrating the Degree and the Duration of the Period of Susceptibility within the Genus Crataegus to G. globosum.

To illustrate further the degree and duration of susceptibility within the different groups, values may be obtained for the relative degrees of susceptibility of the various groups by taking the sum total of the values as expressed by the symbols 0, 1, 2 and 3, and dividing by the number of representatives inoculated.¹ These were obtained from Table I for the COCCINEAE, MACRACANTHAE, and CRUS-GALLI, which are, respectively, typical of the classes very susceptible, moderately susceptible

¹The objection arises that such a method of correlation utilizes arbitrary qualitative symbols to designate quantitative entities. Nevertheless, its usage here is not to be considered from a statistical standpoint and it does present a clearer picture to illustrate both the degree and the duration of the period of susceptibility within any one group of *Crataegus*. It is interesting to note that if such a method be employed in correlating the data obtained from serial inoculations in this genus (under sub-section D) one will arrive at precisely the same conclusions as in the method finally adopted.

and resistant, and have been plotted in Fig. 3. A similar curve (in heavy line) is given for all the inoculated representatives of the genus. The area enclosed by the respective curves would, to a certain extent, be a measure of both the degree of susceptibility and its duration. The

TABLE II

PRESENTING DATA ON THE RELATIVE SUSCEPTIBILITY OF CRATAEGUS TO G. GLOBOSUM, AS INDICATED BY NATURAL INFECTION

	No. Sps.	No. Trees	No.	trees in			
Group			No infect.	Mild infect.	Mod. infect.	Sev. infect.	Rel. degree of susceptibility
Anomalae	19	40	0	19	3	18	2.95
Azaroli	1	1	1	0	0	0	. 00
Bracteatae	2	2	1	1	0	0	. 50
Coccineae	46	82	2	24	20	36	3.22
Crus-galli	71	128	80	46	2	0	. 41
Dilatatae	4	11	1	6	0	4	2.36
Douglasianae	8	19	3	16	0	0	. 84
Flavae	10	11	11	0	0	0	. 00
Intricatae	10	11	8	3	0	0	. 27
Macracanthae	68	99	4	78	10	7	1.44
Microcarpae	1	1	1	0	0	0	. 00
Molles	37	86	10	40	11	25	2.30
Nigrae	2	2	0	2	0	0	1.00
Oxycanthae	10	17	10	6	0	1	. 65
Pinnatifidae	2	4	0	4	0	0	1.00
Pruinosae	58	98	36	57	3	2	. 67
Punctatae	34	37	7	26	2	2	1.14
Rotundifoliae	37	66	14	37	8	7	1.45
Sanguinae	4	4	0	4	0	0	1.00
Silvicolae	35	57	3	42	8	4	1.51
Tenuifoliae	81	175	7	104	32	32	2.06
Triflorae	2	2	2	0	0	0	. 00
Uniflorae	2	2	2	0	0	0	. 00
Virides	18	30	20	9	1	0	. 40

COCCINEAE, characterized by little foliar cuticle, exhibit a much higher degree of susceptibility over a relatively longer period of time than the CRUS-GALLI which have consistently heavy cuticle on the leaves, whereas the MACRACANTHAE, with an intermediate and varying amount of cuticle, assume an intermediate position.

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D. CORRELATION OF THE DATA TO CLASSIFY THE GROUPS OF CRATAEGUS WITH RESPECT TO THEIR RELATIVE SUSCEPTIBILITY

Bearing in mind that the thickness of the cuticle and its rapidity of deposition on the leaves are the primary factors in determining the relative susceptibility of any host, while geographical distribution and physiological antagonism on the part of the host play a very minor part, if any, it is now possible to evaluate the data obtained by the two previously described methods of approach and determine the relative susceptibility of the various groups within the genus *Crataegus*.



FIG. 4. RELATIVE SUSCEPTIBILITY OF THE GENUS CRATAEGUS TO G. GLOBOSUM AS INDICATED BY OBSERVATIONS ON NATURAL INFECTION. The number within each column refers to the number of trees considered within the group.

The relative degrees of susceptibility obtained from observations of natural infection, as previously stated, are presented in Table II, and have been plotted in Fig. 4. In regard to data obtained by serial inoculations, it is quite obvious from Table III that inoculations before the leaves unfurl, and again late in June, result in very little infection. However, as the foregoing discussion on the duration of the period of

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susceptibility demonstrates, such a phenomenon, while interesting, plays an insignificant rôle in determining the amount of infection that might take place on any tree. The two significant inoculations are those made

TABLE III

PRESENTING DATA ON THE RELATIVE SUSCEPTIBILITY OF THE GENUS CRATAEGUS TO G. GLOBOSUM AS INDICATED BY SERIAL INOCULATIONS

Percentage of species within the various groups of <u>Crataegus</u> falling into the different classes of susceptibility, as indicated by serial artificial inoculations

Artificial	inocu	(a)	April :	23 and	24	(b) Artificial inoculation May 7 and 8						
Group s	No. pecies	\$0	species	within 2	classes	Group ape	lo.	* 0	specie	s with	in clas	8688
Anomalae Bracteatae Coccineae Crus-galli Dilatatae Douglasiana Flavae Macracantha Microcarpae Kolles Cxyacanthae Pruinosae Pulcherrima Rotundifolia Silvicolae Tenuifoliae	1 2 43 0 2 6 5 1 6 6 6 1 4 8 0 0 1 4 1 1 1 1 1 1 1 1 1 1 1 1 1	100.0 100.0 0.0 100.0 100.0 100.0 92.3 100.0 83.3 50.0 96.7 100.0 85.7 87.5 40.0	0.0 0.0 100.0 50.0 0.0 7.7 0.0 16.7 50.0 3.3 0.0 14.3 12.5 - 60.0		0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	Anomalae Bracteatae Coccineae Crue-galli Diulatatae Douglasianae Flavae Intricatae Macracanthae Licrocarpae Molles Oxyacanthae Pruinosae Punctatae Rotundifolia e Silvicolae	7 4 48 3 10 11 20 1 16 6 7 18 13 4 14	0.0 0.0 25.0 0.0 10.0 10.0 10.0 10.0 0 100.0 31.6 100.0 5.5 7.7 25.0 0.0	0.0 100.0 39.6 0.0 50.0 36.4 10.0 0.0 12.5 66.7 37.8 0.0 16.7 15.4 50.0 14.3	85.7 0.0 22.9 50.0 66.7 40.0 36.4 30.0 0.0 62.5 33.3 24.3 0.0 38.9 53.8 0.0 21.4	$\begin{array}{c} 14.3\\ 0.0\\ 100.0\\ 12.5\\ 50.0\\ 33.3\\ 0.0\\ 9.1\\ 45.0\\ 0.0\\ 18.8\\ 0.0\\ 16.2\\ 0.0\\ 38.9\\ 23.1\\ 25.0\\ 64.3\end{array}$	
Triflorae Uniflorae Virides	22	100.0 100.0 70.0	0.0 0.0 20.0	0.0 0.0 10.0	0.0	Triflorae Uniflorae Virides	2 2 13	50.0 0.0 0.0	50.0 100.0 30.7	0.0 0.0 23.1	0.0 0.0 46.1	

Artificial inoculation May 22 and 23						Artificial inoculation June 28						
Group spec	ies	10%	specie	s with	in classes	Group spe	No. ecies	% OI	species	within	classes	
Anomalae Bracteatae Coccineae Crus-galli Dilatatae Douglashanae Flavae Macracanthae Macracanthae Microcarpae Molles Oxyacanthae Pruloberrimae Punctatae Rotundifoliae Silvicolae	1 2 4 78 0 3 11 8 16 1 9 11 43 1 20 12 11 14 12 12 11 14 16 11 12 11 12 12 11 12 12 11 12 12	0.0 0.0 69.2 66.7 18.2 37.5 00.0 77.7 27.3 32.6 0.0 25.0 0.0 25.0 0.0 22.2	$\begin{array}{c} 0.0\\ 100.0\\ 0.0\\ 20.5\\ 54.6\\ 62.5\\ 0.0\\ 11.1\\ 54.9\\ 0.0\\ 50.0\\ 50.0\\ 50.0\\ 50.0\\ 50.0\\ 44.4\\ \end{array}$	0.0 0.0 10.3 27.3 25.0 0.0 11.1 18.2 23.3 100.0 10.0 16.7 0.0 11.1	100.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.	Anomalae Bracteatae Coccineae Crus-galli Dilatatae Douglasiana Flavae Intricatae Macracantha Microcarpae Molles Oxyacanthae Pruinosae Pulcherrima Punctatae Rotunifoliae Tenuifolae	10122015361253186010	100.0 100.0 80.0 100.0 83.3 100.0 100.0 100.0 95.7 0.0 87.5 83.3 100.0	0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	0.0 0.0 0.0 0.0 0.0 0.0 16.7 0.0 0.0 4.3 100.0 12.5 0.0 - 0.0 -		
Uniflorae Virides	3	100.0 64.7	0.0	0.0	0.0	Uniflorae Virides	05	100.0	0.0	0.0	0.0	

(8)

in May, (b) and (c), and for fifteen of the major groups the percentage frequency of occurrence of inoculated representatives falling into the respective classes of susceptibility have been plotted in Fig. 5 (p. 118).

In comparing these tables and figures to make a final classification of the groups according to their relative susceptibility, one must remember that these results were obtained from two altogether different meth-

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ods of approach. For those groups the representatives of which have a heavy cuticle, a much lower degree of susceptibility would be indicated by natural infection than by artificial inoculation where the amount of inoculum and the cultural environment are optimum. The number of representatives examined in each group, and especially for natural infection, must also be given consideration.



FIG. 5. RELATIVE SUSCEPTIBILITY OF FIFTEEN GROUPS OF THE GENUS CRATAEGUS TO G. GLOBOSUM AS INDICATED BY SERIAL INOCULATIONS. The results of two inoculations, (b) and (c) respectively, are presented in each sub-graph. The numbers on the abscissae of the sub-graphs refer to the classes of susceptibility. The numbers in parentheses refer to the number of species (with the exceptions noted in text) inoculated in each group.

By correlating the degree of susceptibility as indicated by natural infection, and the frequency of occurrence of inoculated representatives falling into the various classes of susceptibility, the groups may be classified and arranged within each class according to susceptibility as follows:¹

Very susceptible—Anomalae, Coccineae, Tenuifoliae, Dilatatae.

¹In classifying these groups according to their relative susceptibility, values for minor groups, not included in the figures, were taken directly from the tables.

Moderately susceptible—Molles, Macracanthae, Rotundifoliae, Punctatae, Douglasianae, Silvicolae, Pruinosae, Virides, Flavae, Oxyacanthae, Intricatae.

Resistant—Crus-galli, Bracteatae, *Azaroli, *Microcarpae, *Nigrae, *Pinnatifidae, *Sanguineae, *Triflorae, *Uniflorae.¹

Immune-None.

None of the groups examined proved to be wholly immune. No infection was obtained on the one representative of the MICROCARPAE, namely, C. Phaenopyrum (L. f.) Medic. ($= C. \ cordata$ Ait.), but this species has been previously reported as a host to the rust from both Delaware and Tennessee. Of almost five hundred and fifty determined species and varieties studied, less than one percent of the artificial inoculations gave negative results and it is indeed possible that, given optimum conditions for germ-tube penetration, not a single species could be considered totally immune. However, as previously stated, it must be remembered that the conditions favorable for infection set up by artificial inoculation far exceed any that might occur in nature, and many species that are now classed as suscepts would probably never exhibit infection under field conditions.

E. Suggestions for the Selection of Resistant Species and Varieties

The best guide in the selection of Crataegus trees to be planted on estates where *G. globosum* is in the vicinity would be the thickness of the foliar cuticle. A striking example of this was found on an estate at Canton, Massachusetts, where two Crataegus trees, one a COCCINEAE species and the other a CRUS-GALLI species, were planted side by side, surrounded by red cedars bearing heavy infections of *G. globosum*. These have been under observation for the past three years, and each season the foliage on the COCCINEAE species has suffered very severe infection, resulting in more than eighty percent defoliation by the latter part of August. The tree is now in a very weakened condition. The CRUS-GALLI species, on the other hand, has been entirely unaffected by this rust.

In choosing from species of American origin one should definitely avoid the ANOMALAE, COCCINEAE, TENUIFOLIAE and DILATATAE if G. globosum be in the vicinity. Certain of the species within the groups

¹The small number of representatives in the resistant groups indicated by asterisks made it impossible to arrange these groups within the class "Resistant" according to susceptibility and they have been arranged alphabetically.

classed as moderately susceptible have considerable cuticle on the leaves and these may be planted with a relative degree of safety. The CRUS-GALLI, however, are very resistant, and offer a wide variety of species. They are, as Rehder (1927) states, handsome ornamentals with dense, dark green foliage which remains till late in autumn or early winter, and are very attractive in bloom, with decorative bright red fruits that are persistent during the winter. If one desires the Eurasian type, the PINNATIFIDAE offer a group with lustrous leaves and large showy fruit. Some varieties of these are cultivated in northern China for the edible fruit. The OXYACANTHAE will also withstand severe infection unless under abnormal proximity to *Juniperus* rusted by *G. globosum*, with *C. Oxyacantha* Jacq. including some of the most showy garden forms.

This presentation has been confined to foliar lesions, and while infection has been obtained on all parts of the flower as well as the fruit and young twigs, such instances were sufficiently rare that they were not worthy of consideration at this time and have been set aside for a second publication on the life history of *G. globosum* Farl.

No consideration has been given to the possibility of variation in virulence within different strains of this rust. Practically all the inoculum was obtained from two adjacent red cedar trees at Waltham, Massachusetts.

One must also bear in mind that the relative susceptibility of groups within the genus Crataegus to G. globosum is in no respect correlated with their susceptibility to other Gymnosporangium rusts. Crowell (unpublished) has found, for example, that the CRUS-GALLI, so resistant to G. globosum, are quite susceptible to G. clavipes Cke. & Pk.

Pyrus— Relative Susceptibility as Indicated by Serial Inoculations

Studies on relative susceptibility within the genus *Pyrus* were confined to the results obtained from serial inoculations made in 1934. The species represented in the Arboretum were artificially inoculated in a manner similar to that described for *Crataegus*: (a) on April 25, at which time the condition of the foliage varied from buds just bursting through the winter scales to leaves a quarter to a half inch long; (b) on May 9, when the leaves were fairly well expanded on all species; (c) on May 22 when the foliage was fully expanded; and (d) on June 28. Certain of the species which had given negative results in the previous inoculation were omitted in the June inoculation.

In Table IV are given the species inoculated, their distribution, the degree of infection obtained on the respective dates of inoculation, the

stages of the rust produced on the foliage, and finally, a classification of their relative susceptibility.

TABLE IV

PRESENTING DATA ON THE RELATIVE SUSCEPTIBILITY OF SPECIES OF THE GENUS PYRUS TO G. GLOBOSUM, AS INDICATED BY SERIAL INOCULATIONS

Species	Native distrib.	De in in (a)	eg. su dicat ocula (b)	scep ed b ation (c)	t. y (d)	Stages found	Degree suscept.	
P. Balansae Decne.	Eurasian	0	2	0	0	0 & 1	2	
P. betulaefolia Bge.	Eurasian	3	3	2	0	0 & 1	3	
P. Bretschneideri Rehd.	Eurasian	0	1	0	-	0 & 1	1	
P. communis L.	Eurasian	0	1	0	-	0	1	
P. elaeagrifolia Pall.	Eurasian	0	0	0	_		0	
P. Korshinskyi Litv.	Eurasian	1	0	0	-	0	1	
P. Michauxii Bosc. ¹		0	1	0	-	0	1	
P. Lindleyi Rehd.	Eurasian	1	0	0	-	0	1	
P. nivalis Jacq.	Eurasian	0	1	0	-	0	1	
P. phaeocarpa Rehd.	Eurasian	0	1	1	0	0 & 1	1	
P. salicifolia Pall.	Eurasian	0	0	0	-		0	
P. serotina Rehd.	Eurasian	0	2	0	-	0 & 1	2	
P. serrulata Rehd.	Eurasian	1	1	1	0	0	1	
P. syriaca Boiss.	Eurasian	0	1	1	0	0 & 1	1	
P. ussuriensis Maxim.	Eurasian	1	1	0	-	0 & 1	1	

¹P. Michauxii is a 'hybrid (P. amygdaliformis \times P. nivalis).

No consistent correlation between the relative susceptibility of the various species and the type of leaf is evident; all species have considerable cuticle on the foliage, and a few are somewhat tomentose. Nor can the differences in susceptibility be correlated with the distribution of the host.

The lesions in general were found to be much smaller than those exhibited on *Crataegus*, and except in the case of *P. betulaefolia* rarely measured more than one to two millimeters in diameter. Certain species, designated in the table, showed spermogonia only; the lesions were extremely small, and died before any hypertrophy or aecial formation was evident. However, it is possible that with a different strain of the rust some of these might produce aecia; *P. communis*, for example, exhibited only spermogonia in my inoculations but has been reported previously from seven different states.

As in *Crataegus*, there is a definite duration to the period of susceptibility, the degree of which reaches its maximum during and immediately after the period of foliar growth and expansion, and then falls off gradually so that by the end of June all species examined are immune. Classified according to their relative susceptibility, the species examined may be arranged (alphabetically) as follows:

Very susceptible—P. betulaefolia Bge.

Moderately susceptible—P. Balansae Decne., P. serotina Rehd.

Resistant—P. Bretschneideri Rehd., P. communis L., P. Korshinskyi Litv., X P. Michauxii Bosc, P. Lindleyi Rehd., P. nivalis Jacq., P. phaeocarpa Rehd., P. serrulata Rehd., P. syriaca Boiss., P. ussuriensis Maxim.

Immune—P. amygdaliformis Vill., P. elaeagrifolia Pall., P. salicifolia Pall.

Previous reports of *Pyrus* suscepts are confirmed, for the most part, to *P. communis*, to the Kieffer Pear (*P. communis* \times *P. serotina*) and other varieties used commercially in the orchard. Stevens and Hall (1910) report *G. globosum* as being particularly abundant on the Japanese strain of pear (*P. serotina*), while Stewart (1910) reports the Kieffer pear as suffering infection from this rust at Long Island, New York. In particular he finds that both the fruit and leaves are attacked, and that the diseased fruits are very small and misshapen, usually exhibiting circular black areas devoid of aecia, although a few show aecia. On the other hand, Stewart (1910), and Hesler and Whetzel (1917) classify the Bartlett, Bosc, Duchess, and Worden varieties as being for the most part immune, although the fruit of the Worden variety is subject to infection.

While little can be added to the knowledge of the relative susceptibility of the orchard varieties, one may conclude from the foregoing classification that, with the exception of *P. betulaefolia*, *P. Balansae*, *P. serotina*, and as indicated from previous reports, *P. communis*, the remainder of the species can be safely planted in vicinities where the rust is present. This conclusion holds true especially for *P. amygdaliformis*, *P. elaeagrifolia*, and *P. salicifolia*.

Sorbus — Relative Susceptibility as Indicated by Serial Inoculations

Serial artificial inoculations were made in 1934 on species and varieties of *Sorbus* available in the Arnold Arboretum: (a) on April 25, at which time the foliar buds were just beginning to break open and the tiny leaves in many cases exhibited a heavy tomentose covering which was removed without injury to the leaf by rubbing the latter between the fingers, and the inoculum was placed on the exposed green tissue; (b) on May 9, at which time practically all the foliage was going through a period of rapid growth and expansion; (c) on May 24, at which time the leaves were fully expanded (blossoms where present were

also inoculated); (d) on June 28, at which time the leaves for all practical purposes were mature.

The results of these inoculations appear in Table V which presents, where positive results were obtained, the species and varieties inoculated, their native distribution, the degree of infection obtained from the respective inoculations, the stages of the rust exhibited, and finally the resultant classes of susceptibility.

TABLE V

PRESENTING DATA ON THE RELATIVE SUSCEPTIBILITY OF SPECIES AND VARIETIES OF THE GENUS SORBUS TO G. GLOBOSUM, AS INDICATED BY SERIAL INOCULATIONS

Species and varieties	Native distrib.	De in in (a)	eg. su dicat locula (b)	ed b ation (c)	t. y is (d)	Stages found	Degree suscept.
S. americana Marsh.	American	1	3	2	0	0 & 1	3
S. americana var. fructu albo• Hort.	American	1	1	0	_	0 & 1	1
S. americana var. nana Hort.	American	1	0	0	-	0	1
S. arnoldiana Rehd. ¹	Eurasian	1	1	0	-	0	1
S. Aucuparia var. Backhousei Hort.	Eurasian	1	0	0	_	0	1
S. dumosa Greene	American	1	0	0	-	0	1
S. japonica var. calocarpa Rehd.	Eurasian	1	0	0	_	0	1
S. thuringiaca Fritsch ²	Eurasian	1	1	0	-	0 & 1	1

¹S. arnoldiana is a hybrid (S. Aucuparia \times S. discolor).

²S. thuringiaca is a hybrid (S. Aucuparia \times S. Aria).

No infection was obtained on the following (alphabetically arranged) species and varieties, which are all of Eurasian origin: Sorbus alnifolia K. Koch, S. amurensis Koehne, S. Aria Crantz, S. Aria var. angustifolia Hort., S. Aria var. Decaisneana Rehd., S. Aria var. longifolia Pers., S. Aria var. lutescens Hartwig, S. Aria var. magnifica Hort., S. Aria var. salicifolia Myrin, S. Aria var. sulphurea Hort., S. Aria var. theophrasta Hort., S. Aucuparia L., S. Aucuparia var. Dirkenii aurea Hort., S. Aucuparia var. edulis Dieck, S. Aucuparia var. nana Hort., S. Aucuparia var. sulphurea Schneid., S. commixta Hedl., S. commixta Hedl., S. commixta var. rufo-ferruginea Schneid., S. latifolia var. atrovirens Hort., S. Matsumurana Koehne, \times S. Meinichii Hedl., S. pohuashanensis Hedl., S. Zahlbruckneri Schneid.

All species of American origin that were inoculated proved to be susceptible, with *S. americana* as the only species on which the foliage was materially injured by the rust. Of the thirty-one inoculated Eurasian types, infection was obtained on only four, and these proved to be quite resistant.

The lesions in all cases were very small, rarely measuring more than one to two millimeters in diameter, with an average of three to five aecial horns per sorus. Those species on which spermogonia only were obtained (see Table V) exhibited bright yellow lesions until the spermogonia were mature, following which time no further development took place and the infections died. An interesting type of natural infection was observed on Mt. Monadnock in New Hampshire; the lesions were as large as any ever obtained on *Crataegus*, some being as much as ten to twelve millimeters long, each bearing abundant aecial horns. Whether this type of infection results from a more susceptible variety of *S. americana*, or another strain of *G. globosum*, is not known.

With the exception of *S. americana*, no infection was obtained on any of the species after the second inoculation, while practically all the suscepts exhibited some infection from the initial inoculation. It would seem, therefore, that the resistant forms at least are most susceptible during, and immediately after, the period when the foliar buds are unfurling; *S. americana*, however, reached its maximum degree of susceptibility immediately after the leaves had expanded.

It is extremely doubtful that, with the exception of *S. americana* and its varieties within the American types, and possibly the hybrid Eurasian type, *S. thuringiaca*, any representative of the genus *Sorbus* would be seriously affected by *G. globosum* regardless of proximity to the rust. This is certainly true for the species of Eurasian origin.

Malus — Relative Susceptibility as Indicated by Serial Inocu-LATIONS

Serial artificial inoculations were made in 1934, similar to those described for the preceding genera: (a) on April 24, at which time the leaves had already unfurled and were undergoing the period of rapid expansion; (b) on May 9, at which time the foliage was almost mature size, and most of the blossoms were in the pink stage; (c) on May 22, at which time most of the petals had dropped. No inoculation was made in June. Table VI presents the species on which positive results were obtained, the origin of the various species, the results obtained from the respective serial inoculations, the stages of the rust obtained, and finally the relative degree of susceptibility.

TABLE VI

PRESENTING DATA ON THE RELATIVE SUSCEPTIBILITY OF SPECIES AND VARIETIES OF THE GENUS MALUS TO G. GLOBOSUM, AS INDICATED BY SERIAL INOCULATIONS

Species and varieties	Native distrib.	Deg indi inoc (a)	cated culat (b)	cept. d by ions (c)	Stages found	Degree suscept.
M. astracanica DumCours.1	Eurasian	0	1	0	0 & 1	1
M. baccata Borkh.	Eurasian	1	2	0	0 & 1	2
M. coronaria Mill.	American	0	1	0	0	1
M. Dawsoniana Rehd. ²	Hybrid	0	1	1	0 & 1	1
M. glabrata Rehd.	American	0	1	0	0 & 1	1
M. ioensis var. plena Rehd.	American	1	2	1	0 & 1	2
M. magdeburgensis Schoch ³	Eurasian	0	1	0	0	1
M. Soulardi Britt. ⁴	Hybrid	-	2	0	0 & 1	2
M. sublobata Rehd. ⁵	Eurasian	0	1	0	0 & 1	1

¹M. astracanica is a hybrid (M. prunifolia \times M. pumila).

²M. Dawsoniana is a hybrid (M. fusca \times M. pumila).

³M. magdeburgensis is a hybrid (M. pumila \times M. spectabilis).

⁴M. Soulardi is a hybrid (M. ioensis \times M. pumila).

⁵M. sublobata is a hybrid (M. prunifolia \times M. Sieboldii).

The following species, alphabetically arranged according to distribution, gave negative results:

American distribution: Malus angustifolia Michx., M. bracteata Rehd., M. fusca Schneid., M. glaucescens Rehd., M. ioensis Britt., M. lancifolia Rehd., M. platycarpa Rehd.

Eurasian distribution: \times Malus arnoldiana Sarg., M. asiatica Nakai, \times M. atrosanguinea Schneid., M. brevipes Rehd., M. florentina Schneid., M. floribunda Sieb., M. Halliana var. Parkmanii Rehd., \times M. Hartwigii Koehne, M. honanensis Rehd., M. kansuensis Schneid., M. micromalus Mak., M. hupehensis (Pamp.) Rehd. (= M. theifera Rehd.), M. pumila Mill., M. prunifolia Borkh., \times M. purpurea var. Eleyi Rehd., \times M. robusta Rehd., M. Sargenti Rehd., M. Sieboldii Rehd., M. sikkimensis Koehne, M. spectabilis Borkh., M. sylvestris Mill., M. toringoides Hughes, M. Tschonoskii Schneid., M. yunnanensis var. Veitchii Rehd., \times M. zumi Rehd.

A variety of an American species, M. *ioensis* var. *plena*, and the hybrid M. *Soulardi* proved to be moderately susceptible to G. *globosum*, while two species, M. *coronaria*, and M. *glabrata*, and the hybrid M. *Dawsoniana*, may be classed as mildly susceptible. On the remainder of the American species inoculated no infection could be observed; nevertheless, Thaxter (1889) obtained aecia on M. *pumila* Mill. (= M.

Malus Britt.). Of all the Eurasian species inoculated only one proved to be moderately susceptible, namely M. baccata, and three hybrids between Eurasian species, M. astracanica, M. magdeburgensis and M. sublobata, proved to be mildly susceptible.

Although a higher percentage of the American species proved to be susceptible, no outstanding correlation could be observed between relative susceptibility and geographic distribution. Nor can susceptibility be correlated with the type of leaf or type of infection produced. In all cases the lesions were small; they were rarely more than one to two millimeters in diameter.

The serial inoculations indicated a definite duration to the period of susceptibility which reaches a maximum about the time the blossoms are in the pink stage, and falls off to almost zero within a period of two weeks.

Excluding the species found to be susceptible it is very doubtful that any of the remaining species considered would suffer from the rust regardless of proximity to red cedars infected by *G. globosum*.

Previous reports would indicate that the commercial varieties of apple are more susceptible than the above ornamental types. Bliss (1931) using telial material from Iowa culturally obtained flecking on the varieties Baldwin, Delicious, Fameuse, Greening, McIntosh, Tolman, Wealthy, Yellow Transparent, and York Imperial. From reports of Clinton (1934), Thomas and Mills (1930), Sherbakoff (1932), Miller, Stevens and Wood (1933), and others, the relative susceptibility of the commercial varieties of apple may be classified as follows:

Varieties on which moderate to severe infection has been observed: Fallawater, Fameuse, Hubbardston, Northwestern Greening, Rhode Island Greening, and Wealthy.

Varieties reported susceptible: Baldwin, Cortland, Esopus, Spitzenburg, Fall Pippin, Gano, Golden Delicious, Jonathan, McIntosh, Newton, Northern Spy, Pewaukee, Rome Beauty, Russett, Stark, Tolman Sweet, Tompkins King, Wagener, Winesap, and York Imperial.

Resistant variety: Ben Davis.

Amelanchier¹

Farlow (1885) obtained spermogonia on leaves of Amelanchier canadensis Med. and Harshberger (1902) lists the same species as a suscept to G. globosum, exhibiting both spermogonia and aecia. Stone (1908) lists A. alnifolia² as a suscept from Alabama. The following species and

¹Relative susceptibility in this and the following genera was determined by non-serial inoculations.

²This probably refers to A. canadensis or A. laevis, since A. alnifolia is not native in Alabama.

varieties of Amelanchier were inoculated early in May, 1933: Amelanchier amabilis Wieg., A. asiatica Endl., A. Bartramiana Roem., A. Bartramiana \times A. laevis, A. canadensis Med., A. florida Lindl., \times A. grandiflora Rehd., A. humilis Wieg., A. humilis \times A. sanguinea, A. intermedia Spach, A. laevis Wieg., A. oblongifolia Roem., A. ovalis Med., A. sanguinea DC., A. sera Ashe, A. spicata K. Koch, A. stolonifera Wieg. All the inoculations gave negative results.

No reports can be found indicating that any of the species and varieties of *Amelanchier* are very susceptible to *G. globosum*.

Cydonia

Thaxter (1888) by culture obtained spermogonia on Cydonia oblonga Mill. (= C. vulgaris Pers.). Cook (1913) reports G. globosum as being of common occurrence on quince in New Jersey. Harshberger (1902), Clinton (1904), and Güssow (1915) report this rust on quince from two other states and from the Niagara Peninsula. Cydonia oblonga, inoculated by the writer in early May, 1933, proved to be moderately susceptible to G. globosum, producing both spermogonia and aecia. None of the varieties of Cydonia oblonga was inoculated, and no information can be given with respect to their relative susceptibility.

The remaining smaller genera were artificially inoculated and the results from these inoculations may be summarized and tabulated as follows:

Comptonia

Comptonia aspleniifolia Ait.-immune.

Crataegomespilus

Crataegomespilus grandiflora Bean (Crataegus Oxyacantha \times Mespilus germanica)—very suceptible; both spermogonia and aecia obtained; severe leaf killing resulted. Natural infection was also observed.

Mespilus

Mespilus germanica L.—moderately susceptible; both spermogonia and aecia obtained.

Myrica

Myrica caroliniensis Mill.-immune. M. Gale L.-immune.

Photinia

Photinia villosa DC.--immune.

Sorbaronia

Sorbaronia alpina Schneid. f. superaria Zabel (Aronia arbutifolia imes

Sorbus Aria)—resistant; exhibited spermogonia only. Aronia floribunda \times Sorbus Aucuparia—no infection obtained.

Sorbopyrus

Sorbopyrus auricularis Schneid. (Pyrus communis \times Sorbus Aria)—resistant; exhibited spermogonia only.

III. RELATIVE SUSCEPTIBILITY OF HOSTS WITHIN THE GENUS JUNIPERUS

To our present knowledge of the relative susceptibility of *Juniperus* little can be added by the writer. From previous reports, including those of Adams (1919), Arthur (1926) (1927), Bliss (1933), Claassen (1897), Connors (1934), Hunt (1926), Kern (1929), Martin (1922) (1925), Stone (1909), and others, and from an examination of the material in the Farlow Herbarium and the herbarium of Professor J. H. Faull, the host list includes at least six species of *Juniperus*, and at least four varieties of *Juniperus virginiana*. These have been presented in the subsequent host list.

It may be added here that Martin (1922) lists *Larix* species as hosts to *G. globosum* from nine states. No infection by this rust has ever been observed on *Larix* in the Arnold Arboretum.

Juniperus virginiana is the most common telial host throughout the eastern and central part of North America, having been reported from twenty-five states and from Ontario. Severe infection may occur, as exemplified at the Morton Arboretum, Lisle, Illinois and from many estates and nurseries surrounding Boston. The writer has observed trees that were killed by the abundance of galls present. Other trees, while not killed, were disfigured to such an extent that they were no longer of ornamental value and had to be removed. Juniperus scopulorum has also been reported as suffering from infection by G. globosum at the Morton Arboretum.

As far as the eastern and central part of North America are concerned no information to date would indicate that any species other than *Juniperus virginiana* and *Juniperus scopulorum* and their varieties would suffer to any extent from infection by *G. globosum*.

IV. THE HOSTS OF GYMNOSPORANGIUM GLOBOSUM FARL.

The following list includes as far as can be ascertained all the known hosts of G. globosum. The hosts have been arranged alphabetically by genera and their included species. Within the genus *Crataegus* the species and varieties have been arranged within their respective groups.

Following each host name in parentheses are symbols which may be defined as follows:

- a—as obtained by inoculations made by the writer; the inclusion of an author's name and reference indicates that this host has been determined previously by inoculation.
- n—as determined by observations of natural infection made by the writer.
- The inclusion of the abbreviated name of a State implies that this species has been reported previously as a host from that State.
- All new hosts submitted would necessarily be records for the State of Massachusetts, as all studies were made in the Arnold Arboretum, Boston.

HOSTS FOR THE 0 & 1 STAGE

An asterisk preceding a host indicates that the 0 stage only was found.

AMELANCHIER:

Amelanchier alnifolia Nutt. (Ala.),¹ A. canadensis Med. (Thaxter [1885]; Penn.).

CRATAEGOMESPILUS:

Crataegomespilus grandiflora Bean (a; n).

CRATAEGUS (by groups):

ANOMALAE:

Crataegus affinis Sarg. (a; n), C. asperifolia Sarg. (a; n; Vt.), C. Brockwayae Sarg. (a; n), C. Coleae Sarg. (n), C. cyclophylla Sarg. (a; n; Vt.), C. Dunbari Sarg. (a; n), C. Egglestonii Sarg. (a; n; N. Y., Vt.), C. errata Sarg. (a; n), C. honesta Sarg. (n), C. Ideae Sarg. (n), C. improvisa Sarg. (n), C. misella Sarg. (n), C. pinguis Sarg. (n; Mich.), C. putata Sarg. (n), C. repulsans Sarg. (n), C. Saundersiana Sarg. (n), C. scabrida Sarg. (a; n; Vt.), C. shirleyensis Sarg. (a; n), C. urbana Sarg. (n).

AZAROLI:

Crataegus Heldreichii Boiss. (a), C. tanacetifolia Pers. (N. Y.).

BRACTEATAE:

Crataegus Ashei Beadle (a; n), C. Harbisonii Beadle (a; Tenn.).

Coccineae:

Crataegus acclivis Sarg. (n), C. arcuata Ashe (n; Penn.), C. assurgens Sarg. (a; n), C. aulica Sarg. (n), C. caesa Ashe (n), C. chippewaensis Sarg. (n), C. confinis Sarg. (n), C. conspecta Sarg. (n),

¹See foot-note on page 126.

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C. contigua Sarg. (n), C. cristata Ashe (n), C. Dayana Sarg. (n), C. delecta Sarg. (n; Ill.), C. densiftora Sarg. (n), C. Eamesii Sarg. (n; Conn.), C. elongata Sarg. (n), C. fluviatilis Sarg. (a; n), C. fretalis Sarg. (n; Conn.), C. Hillii Sarg. (n), C. Holmesiana Ashe (a; n; Conn., N. Y., Vt.), C. Holmesiana var. tardipes Sarg. (n), C. Holmesiana var. villipes Ashe (n), C. irrasa Sarg. (n), C. lenta Ashe (n), C. lobulata Sarg. (n), C. Macounii Sarg. (n), C. lenta Ashe (n), C. lobulata Sarg. (n), C. Macounii Sarg. (n), C. miranda Sarg. (n), C. neolondinensis Sarg. (n; Conn.), C. pedicellata Sarg. (a; n), C. pedicellata var. gloriosa Sarg. (n), C. perrara Sarg. (n), C. polita Sarg. (n; previously reported, state not given), C. polita var. Tatnalliana (Sarg.) Eggl. (Mo., N. Y.), C. Pringlei Sarg. (a, Arthur [1907]; n; Conn., Ind., N. Y.), C. pura Sarg. (n), C. sejuncta Sarg. (n), C. sertata Sarg. (n), C. Thayeri Sarg. (n), C. uticaensis Sarg. (n), C. vivida Sarg. (n).

CRUS-GALLI:

Crataegus algens Beadle (a; n), C. arborea Beadle (a; n), C. arduennae Sarg. (a; n; Ind.), C. armata Beadle (a), C. arta Beadle (a), C. attenuata Ashe (a; n), C. barbata Sarg. (a), C. barrettiana Sarg. (a), C. Bartramiana Sarg. (a), C. bellica Sarg. (a), C. calophylla Sarg. (a), C. Canbyi Sarg. (a; n), C. cerasina Sarg. (n), C. consueta Sarg. (a; Mo.), C. crus-galli L. (a, Thaxter [1891]; n; Ind., Ky., Maine, Mass., Miss., Mo., N. Car., Ohio, Penn., Tenn., Va.), C. crus-galli var. arbutifolia Hort. (a), C. crus-galli var. exigua (Sarg.) Eggl. (n), C. crus-galli var. pyracanthifolia Ait. (a; n), C. crus-galli var. rubens Sarg. (a), C. efferta Sarg. (a), C. effulgens Sarg. (a), C. Engelmannii Sarg. (a; n; Mo.), C. erecta Sarg. (a; n), C. Farwellii Sarg. (a; n), C. fecunda Sarg. (n), C. Fontanesiana (Spach) Steud. (a; n), C. geneseensis Sarg. (a), C. hamata Sarg. (a), C. hirtella Sarg. (a), C. infesta Sarg. (a; n), C. insignis Sarg. (a), C. jasperensis Sarg. (a), \times C. Lavallei Herincq (a; n), C. lawrencensis Sarg. (a), C. leptophylla Sarg. (a; n), C. livoniana Sarg. (a; n), C. macra Beadle (a), C. Mohrii Beadle (a; n; Ga.), C. munita Sarg. (a), C. pachyphylla Sarg. (a), C. Palmeri Sarg. (a; n), C. paradoxa Sarg. (a), C. parciflora Sarg. (a; n), C. Parkae Sarg. (a), C. Pennypackeri Sarg. (a; n), C. peoriensis Sarg. (n), C. permera Sarg. (a; n), C. persimilis Sarg. (n), C. persistens Sarg. (a; n), C. phlebodia Sarg. (a; n), C. pilifera Sarg. (a), C. polyclada Sarg. (a), C. regalis Beadle (a; n), C. Reverchonii Sarg. (Tex.), C. rivalis Sarg. (a; n), C. robusta Sarg. (a; n), C. rotunda Sarg. (a), C. rubrifolia Sarg. (a; n), C. rudis Sarg. (a), C. setosa Sarg. (a), C. severa Sarg. (a), C. signata

Beadle (a), C. sinistra Beadle (a), C. sublobulata Sarg. (a; n), C. tardiflora Sarg. (a), C. tetrica Beadle (a; Tenn.), C. triumphalis Sarg. (a; n), C. uniqua Sarg. (a), C. vallicola Sarg. (a; n), C. villiflora Sarg. (a), C. Wilkinsoni Ashe (a).

DILATATAE:

Crataegus coccinioides Ashe (a; n; Mo.), C. dilatata Sarg. (= C. coccinioides var. dilatata [Sarg.] Eggl.) (a; Mass., N. Y., Penn., Vt.), C. durobrivensis Sarg. (n), C. hudsonica Sarg. (n).

DOUGLASIANAE:

Crataegus colorado Ashe (n), C. columbiana Howell (a), C. Douglasii Lindl. (a, Farlow [1885]; n), C. Douglasii f. badia Sarg. (n), C. Douglasii var. Suksdorfii Sarg. (n), C. erythropoda Ashe (n), C. Piperi Britt. (a), C. rivularis Nutt. (n).

FLAVAE:

Crataegus arrogans Beadle (a), C. colonica Beadle (a), C. dispar Beadle (a; S. Car.), C. elliptica Ait. (a), C. frugiferens Beadle (a), C. ignava Beadle (a; n), C. impar Beadle (a), C. insidiosa Beadle (a), C. limata Beadle (a), C. visenda Beadle (a).

INTRICATAE:

Crataegus apposita var. Bissellii (Sarg.) Eggl. (a; Conn.), C. biltmoreana Beadle (Mo.), C. Boyntonii Beadle (N. Car.), C. Buckleyi Beadle (a; N. Car.), C. Delosii Sarg. (a), C. foetida Ashe (a), C. fortunata Sarg. (a), C. laetifica Sarg. (a; n), C. macilenta Beadle (Ala.), C. modesta Sarg. (a), C. neobushii Sarg. (n), C. Painteriana Sarg. (a; n), C. rubella Beadle (a), C. Sargentii Beadle (a), C. scabra Sarg. (a; n), C. Schweinitziana Sarg. (Penn.), C. straminea Beadle (Penn.), C. tecta Beadle (Ala.), C. villicarpa Sarg.

MACRACANTHAE:

Crataegus ambrosia Sarg. (n), C. aquilonaris Sarg. (n), C. ardua Sarg. (n), C. baccata Sarg. (n), C. Balkwillii Sarg. (n), C. Beckiana Sarg. (n), C. bristolensis Sarg. (n), C. calpodendron (Ehrh.) Medic. (Penn.), C. chadfordiana Sarg. (n), C. Chapmanii (Beadle) Ashe (a; n; N. Car.), C. conspecta Sarg. (n), C. conspicua Sarg. (n; Vt.), C. corporea Sarg. (n), C. delectabilis Sarg. (Ont.), C. Deweyana Sarg. (a; n), C. divida Sarg. (n), C. dumicola Sarg. (n), C. Emersoniana Sarg. (a; n), C. ferentaria Sarg. (a; n), C. ferta Sarg. (n), C. fertilis Sarg. (a; n), C. finitima Sarg. (a; n), C. flagrans Sarg. (n), C. flammea Sarg. (n), C. frutescens Sarg. (n), C. fulgens Sarg. (a; n), C. fulgida Sarg. (n), C. Gaultii Sarg.

(a; n), C. gemmosa Sarg. (n), C. glabrata Sarg. (n), C. globosa Sarg. (a; n), C. Halliana Sarg. (n), C. hystricina Ashe (n), C. illinoiensis Ashe (n), C. integriloba Sarg. (n), C. Laneyi Sarg. (a; n), C. laurentiana Sarg. (n), C. macracantha Lodd. (a; n; Conn., N. Y., S. Dak., W. Va., Wis.), C. macracantha var. succulenta Rehd. (= C. succulenta Schrad.) (n; Penn., Wis.), C. membranacea Sarg. (n; Vt.), C. michiganensis Ashe (n), C. microsperma Sarg. (n), C. missouriensis Ashe (a; n), C. neofluvialis Ashe (n; Penn.), C. nuda Sarg. (n), C. ogdensburgensis Sarg. (n), C. Peckietta Sarg. (N. Y.), C. pellucidula Sarg. (n), C. peramoena Sarg. (n), C. pertomentosa Ashe (Iowa, Kansas), C. pisifera Sarg. (n; Vt.), C. praeclara Sarg. (a), C. propixa Sarg. (a), C. prunifolia (Marsh.) Pers. (a; n), C. pudens Sarg. (a; n), C. rhombifolia Sarg. (n; Conn., N. Y., Mass., Vt.), C. Robinsonii Sarg. (n), C. rupicola Sarg. (a), C. saeva Sarg. (n), C. Searsii Sarg. (n), C. simulata Sarg. (n), C. spatiosa Sarg. (n), C. spinulosa Sarg. (a; n), C. structilis Ashe (n), C. tomentosa L. (a, Thaxter [1880]; n; Ill., Iowa, Ky., Maine, Miss., Mo., Ohio, Ont., Que., Wis.), C. truculenta Sarg. (n), C. vaga Sarg. (a; n), C. vegeta Sarg. (a; n), C. venulosa Sarg. (a; n), C. venustula Sarg. (n), C. Wilsonii Sarg. (n).

MACROSPERMAE:

Crataegus Handyae Sarg. (n).

MICROCARPAE:

Crataegus Phaenopyrum (L. f.) Medic. ($\equiv C. cordata$ Ait.) (Del., Tenn.).

MOLLES:

Crataegus anomala Sarg. (n; Conn., N. Y.), C. arnoldiana Sarg. (a; n), C. Berlandieri Sarg. (n), C. canadensis Sarg. (n), C. champlainensis Sarg. (a; n; N. Y.), C. contortifolia Sarg. (n), C. corusca Sarg. (Ill.), C. digna Sarg. (n), C. dispessa Ashe (a; Mo.), C. dumetosa Sarg. (a; Mo.), C. Ellwangeriana Sarg. (a; n), C. exclusa Sarg. (n), C. Fulleriana Sarg. (n), C. Greggiana Eggl. (a), C. induta Sarg. (a), C. invisa Sarg. (n), C. lanigera Sarg. (n), C. lanuginosa Sarg. (a; n), C. lasiantha Sarg. (a; n; Mo.), C. lauta Sarg. (n), C. limaria Sarg. (a; n), C. macrophylla Sarg. (n), C. meridionalis Sarg. (n), C. mollipes Sarg. (n), C. mollis (Torr. & Gr.) Scheele (a, Bliss [1931]; n; Ill., Ind., Iowa, Kan., Ky., Mass., Mo., Nebr., Ohio), C. noelensis Sarg. (n), C. nutans Sarg. (n), C. pennsylvanica Ashe (n), C. peregrina Sarg. (a; n), C. Robesoniana Sarg. (n), C. sera Sarg. (a; n), C. submollis Sarg. (a; n; Vt.),

C. Tatnalliana Sarg. (n), C. Tracyi Ashe (a), C. transmississippiensis Sarg. (n), C. Treleasei Sarg. (Mo.), C. umbrosa Sarg. (n), C. urbica Sarg. (n).

NIGRAE:

 \times Crataegus hiemalis Lge. (n), C. nigra Kit. (n).

OXYACANTHAE:

Crataegus monogyna Jacq. (a; n; Mass.), C. monogyna var. inermis Rehd. (a), C. monogyna var. laciniata (Stev.) Regel (a; n), C. monogyna var. pteridifolia Rehd. (a; n), C. Oxyacantha L. a, Farlow [1885]; n; Maine, Mass., Ont.), C. Oxyacantha var. Gireoudii Bean (a), C. Oxyacantha var. leucocarpa Loudon (a), C. Oxyacantha var. rubra Hort. (a), \times C. sorbifolia Lge. (a; n).

PINNATIFIDAE:

Crataegus pinnatifida Bge. (n), C. pinnatifida var. major N. E. Br. (n).

PRUINOSAE:

Crataegus alacris Sarg. (a), C. amoena Sarg. (a), C. arcana Beadle (n), C. aridula Sarg. (a), C. aspera Sarg. (a; n), C. ater Ashe (a), C. beata Sarg. (n), C. bellula Sarg. (n), C. bracteata Sarg. (a), C. caerulescens Sarg. (n), C. cestrica Sarg. (a), C. Clintoniana Sarg. (n), C. cognata Sarg. (n), C. comata Sarg. (n), C. comparata Sarg. (n), C. confragosa Sarg. (n), C. conjuncta Sarg. (a; n; Conn., Mass.), C. delawarensis Sarg. (a), C. deltoides Ashe (a; n), C. disjuncta Sarg. (a; Mo.), C. divisifolia Sarg. (n), C. exornata Sarg. (n), C. Ferrissii Ashe (n), C. festiva Sarg. (Conn., Vt.), C. formosa Sarg. (a; n), C. fusca Sarg. (a), C. georgiana Sarg. (a; n), C. glareosa Ashe (n), C. horridula Sarg. (a; n), C. incisa Sarg. (a; n), C. inusitula Sarg. (a; n), C. iracunda Beadle (a; n), C. Jesupii Sarg. (Penn.), C. Kellermanii Sarg. (a), C. latifrons Sarg. (n), C. latisepala Ashe (a; n), C. leiophylla Sarg. (a; n; N. Y.), C. levis Sarg. (a; n), C. littoralis Sarg. (a), C. locuples Sarg. (a; n), C. numerosa Sarg. (a; n), C. oblita Sarg. (a; n), C. Pequotorum Sarg. (a; n; Conn.), C. perampla Sarg. (a; n), C. perjucunda Sarg. (a), C. philadelphica Sarg. (a; n), C. pilosa Sarg. (n), C. platycarpa Sarg. (a), C. Porteri Britt. (n), C. procera Sarg. (a; n), C. pruinosa (Wendl.) K. Koch (a; n; Conn., Mo., N. Y., Ohio, S. Car., Penn.), C. pruinosa var. latisepala (Ashe) Eggl. (Mass., Mich.), C. pulchra Sarg. (a; n), C. quinebaugensis Sarg. (Conn.), C. radiata Sarg. (a; n), C. relicta Sarg. (n), C. remota Sarg. (n), C. rubicundula Sarg. (a; n), C. scitula Sarg. (n), C. sicca Sarg. (n), C. sitiens Ashe (a; n), C. tribulosa Sarg.
(n), C. uplandia Sarg. (n), C. virella Ashe (a).

PRUNIFOLIAE:

Crataegus decorata Sarg. (n; Mo.).

PULCHERRIMAE:

Crataegus ancisa Beadle (Ala.), C. illustris Beadle (a).

PUNCTATAE:

Crataegus amnicola Beadle (a; n), C. angustata Sarg. (a), C. barbara Sarg. (a; n), C. Brownietta Sarg. (n), C. calvescens Sarg. (n), C. celsa Sarg. (n), C. collina Chapm. (Ga., Va.), C. compacta Sarg. (n), C. Dewingii Sarg. (n), C. Eatoniana Sarg. (n), C. Eastmaniana Sarg. (a; n), C. florifera Sarg. (a; n), C. glabrifolia Sarg. (a; n), C. incerta Sarg. (n), C. Lettermanii Sarg. (a), C. macropoda Sarg. (a; n), C. notabilis Sarg. (n), C. pausiaca Ashe (a; n), C. porrecta Ashe (n), C. praestans Sarg. (a; n), C. pratensis Sarg. (a; n), C. punctata Jacq. (a; n; Ill., Ind., Iowa, Maine, Mass., Mich., Mo., N. Y., N. Car., Ohio, Ont. Penn., Vt., W. Va.), C. punctata var. aurea Ait. (a; n), C. punctata var. canescens Britt. (n), C. punctata var. maliformis ? (n), C. punctata mutabilis Gruber (a; n), C. secta Sarg. (a; n), C. sordida Sarg. (a), C. suborbiculata Sarg. (a; n), C. succincta Sarg. (a), C. sucida Sarg. (Mo.), C. swanensis Sarg. (a; n), C. tenax Ashe (a; n), C. umbratilis Sarg. (a; n), C. verruculosa Sarg. (n), C. vicina Sarg. (a).

ROTUNDIFOLIAE:

Crataegus Bicknellii Eggl. (n), C. Blanchardii Sarg. (n), C. Brainerdii Sarg. (a; n; Vt.), C. Brunetiana Sarg. (a), C. caliciglabra Schuette (a), C. chrysocarpa Ashe (N. Y.), C. coccinata Sarg. (n), C. crassifolia Sarg. (n), C. cupulifera Sarg. (n), C. divergens (Peck) Sarg. (a), C. Dodgei Ashe (n), C. Evansiana Sarg. (a; n), C. Faxonii Sarg. (n), C. illuminata Sarg. (n), C. inaudita Sarg. (a), C. insolens Sarg. (n), C. Jackii Sarg. (n), C. Jonesae Sarg. (a; n), C. Keepii Sarg. (n), C. Kennedyi Sarg. (n), C. kingstonensis Sarg. (n), C. lemingtonensis Sarg. (n), C. maligna Sarg. (n), C. mansfieldensis Sarg. (n), C. Margaretta Ashe (n; Iowa, Mo.), C. Margaretta f. xanthocarpa Sarg. (n), C. Maribella Sarg. (n), C. Oakesiana Eggl. (a), C. praecoqua Sarg. (= C. praecox Sarg.) (n; N. Y.), C. Proctoriana Sarg. (n), C. propria Sarg. (n), C. rotundata Sarg. (n), C. rotundifolia Moench (= C. coccinea L. p. p.) (a, Thaxter [1889]; n; Iowa, Mo., N. Y., Ont., Vt.), C. rotundifolia var.

aboriginum Sarg. (n), C. rotundifolia var. pubera Sarg. (n), C. rotundifolia f. rubescens Sarg. (n), C. varians Sarg. (n), C. Websteri Sarg. (n), C. Williamsii Eggl. (n).

SANGUINEAE:

Crataegus altaica Lange (n), C. dsungarica Zab. (n), \times C. Lambertiana Lge. (n), C. Maximowiczii Schneid. (n), C. sanguinea Pall. (Ont.).

SILVICOLAE:

Crataegus aemula Beadle (n), C. allecta Sarg. (n), C. Barryana Sarg. (n), C. blairensis Sarg. (n), C. congestiflora Sarg. (a; n), C. cruda Sarg. (n), C. delectata Sarg. (n), C. diffusa Sarg. (= C. silvicola var. Beckwithae [Sarg.] Eggl.) (n; Conn., Vt.), C. dissona Sarg. (n; Mass., N. H., N. Y.), C. effera Sarg. (n), C. filipes Ashe (n), C. foliata Sarg. (n), C. Fretzii Sarg. (n), C. filipes Ashe (n), C. foliata Sarg. (n), C. Fretzii Sarg. (n), C. gravis Ashe (n), C. iterata Sarg. (n), C. laetans Sarg. (n), C. Livingstoniana Sarg. (n), C. luxuriosa Sarg. (n), C. macera Sarg. (n), C. Maineana Sarg. (n), C. medioxima Sarg. (n), C. opulens Sarg. (n), C. promissa Sarg. (a; n), C. prona Ashe (n), C. puta Sarg. (n), C. radina Sarg. (n), C. recordabilis Sarg. (n), C. Robbinsiana Sarg. (Vt.), C. ruricola Sarg. (n), C. stolonifera Sarg. (n), C. strigosa Sarg. (n), C. tortuosa Sarg. (n), C. xanthophylla Sarg. (a; n).

TENUIFOLIAE:

Crataegus acuminata Sarg. (a; n), C. acutiloba Sarg. (a; n; N. Y., Vt.), C. alnorum Sarg. (n), C. apiomorpha Sarg. (n), C. ascendens Sarg. (n), C. asperata Sarg. (n), C. basilica Beadle (a), C. bella Sarg. (a; n), C. benigna Sarg. (a; n), C. blandita Sarg. (n), C. Boothiana Sarg. (n), C. colorata Sarg. (a; n; Ont.), C. conferta Sarg. (n), C. crudelis Sarg. (n), C. cyanophylla Sarg. (a; n), C. Damei Sarg. (n), C. delucida Sarg. (n; Vt.), C. demissa Sarg. (n; Mass., Vt.), C. dissimilis Sarg. (a; n; Conn., Mass., Vt.), C. Edsoni Sarg. (n; N. H., Vt.), C. Eganii Ashe (n), C. firma Sarg. (n), C. flabellata (Bosc.) K. Koch (a; n), C. florea Sarg. (n), C. Forbesae Sarg. (a; n; Conn.), C. fucosa Sarg. (n), C. genialis Sarg. (a; n; Vt.), C. glaucophylla Sarg. (a; n; Conn., N. Y.), C. gracilipes Sarg. (n), C. Gruberi Ashe (n), C. Habereri Sarg. (n), C. Hadleyana Sarg. (n), C. heidelbergensis Sarg. (n), C. insolita Sarg. (n), C. leptopoda Sarg. (n), C. lucorum Sarg. (n), C. luminosa Sarg. (n), C. macrosperma Ashe (n; N. Y., Penn.), C. marcida Ashe (n), C. matura Sarg. (n), C. media Sarg. (n), C. merita Sarg. (n), C. miniata Ashe (n), C. modica Sarg. (n), C. monstrata Sarg. (n), C. Napaea Sarg. (n), C. nescia Sarg.

(n), C. otiosa Ashe (n), C. Paddockeae Sarg. (n), C. Paineana Sarg. (n), C. pallidula Sarg. (n), C. parviflora Sarg. (n), C. pastorum Sarg. (a; n), C. paucispina Sarg. (a), C. pentandra Sarg. (a; n; Vt.), C. perlevis Ashe (n), C. populnea Ashe (n), C. pumila Sarg. (n), C. retrusa Ashe (n), C. roanensis Ashe (Ky., Vt.), C. rubicunda Sarg. (n), C. rubrocarnea Sarg. (n), C. rufipes Ashe (n), C. sarniensis Sarg. (n), C. saturata Sarg. (n), C. serena Sarg. (n), C. sextilis Sarg. (n), C. siderea Sarg. (n), C. Slavini Sarg. (n), C. streeterae Sarg. (n), C. tenella Ashe (n; Conn.), C. tenera Ashe (n), C. tenera Ashe (n), C. tenera Sarg. (n), C. tenera Ashe (n), C. tenera Ashe (n), C. tenera Ashe (n), C. tenera Ashe (n), C. tenera Sarg. (n), C. trachyphylla Sarg. (n), C. uber Ashe (n), C. viridimontana Sarg. (n), C. vittata Ashe (a).

TRIFLORAE:

Crataegus austromontana Beadle (a).

UNIFLORAE:

Crataegus armentalis Beadle (a), C. Brittonii Eggl. (a).

VIRIDES:

Crataegus abbreviata Sarg. (a; n), C. atrorubens Ashe (a; n), C. blanda Sarg. (a), C. enucleata Sarg. (a; n), C. lanceolata Sarg. (a; n), C. larga Sarg. (a), C. lutensis Sarg. (a), C. nitens Sarg. (a), C. nitida (Engelm.) Sarg. (a; n), C. ovata Sarg. (a; n), C. penita Beadle (a), C. poliophylla Sarg. (a), C. uvaldensis Sarg. (a), C. velutina Sarg. (a), C. viridis L. (a; n; Okla.), C. vulsa Beadle (a; n).

CYDONIA:

Cydonia oblonga Mill. ($\equiv C.$ vulgaris Pers.) (a; Thaxter [1889]; Conn., Niagara Peninsula, N. J., Penn.).

MALUS:

Malus angustifolia Michx. (S. Car.), $\times M$. astranica Dum.-Cours. (a), M. baccata Borkh. (a), M. coronaria Mill. (a, Arthur [1907]), $\times M$. Dawsoniana Rehd. (a), M. glabrata Rehd. (a), M. glaucescens Rehd. (Ind.), M. ioensis var. plena Rehd. (a), $\times *M$. magdeburgensis Schoch (a), M. pumila Mill. (= M. Malus [L.] Britt.) (Thaxter [1886]; Conn., Maine, Mass., Mo., N. H., N. J., N. Y., Vt.), $\times M$. Soulardi Britt. (a), $\times M$. sublobata Rehd. (a). MESPILUS:

Mespilus germanica L. (a).

PYRUS:

Pyrus Balansae Decne. (a), P. betulaefolia Bge. (a; n), P. Bretschneideri Rehd. (a), P. communis L. (a; Conn., Ind., Iowa, Mass.,

N. Car., N. Y., Penn., R. I.), *P. elaeagrifolia* Pall. (a), **P. Korshinskyi* Litv. (a), **P. Michauxii* Bosc (a), **P. Lindleyi* Rehd. (a), **P. nivalis* Jacq. (a), *P. phaeocarpa* Rehd. (a), *P. salicifolia* Pall. (a), *P. serotina* Rehd. (a), **P. serrulata* Rehd. (a), *P. syriaca* Boiss. (a), *P. ussuriensis* Maxim. (a).

SORBARONIA:

 \times *Sorbaronia alpina Schneid. f. superaria Zabel (a).

SORBOPYRUS:

 \times *Sorbopyrus auricularis Schneid. (a).

SORBUS:

Sorbus americana Marsh. (a; Thaxter [1887 and 1891]; Maine, Mass., N. Y., Penn., Vt.), S. americana var. fructu albo Hort. (a), *S. americana var. nana Hort. (a), \times *S. arnoldiana Rehd. (a), *S. Aucuparia L. var. Backhousei Hort. (a), *S. dumosa Greene (a), *S. japonica var. calocarpa Rehd. (a), \times S. thuringiaca Fritsch (a).

HOSTS FOR THE III STAGE

JUNIPERUS:

Juniperus lucayana Britt. (= J. barbadensis Auth., not L.) (Ala.), J. communis L. (Penn.), J. fragrans Hort. (Ont.), J. horizontalis Moench (= J. prostrata Pers.) (N. Dak.), J. scopulorum Sarg. (Colo., Ill., Iowa, N. Dak.), J. virginiana L. (Ala., Conn., Ill., Ind., Iowa, Kansas, Ky., La., Mass., Mich., Minn., Miss., Mo., N. H., N. Y., N. Car., N. Dak., Ohio, Okla., Ont., Penn., S. Car., Tex., Vt., W. Va., Wis.), J. virginiana var. Burkii Hort. (Ill.), J. virginiana var. Canaertii Sénécl. (Ill.), J. virginiana var. elegantissima Hochst. (Ill.), J. virginiana var. glauca Carr. (Ill.).

LARIX:

Larix sp. (Conn., Kan., Minn., Miss., N. Y., Okla., Tex., Va., W. Va.).

V. SUMMARY

1. At least ten genera, all within the Pomoideae, include hosts on which the aecial phase of *Gymnosporangium globosum* may occur. One genus only, *Juniperus*, is known with certainty to include hosts for the telial phase.

2. Relative susceptibility to G. globosum within the respective host genera has been studied by the writer to determine: (1) immune species; (2) resistant species which suffer no material harm from this rust; (3) moderately susceptible species which may be infected but not to the extent of defoliation; and (4) very susceptible species whose foliage can be ruined by G. globosum. 3. These investigations were carried out by means of artificial inoculations, substantiated by observations of natural infection where present, in the Arnold Arboretum of Harvard University.

4. The results of these investigations on relative susceptibility, added to those of previous writers, may be summarized as follows:

A. On host genera for the aecial phase of G. globosum.

(a) On the genera on which serial inoculations were made.

Cratacgus. A marked variation in susceptibility was found within the genus, the degree of which is dependent primarily on the thickness and the rapidity of deposition of the foliar cuticle. Due to the large number of species and the unstable condition of taxonomy within the genus, the classification according to susceptibility to *G. globosum* was made by groups rather than by species. The observations on natural infection substantiated the results obtained by artificial inoculation. Suggestions have been made for the selection of resistant species and varieties within the respective groups.

Pyrus. Of seventeen species inoculated, one proved to be very susceptible, two moderately susceptible, ten resistant, and three immune. Certain of the commercial varieties are classified from previous reports according to their susceptibility to *G. globosum*.

Sorbus. Infection was obtained on all the species and varieties of American origin inoculated. Of thirty-one species and varieties of Eurasian origin inoculated four are resistant, the remainder are immune.

Malus. Of seven American species inoculated three proved to be susceptible, while infection was obtained on only one species and three hybrids of the twenty-seven Eurasian types considered. Infection was obtained also on two hybrids between Eurasian and American species. Certain of the commercial varieties are classified from previous reports according to their susceptibility to *G. globosum*.

(b) On the genera otherwise inoculated.

Amelanchier. Seventeen species and varieties were inoculated; all inoculations gave negative results. Nevertheless, the rust has been reported on two species, A. canadensis and A. alnifolia.¹ It is not probable that any species in this genus would suffer severely from infection by G. globosum.

Cydonia. Gymnosporangium globosum has been reported as occurring commonly on quince in New Jersey. Cydonia oblonga by culture proved to be moderately susceptible to G. globosum.

Crataegomespilus, Mespilus, Sorbaronia and Sorbopyrus. The re-

¹See foot-note on page 53.

sults obtained by inoculations on representatives of these more or less susceptible genera have been tabulated on page 127.

Comptonia, Myrica and Photinia. These genera were found by inoculation to be immune.

B. Host genera for the telial phase of G. globosum.

Juniperus. No information to date would indicate that any species other than J. virginiana and J. scopulorum and their varieties would suffer to any extent from infection by G. globosum.

5. In the genera *Crataegus*, *Malus*, *Pyrus* and *Sorbus* there is a definite duration to the period of susceptibility reaching a maximum during or immediately after foliar expansion.

6. In selecting ornamentals to plant in vicinities where *Gymnosporangium* rusts are present, it must be remembered that the relative susceptibility of any host to *G. globosum* is not necessarily correlated with its susceptibility to other Gymnosporangium rusts.

7. No consideration has been given to the possibility of variation in virulence within different strains of G. globosum. Such may very well occur.

8. A complete list of all the known hosts of *G. globosum* is recorded in this paper.

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VIII. EXPLANATION OF PLATES

Plate 125

Illustrations of the tendency of the mycelium to follow along the veins of Crataegus leaves:

- Fig. 1. A series of lesions obtained by inoculation on a waxy-type of leaf (*Crataegus fecunda*), giving the appearance of systemic infection along the veins.
- Fig. 2. A single lesion at the spermogonial stage on *Crataegus suavis*. The rust mycelium concentrates along the vascular strands causing the latter to show as bright yellow lines within the lesion.
- Fig. 3. A single lesion extends along a lateral vein, forking at the junction with a sub-lateral vein.
- Fig. 4. A typical vein infection; the long axis of the lesion corresponding with that of the vein.

Plate 126

Types of infections and their resultant effects on Crataegus leaves (explanations in text):

- Fig. 1. Illustrates the relative amount of leaf killing caused by vein infections, and by infections not primarily associated with the main veins.
- Fig. 2. A single infection on the mid vein resulting in the death of over one-half of the leaf.
- Fig. 3. A very small type of lesion, exhibiting no hypertrophy and producing a single aecial horn.
- Fig. 4. A single vein infection (indicated by the black spot on the plate), killing the leaf behind the lesion along the vein; suggesting a toxic agent on the part of the rust.
- Fig. 5. A large single lesion which died shortly after spermogonia appeared; suggesting hypersensitivity on the part of the host.

Plate 127

- Figs. 1, 2, 3 and 4, illustrate the relative degree of susceptibility of *Cratae*gus Pringlei, as indicated by serial inoculations on April 25, May 9, May 23 and June 28, 1934, respectively.
- Fig. 5. The type of chamber used in all the inoculations. (Explanations in the text.)

Plate 128

Serial inoculations on *Crataegus Jonesae* to illustrate the period of susceptibility (explanations in text):

- Fig. 1. Inoculated May 7, at which time the two upper leaves were very small, while the five basal leaves were well expanded. As indicated by the number of lesions the latter are the more susceptible.
- Fig. 2. Inoculated June 8, at which time all leaves were fully expanded; the two upper (youngest) leaves are now the more susceptible.

LABORATORY OF PLANT PATHOLOGY,

ARNOLD ARBORETUM, HARVARD UNIVERSITY.

Plate 125



THE HOSTS OF GYMNOSPORANGIUM GLOBOSUM Farl.

Plate 126



THE HOSTS OF GYMNOSPORANGIUM GLOBOSUM Farl.



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