Beet Mosaic and Beet Yellows Virus Transmission by the Green Peach Aphid

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For a period of years, vector-virus relationship studies have been in progress in many areas of the world, and much of this work has been with virus diseases of sugar beets. The knowledge that has been accumulated is still far from complete, but it is at a stage which allows for some speculation concerning the phylogeny of vector-virus relationships. The following remarks will be confined to a relatively narrow portion of the phylogenetic continuum which seems to be emerging within the aphid-borne viruses. However, it appears likely that the other vector-virus relationships will fit into the same general scheme.

In general, present day classification puts vector-virus associations into two broad, relatively inclusive, groups; namely, the *persistent* and the *nonpersistent*. The implications of the terminology are that the former are retained for long periods of time by vectors, while the latter are not.

Beet mosaic virus, in its vector association, might be cited as being typical of the nonpersistent group, while the yellow-net virus might be said to be representative of the persistent group. Yellows, in its vector-virus relationships, is neither typically persistent, nor is it typically nonpersistent. Being somewhat intermediate between the two extremes, it might be called *semi-persistent*. The resemblances and differences between these two viruses, *i.e.,* beet mosaic and beet yellows, perhaps can be best illustrated by taking up three fundamental phases of aphid transmission: acquisition, inoculation, and retention.

Acquisition

Beet mosaic is a virus that can be acquired by aphids within a few seconds of feeding on diseased tissue. The graph (Figure 1), illustrates a theoretical curve which might be derived from the published data (4, 5) on the acquisition threshold period of beet mosaic and the green peach aphid, *Myzus persicae* (Sulz.). It should be emphasized that the time scale is in *seconds*. As can be seen, between 5 and 10 seconds the insects begin to acquire virus. The probability of virus acquisition rises to a maximum in the 20 to 30 second range, and then, if the feeding period is prolonged, loss of infectivity occurs. This is of importance, since the usual interruption of a trial penetration by an aphid which has previously been fasted occurs in the 15 to 20 second range.

Recent evidence by Bradley (2) and others (1), indicates that the insects acquire such viruses as beet mosaic from the epidermal tissues of the plants, and that as aphids penetrate into deeper tissues, they begin to feed in areas which are relatively poor sources of virus. Thus, it would appear that beet mosaic is a virus which reaches the most favorable concentrations for insect transmission in the epidermal layers of the plant.

An examination of the limited data on the acquisition of beet yellows virus by the green peach aphid would indicate that the same type of curve

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[2] Numbers in parentheses refer to literature cited.

could be fitted, and such a graphic representation is seen in Figure 2. The main difference is in the time scale. With beet mosaic, the time scale was in *seconds,* while in yellows, the time scale was in *hours.* These data indicate that as aphids feed for a period of hours on a yellows infected plant, there is a gradual rise in the probability of virus acquisition until a maximum is reached between 12 and 24 hours. Extension of the curve is hazardous, and whether or not prolonged feeding on the diseased source will cause a gradual decrease in vector efficiency is not known at the present time. The only indications are from limited experiments where the performance of insects fed on a virus source plant for a single 24 hour period was com-

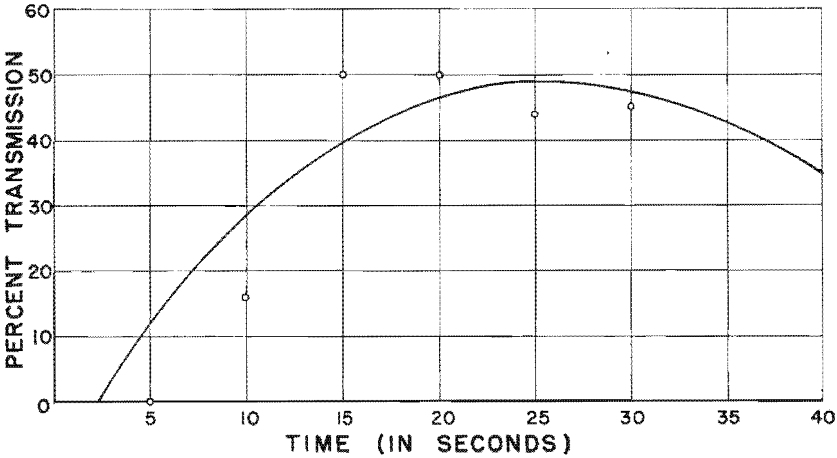

Figure 1.—Theoretical curve calculated from published data on the acquisition threshold period of beet mosaic virus and the green peach aphid. $\hat{Y} = 29.37 + 4.3\ (X - 50) - 0.08\ (X^2 - 1083.3)$.

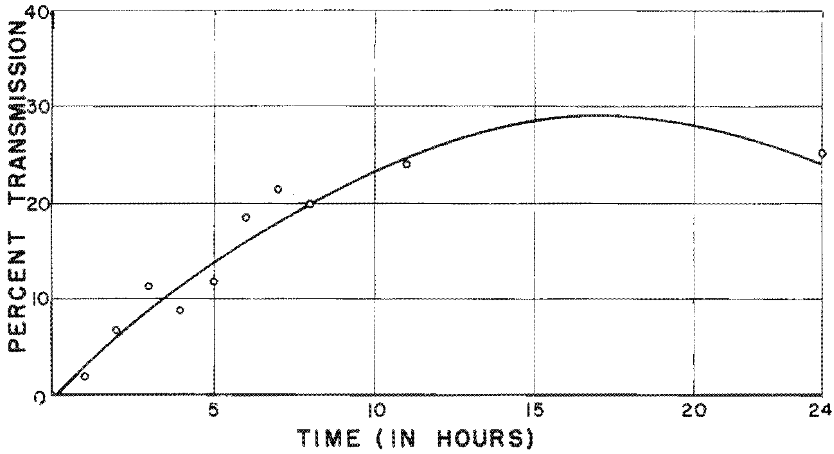

Figure 2.—Theoretical curve calculated from data gathered on the acquisition threshold period of the beet yellows virus and the green peach aphid. $\hat{Y} = 14.23 + 3.34\ (X - 6.55) - 0.095\ (X^2 - 84)$.

pared to that of insects fed on the same virus source plant for 2 consecutive 24 hour periods. In this case the 24 hour fed insects transmitted virus at about 30 percent efficiency, while the 48 hour fed insects transmitted virus at about 11 percent efficiency (41 infections out of 140 plants tested, versus 16 infections out of 140 plants tested, adjusted $X^2 = 12.68$, d.f. 1, $p = .001$).

However, using the 48 hour result in the calculation of the parabola, it is evident that the estimated parabola decreases too fast. However, the hypothesis that a parabolic curve, or some portion thereof, could be used to represent the manner in which the beet yellows virus is acquired by feeding green peach aphids has yet to be disproven.

Thus, it is quite possible that a similar pattern of virus acquisition exists for both the beet mosaic and the beet yellows viruses, except that the time scales are entirely different, one being in seconds, and the other being in hours. With this as a basis, it might be speculated that the acquisition of the mosaic virus is best when the aphid stylets are in the epidermal region, while acquisition of the yellows virus is best when the insects are penetrating into the mesophyll or mesophyll-phloem area. In any event, it would seem that in the field, the prevention of insects from acquiring beet yellows virus would be a much easier task than the prevention of the acquisition of beet mosaic virus by migrating alatae.

Inoculation

The inoculation threshold period of beet mosaic virus by the green peach aphid, like that of the acquisition threshold period, is a matter of seconds. The curve (Figure 3) rises rapidly to a maximum, and further increase in penetration time is of no benefit. The same type of curve (Figure 4) is applicable to data on the inoculation threshold period of beet yellows virus, but, as in the case of the acquisition period, the time scale is in hours. However, based upon the available evidence, the rapid

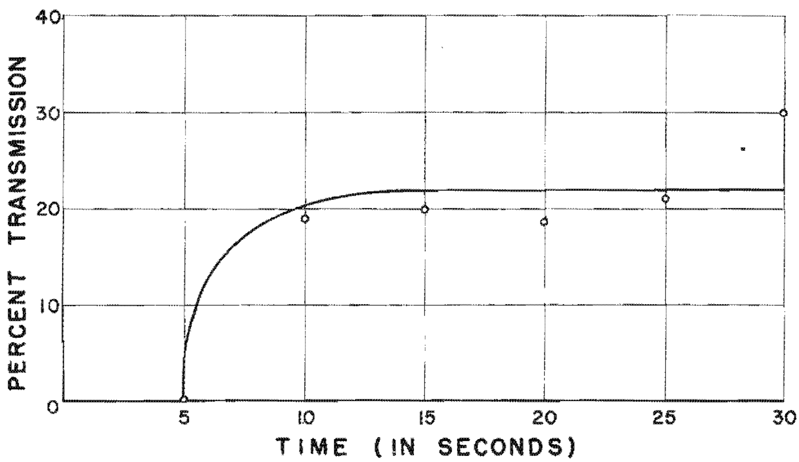

Figure 3.—Theoretical curve ($\hat{Y} = 1 - e^{-\alpha t}$, $\alpha = 0.60$, t = seconds — 5) calculated from data published on the inoculation threshold period of the beet mosaic virus and the green peach aphid; 22 percent transmission was taken as unity.

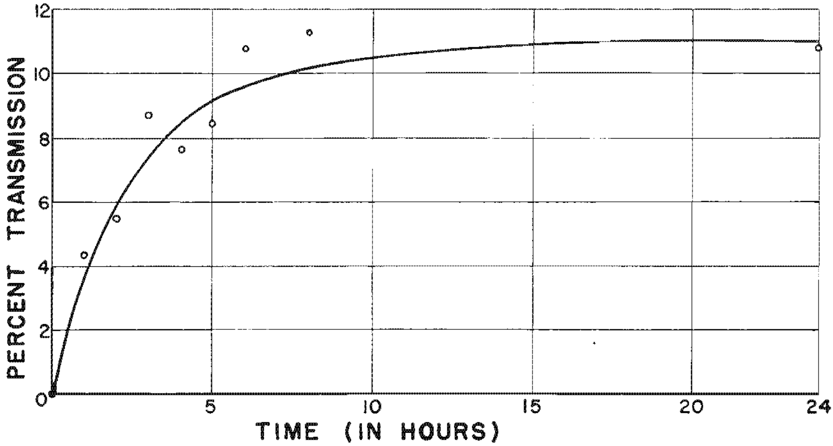

Figure 4.—Theoretical curve ($\hat{Y} = 1 - e^{-\alpha t}$, $\alpha = 0.345$, t = hours) calculated from data gathered on the inoculation threshold period of the beet yellows virus and the green peach aphid; 11.44 percent transmission was taken as unity.

initial rise of the curve indicates that the inoculation threshold period is a matter of minutes, with a maximum efficiency in virus inoculation being reached in about 3 hours.

It would appear that the inoculation of virus is not as rigidly dependent upon a particular tissue as is acquisition, *i.e.*, the probability of successfully establishing an infection is not as precisely governed by specific tissue regions as is that of acquiring virus. This may mean that the virus when once introduced into a favorable tissue can survive with low levels of multiplication until such time as it is translocated to the more favorable regions for virus increase.

Virus Retention by Aphids

Since the beet mosaic virus is rapidly acquired and rapidly inoculated, it is not particularly surprising to find that the period of retention of a virus charge by an infective insect is brief. The actual time which a given aphid will retain a virus charge sufficiently large to insure infection depends to a considerable extent upon the treatment of the vector, *e.g.*, whether the aphid is feeding or fasting after acquisition, as well as the temperature. However, for practical simplicity, beet mosaic is not retained by the green peach aphid for much more than a half hour. The data can be reduced to an exponential curve of the order $p = e^{-\alpha t}$ [3], and estimating the half-life from limited data gathered at Berkeley, it would place the half-life of beet mosaic virus in a feeding insect at approximately 5 minutes. This would mean that there is a 50 percent reduction in the probability of having an infective insect for every 5 minutes that it feeds on a healthy plant. A graphic representation of such data is given in Figure 5.

The same type of curve can be developed using the beet yellows virus and the green peach aphid, but here again the time scale is different. In

[3] In the equation, p = the probability of obtaining an infection, e is the base of natural logarithms, α is a constant, and t = time.

the case of the beet yellows virus, the half-life is approximately 8 hours, instead of 5 minutes, as is illustrated in Figure 6.

Thus, it can be seen that the basic type of relationship existing between the beet mosaic and the beet yellows viruses and the vector *Myzus persicae* (Sulz.) under the experimental conditions imposed, differs mainly in a quantitative way, rather than in a qualitative way. This is not a new concept. It has been suggested and advocated with various lines of reasoning by the English workers for a period of years, mainly K. M. Smith (3) and M. A. Watson (6). It must be remembered, however, that data are not

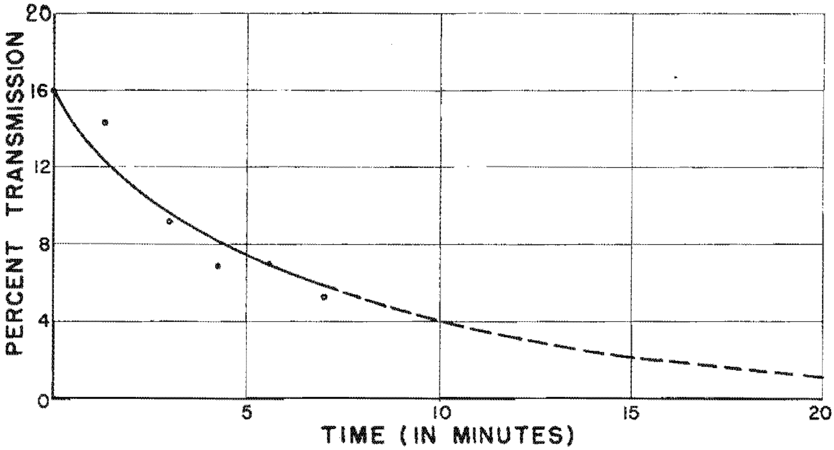

Figure 5.—Theoretical curve ($\hat{Y} = e^{-at}$, $a = 0.143$, t = minutes) calculated to fit data published on the retention of beet mosaic virus by the green peach aphid. The curve was calculated to fit 16 percent transmission at zero time. The dotted portion represents extrapolation.

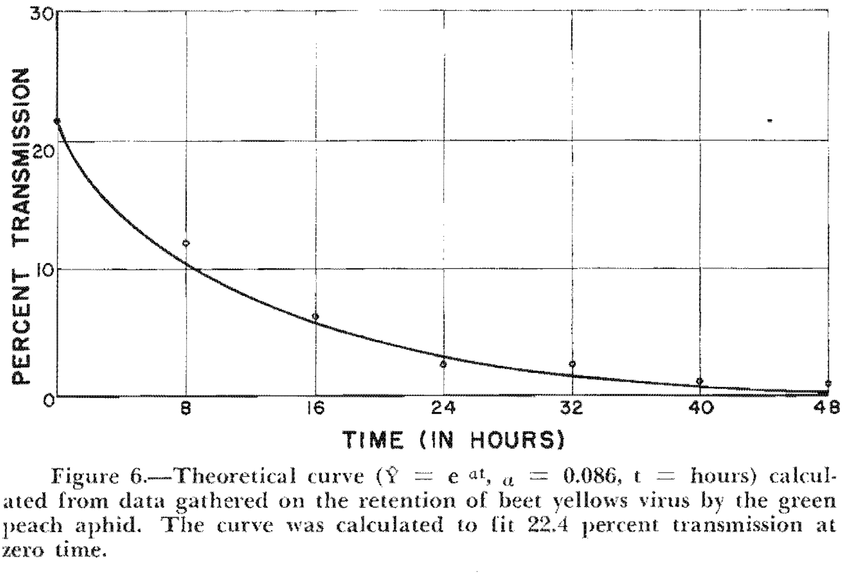

Figure 6.—Theoretical curve ($\hat{Y} = e^{at}$, $a = 0.086$, t = hours) calculated from data gathered on the retention of beet yellows virus by the green peach aphid. The curve was calculated to fit 22.4 percent transmission at zero time.

available to date which permit proper assessment of the limitations of the concept.

Speculating further, it might be suggested that the more dependent a virus has become upon a particular host plant, or the more specific are the demands of the virus for certain tissue regions, the more tenacious are the vector-virus relationships likely to be.

Beet mosaic, a virus which reaches maximum concentration for vector transmission within the epidermal tissues of the plant, but a virus which has not yet become specialized to the extent that it can be readily transmitted from plant to plant by wind-blown leaf contact, is still dependent upon insects for its transmission and prepetuation. Evolution (without any implied teleology) has admirably fitted beet mosaic virus to transport by means of aphids, since these insects apparently find their host plants largely by chance and random probing in epidermal tissues of plants. Favoring the transmission are the low degree of vector specificity, the rapid acquisition during a trial feeding penetration, and the rapid inoculation by a similar feeding attempt. What is lost in advantage by the inability of the virus to survive for long periods within the vectors is gained in the lack of vector specificity.

Beet yellows virus, one which apparently requires a slightly different tissue for optimum multiplication and survival in transmission concentrations, presumably the mesophyll or the mesophyll-phloem tissue, is more dependent on insect vectors for survival. In this case, the vector-virus relationships, *i.e.*, acquisition, inoculation, and retention, are less ephemeral. Since the vectors, to acquire the virus, must penetrate more deeply into the tissues of the plant and since only those vectors which can use beet for a host plant for their own benefit are likely to penetrate the beet tissue for long periods, the vector specificity found in beet yellow is likely to be stronger. However, in the case of beet yellows virus, the greater restriction of vector specificity is compensated by an increase in the time which the virus is retained.

References

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