the masers detected by Claussen *et al.* had components spread over a range of 600 km s⁻¹. To determine the velocity to an accuracy of 30 km s⁻¹, for a source at 5 Mpc, the measurement accuracy must be 1 microarc second per year. Such a motion can be detected from measurements of the relative positions of maser spots over time scales of several years. Measurements of such accuracy are barely possible with current VLBI techniques, but these techniques are improving rapidly. The accuracy of the estimate of the distance using the described statistical parallax technique, for the case where the velocities are well determined, is about $DN^{-1/2}$, where D is the distance and N is the number of maser spots measured. Thus, an analysis of a maser with 100 spots should give a formal estimate of the distance to an accuracy of 10 per cent. This technique could lead to an improved

distance scale to the nearby galaxies and an improved value of the Hubble constant. □

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Plant life history

Death of the elusive biennial

from Jonathan Silvertown

FOR the purposes of analysis, ecologists have tended to classify plants as annuals, biennials or perennials. Annuals arise from seed, grow, flower and die within a year; biennials flower and die in the second year after germination; and perennials live for many years and flower many times. Annuals may increase at a yearly rate equal to the fraction of plants which survive till flowering, multiplied by their seed production. This gives an annual a strong advantage over a biennial which, living longer but, for the sake of argument, surviving just as well to flowering and producing as many seeds, will take two years to accomplish the same seed output. Assuming the same mortality and seed production, perennials are favoured over both annuals and biennials because they combine regular yearly seed production with survival of the flowering plant; the magnitude of their advantage depends on the ratio of seedling mortality in the first year of life to that of older plants¹. With such a disadvantage, why do biennials exist at all?

First, a clarification is necessary. Several vegetable crops, among them the leek, behave as biennials but all, but one², demographic studies of purported biennials have demonstrated that, outside cultivation, so-called biennials often live three, four or more years before flowering and dying. These plants are more properly described as semelparous (single-reproducing) perennials and should have even lower fitness than true biennials in normal conditions. Foxglove, once a famous 'biennial', is actually an iteroparous (multiple-reproducing) perennial in early recolonization of forest gaps, although the cohorts that arise late in succession behave rather like biennials³.

If the theoretical disadvantages of their life history are such that the paucity of biennials is understandable, the existence of semelparous perennials, which delay reproduction for longer still, is even more

FOXGLOVE

curious. Though semelparous perennials are rare in floras as a whole (only 1.4 per cent of the North American flora are semelparous perennials compared with 21.3 per cent of annuals)⁴, they are very common in some families. Thirty per cent of European umbellifer species show this behaviour. So the disadvantages of this life history cannot be as great as they seem.

Some of the disadvantage is overcome because semelparous perennials produce more seeds than annuals, as theory predicts they should. Delayed reproduction is favoured when seed production increases

disproportionately with the length of the delay. This appears to account for the semelparous perennial behaviour of fuller's teasel⁵. But are there also ecological conditions which favour them?

Semelparous perennials are particularly common in certain habitats, notably where there is intermittent disturbance of the vegetation such as treefall gaps in forests. Seedlings require a gap in which to regenerate successfully⁶ and it so happens that intermittent gaps are just the kind in which annuals lose their advantage because, without annually available space, they are unable to produce a new generation every year. In the same circumstances, however, established semelparous perennials are still able to accumulate the resources needed for seed production⁷.

Semelparous perennials are also common in the early stages of succession but they are eventually squeezed out by iteroparous perennials. Harper⁸ first pointed out that the disadvantage of delayed reproduction disappears in declining successional populations because biennials die more slowly than annuals; van der Meijden and van der Waals-Kooij⁹ have shown that even greater reproductive delays can be an advantage in a declining population. The results of stochastic simulations point in the same direction¹⁰. A recent demographic analysis shows that the 'biennial' habit of wild carrot is favoured over the annual one when successional changes in the habitat are taken into account¹¹.

Another discovery, first reported for teasel¹² and now for many semelparous perennials, is that plants must reach a minimum size before flowering and that this can largely account for the length of their reproductive delays. A life history model which compares the fitness of semelparous perennials that cue reproduction by size with those that cue it by age (as must a true biennial) has shown that cueing by size is a superior strategy in a deteriorating environment. A reduction in available resources causes a delay in reproduction for size-cueing plants, which is less damaging to fitness than the reduction in seed output that it causes in age-cueing ones¹³. All the recent studies point to the same conclusion: the biennial is dead — long live the semelparous perennial. □

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