Dear Prof. Fisher,

Thankyou very much for your solution of the case in which inviable zygotes are not replaced. I had come to the conclusion, from my graphical attempts at solution, that there must be a continuum of equilibria, but the precise mathematical demonstration of this had escaped me. I realise now that this should have been a simple matter, and I am beginning to regret my lack of mathematical training. It is interesting that in this example the position of equilibrium is reached relatively rapidly. This compares with the rapidity with which, in those cases where we have only one equilibrium position, a population whose proportions lie off the curve along which it moves towards equilibrium, moves back onto that curve.

While the whole of the continuum of equilibria is of theoretical interest, in practice only the cases where $\frac{Q}{R}$ is large are of importance, since we have to deal with the appearance in a normal population of one, or at most only a few, homostyle plants. With $\frac{Q}{R}$ large, the value of $R$ will decrease very slightly to equilibrium. Two factors will work to alter the equilibrium value of $R$, - mutation of heterostyle to homostyle and the reverse, and fortuitous variation in numbers from generation to generation. Of these, the latter will be the greater. There will therefore be a fluctuation in the value of $R$ about its original equilibrium value, and the equilibrium will vary along the continuum. If in one generation $R$ shows an increase, it may quite easily decrease in the next...But if we have only one homostyle plant in the population, a fall in the value of $R$ means loss of homostyles until the mutation again occurs.
Thus if the homostyle gene or gene combination arise once in a large population, and the conditions of viability and seed production are such as we have assumed, it would stand a very good chance of being lost in a few generations, were the life of the individual plant short.

But this possibility, and those based on any other assumptions, will be modified by the perennial life of the Primrose. One effect of perennation will be to smooth out the effect of fortuitous variation from one generation to the next, but the equilibrium proportions will not be altered. Without data on the length of life, it is difficult to assess the importance of this factor.

I was not surprised to find that the Somerset data do not fit in with the assumption of inviability, whatever the conditions of seed production. While I have not been working long enough on this problem to be able to make any statement on the question of viability, it is known that in *P. sinensis* a certain proportion of homozygous thrums live, and one would not expect homozygous homostyles to be less viable.

The graphically obtained results, assuming low viability of the homozygote, were much closer to the Somerset data. There is a method by which one can obtain some idea of the validity of one's assumptions. As a population moves towards its equilibrium, the ratio \( \frac{P}{Q} \) will change regularly, and \( Q \) plotted against \( P \) will give a smooth curve. The position of this curve will change as one changes one's assumptions.

If one takes the view that different proportions in different populations represent stages in progression towards equilibrium, then by plotting observed values of \( P \) and \( Q \) against each other, we shall obtain the actually occurring curve which can be matched
against the theoretical ones.

Three such theoretical curves have been plotted, and are enclosed, and the Somerset data have been inserted; they do not fit very well with the trend of the theoretical curves, but this may be due to chance variation as the excess of thrums at Maperton would seem to suggest. A greater number of observations might show much closer correspondence.

If one assumes, on the inviability non-replacement hypothesis, that the different proportions are due to different equilibria, the P Q curve should be in agreement with the equation

\[(1 - P)(3 + P + Q) = 2\]

which is the equation of the upper curve drawn. As you have pointed out, the Somerset figures do not approach this curve.

I hope that I shall be able to do some extensive counting in Somerset next Spring, and obtain other data which will assist in the elucidation of this problem, but this is naturally doubtful. It is even uncertain how much time I shall be able to spend on theoretical considerations in the immediate future, because I am shortly going to turn chemist, and take up a post in a munitions works under the Ministry of Supply. At present, I am busy getting everything in order, so that it can be safely left, and I don't expect that I shall get a great deal of spare time when I become a chemist. This problem is a very intriguing one, and I regret that I shan't be able to devote all my energy to it just yet, but I intend to do as much to it as I can, even when I am engaged in making materials of war.

Yours very sincerely, and with many thanks,

J. L. Crooey