

SEED PRODUCTION AND SEX RATIO IN ANEMOPHILOUS PLANTS

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1. INTRODUCTION

THE selective consequences and effects of population sex ratios have been reviewed by Edwards (1962) and additionally discussed by Jain (1963) and MacArthur (1965). A closely related topic is how changes in the sex ratio influence seed production. Recently Mulcahy (1967) demonstrated the importance of sex ratios and their effect on seed production in an insect-pollinated plant species and found that maximum seed production occurs when the proportion of staminate plants is less than one-half.

Presumably the effect of sex ratios on seed production holds true for wind-pollinated plant species as well. It should, however, be considered that wind pollination differs from insect pollination in that in general pollen distribution of entomophilous plants changes as plant density changes, while with anemophilous plants the pollen distribution apparently remains constant (Levin and Kerster, 1969).

This paper analyses the relationship between sex ratio and maximum seed production in plants where pollen distribution is independent of plant density. Most wind-pollinated plants have uniovulate ovaries, or produce but one seed per ovary. Thus, as a simplification, one functional ovule per ovary is assumed.

2. ANALYSIS

Using T as the plant density or total number of plants per unit area and m as the number of staminate or "male" plants per unit area obviously

$$\text{Number of "female" (pistillate) plants} = T - m. \quad (1)$$

If s is the number of seeds per unit area and V the average number of ovules/plant and where seeds/ovule is the probability of producing a seed per ovule for each plant,

$$s = (T - m) \cdot V \cdot (\text{seeds/ovule}). \quad (2)$$

As the concentration of pollen increases the number of seeds/ovule also increases, approaching, asymptotically, unity as a limit (Mulcahy, 1967). Since one pollen grain or more produces only one seed the probability that an ovule will be fertilized is equal to one minus the probability that no pollen grain will be present. This can be described as:

$$\text{seeds/ovule} = 1 - e^{-\mu}, \quad (3)$$

where $e^{-\mu}$ is the Poisson probability function for no objects being present in an area where $\mu =$ the average concentration of objects present.

Assuming that the distribution of pollen is the same for all staminate plants in a population and that each plant produces an equal number of pollen grains, then μ is proportional to m . Letting C be the rate of increase of functional pollen grains per stigma as the number of staminate plants increases

$$C = \frac{\mu}{m} \tag{4}$$

and p equal the proportion of staminate plants (*i.e.* the sex ratio)

$$m = T \cdot p. \tag{5}$$

Then equation (2) is

$$s = (T - T \cdot p) \cdot V \cdot (1 - e^{-C \cdot T \cdot p}). \tag{6}$$

Taking the derivative of s with respect to p (ds/dp) and setting the equation to zero

$$e^{C \cdot T \cdot p} + C \cdot T \cdot p = 1 + C \cdot T. \tag{7}$$

Table 1 shows the solution of this equation for p at several values of $C \cdot T$. Here it can be seen that when $C \cdot T$ is close to zero p is close to $\frac{1}{2}$ and as $C \cdot T$ increases p becomes smaller. For any value of p , the higher C is, the lower T is, and with higher C values optimal sex ratios removed from $\frac{1}{2}$ will occur at lower T values.

TABLE 1

Values of p satisfying equation (7) for several values of C · T. C · T represents the product of rate of increase of pollen grains/stigma with increasing sex ratio and plant density, while p represents the sex ratio producing maximum seeds

If $C \cdot T =$	0.05	0.1	0.5	0.2	0.3	0.4	0.5	0.8	1.0
Then $p =$	0.497	0.494	0.491	0.488	0.482	0.476	0.470	0.453	0.443
If $C \cdot T =$	1.5	2.0	3.0	4.0	5.0	8.0	10.0	20.0	
Then $p =$	0.419	0.396	0.357	0.327	0.301	0.244	0.218	0.145	

It should also be noted that m and T represent integers and therefore at certain densities some sex ratios cannot occur, thus the real optimal sex ratio will only be close to the calculated optimal. These last two points can be illustrated by substituting m for $T \cdot p$ in equation (7)

$$e^{C \cdot m} + C \cdot m = 1 + C \cdot T. \tag{8}$$

This equation cannot be solved explicitly, but, if we know C , we can, by inserting values of m , find the number of staminate plants which gives maximum seeds (s) for any density (T). Since we do not have an estimate of C we must try this at various values of C . For any value of C each side of equation (8) can be computed independently of the other side and the values of each side can be listed over a wide range of m or T . The value of m which produces a result on the left side of equation (8) closest to the result on the right side of the density in question gives the sex ratio (m/T) producing maximum seed production at that density. This is done in table 2 for two arbitrarily chosen values of C . Clearly these values may or may not be real values; however, they do indicate how C affects the denouement. Values of p satisfying equation (7) are presented for comparison, since here $C \cdot T$ is obviously 1 minus the "right side" of equation (8).

3. CONCLUSION

The following conclusions may be drawn:

1. The best sex ratio is always $< 1/2$, but, especially at low densities, may equal $1/2$ for practical purposes.

2. The higher the value of C (rate of increase of pollen grains/stigma with increasing sex ratio) the smaller the population density at which an achievable sex ratio $< 1/2$ will give maximum seed production.

4. DISCUSSION

If C (the rate of increase of pollen grains/stigma with increasing proportion of staminate plants) is constant for a species in a given unit area, then population at low densities will produce maximum seeds when the sex ratio is $1/2$ while at high densities maximum seed production will occur with a preponderance of pistillate plants. Some factors, such as local air currents, may alter C values between populations, while others, efficiency of pollen trapping, pollen buoyancy, pollen production and plant distribution for example, will alter C values between species. Because of this a great amount of variability exists and "sub-optimal" sex ratios may frequently produce seeds at or above the theoretically maximum number. Thus maximum seed production may be accomplished over a range of sex ratios. This is especially true at low C values.

The number of ovules/plant should have no effect on the relationship between sex ratio and maximum seed production but should alter the actual number of seeds produced in each case. Johnson and Cook (1968) found that the carpel production of the uniovulate *Ranunculus flammula* L. is "consistent with the amount of food reserve that can be accumulated by the plant for endosperm production". If this is true for most uniovulate plants and if all other factors are equal, then we should expect that populations with a low C value and hence a low seed/ovule production should produce more ovules (and therefore more carpels) than those with a high C value. Consider a situation where two plants have enough food reserve for 4 seeds. Plant A has a more efficient pollen trapping mechanism, and thus a higher C value than plant B. At the optimal sex ratio μ is such that for the two plants seeds/ovule is $1/2$ and $1/4$ respectively (see equations (3) and (4)). It would be more efficient for plant A to have 8 ovules and plant B to have 16 ovules.

5. SUMMARY

1. A mathematical model relating seed production to sex ratio for uniovulate wind-pollinated plants is presented which indicates that at low densities the sex ratio giving maximum seed production is about $1/2$ while at higher densities this maximum occurs at lower ratios.

2. The density at which this shift occurs and the extent of the shift is dependent upon the rate of increase of number of pollen grains/stigma as the number of staminate plants increases. Thus, anemophilous plants with different floral and pollen features may exhibit different degrees of this phenomenon.

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