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STUDIES ON PLANT DEMOGRAPHY:
RANUNCULUS REPENS L., R. BULBOSUS L. AND
R. ACRIS L.

III. A MATHEMATICAL MODEL INCORPORATING MULTIPLE
Modes of reproduction

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INTRODUCTION

Any attempt to go beyond a simple description of biological events towards an understand-
ing of their relationships can follow either the experimental or the comparative
approach. Much of our present understanding of population dynamics is based on the
experimental approach initiated by Raymond Pearl with Drosophila populations.
Studies on plant population dynamics have largely followed this experimental approach
and, because so many of the parameters involved have agronomic implications, have
dealt mostly with crops or weeds (Harper 1967a, b). The majority of such studies refer to
single or two species systems.

These investigations have followed the plant populations from the stage of the seed
in the soil (Harper 1957; Roberts 1963) through the stage of germination and establish-
ment (Harper, Williams & Sagar 1965; Cavers & Harper 1967; Putwain & Harper 1970;
Harper & White 1972) to an analysis of mutual interference as it affects growth and
mortality in a density regulated system (Yoda et al. 1963; Harper 1964; Obeid 1965;

Comparative studies of the dynamics of populations have so far contributed little to
our understanding of the subject. Bevteron & Holt’s (1959) comparative study of the
mortality rates and growth rates for a large number of exploited fish populations is
perhaps the best example of this approach. They documented a positive correlation
between the mortality rate and the scale factor $K$ of the von Bertallanify growth equation.
Unfortunately, the estimation of the relevant parameters is rather inaccurate and the
species compared are often very distantly related; in consequence the trends suggested
are rather unclear. There has been no work along these lines for plant populations. The
present paper constitutes one of a series describing a detailed comparative study of the
dynamics of several populations of each of three closely related species of Ramunculus in
a lowland grassland in North Wales (Sarukhán & Harper 1973; Sarukhán 1974 and
in preparation). This study is based on an investigation of the behaviour of the seed
populations of the three species under field conditions and a continuous monitoring of
establishment, reproduction and survival of nearly nine thousand individually identified
plants in twenty-one permanent plots each of 1 m$^2$ over a period of 2½ years. This has

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served to provide extremely accurate estimates of the demographic parameters and this paper presents an analysis of these data employing an extension of the matrix method for the computation of the population growth rates (Bernardelli 1941; Lewis 1942; Leslie 1945). This extension made it possible to deal simultaneously with seed production and vegetative propagation. The analysis reveals a striking relationship between the degree of stability of the population of a species and the reliance by that species on seed as opposed to vegetative reproduction.

**MATERIALS AND METHODS**

The present study deals with three closely related ‘buttercups’ (*Ranunculus repens*, *R. bulbosus* and *R. acris*). They are perennial weeds of grasslands and have widely different life cycles and reproductive behaviour. A detailed account of their biology is given by Harper (1967a) and some of the most relevant characters from the demographic point of view are discussed by Sarukhán & Harper (1973) together with the general methodology used to study the plant populations. An account of the reproductive behaviour and seed population dynamics of the three species is given by Sarukhán (1974). The main life cycle characteristics of the three buttercups are as follows.

<table>
<thead>
<tr>
<th></th>
<th><em>R. repens</em></th>
<th><em>R. bulbosus</em></th>
<th><em>R. acris</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Type of stem</strong></td>
<td>Short vertical rhizome</td>
<td>Corm</td>
<td>Short vertical or oblique rhizome</td>
</tr>
<tr>
<td><strong>Summer rest</strong></td>
<td>None</td>
<td>From July to September</td>
<td>None</td>
</tr>
<tr>
<td><strong>Reproduction</strong></td>
<td>Mostly vegetative, some by seed</td>
<td>Exclusively by seed</td>
<td>Mostly by seed, some vegetative</td>
</tr>
<tr>
<td><strong>Germination</strong></td>
<td>Late April–late July</td>
<td>Late September–mid-November</td>
<td>Late March–May</td>
</tr>
<tr>
<td><strong>Physiological renewal</strong></td>
<td>Large proportion of adults replaced by new vegetative units in late summer</td>
<td>All adults renew their tissues in winter and spring</td>
<td>Only leaves renewed</td>
</tr>
</tbody>
</table>

*Demographic analysis*

The primary aim of demographic studies is to understand the way in which the size of a population changes in time, i.e. to estimate $dN/dt$, where $N$ = the number of individuals in the population and $t$ = time. The simplest formulation of population dynamics is $dN/dt = f(n)$. Elaborations of this statement lead to the development of the exponential or logistic models (Verhulst 1838; Lotka 1925). A further sophistication may be introduced into the formulation by recognizing that the change in population size is not a function of the population size alone, but depends also on the structure of the population (Lotka 1925; Birch 1948). The structure of a population may be specified by the relative number of organisms belonging to various categories such as age groups or developmental and functional stages. In a plant population these categories may be seeds, seedlings, ramets (vegetative offshoots), non-flowering adults, flowering adults of one year in age, flowering adults of two years in age and so on. The precise number of categories
distinguished depends on the extent of difference in the relevant behaviour, e.g. the survivorship of different individuals belonging to potential categories, the ability to recognize the different potential categories in the field, and ease of computation. Now, if \( N_i \) is the number of individuals belonging to the \( i \)th category and \( m+1 \) is the total number of categories into which the population is divided, then,

\[
dN_i/dt = f(N_0, \ldots, N_i, \ldots, N_m).
\]

(1)

For a discrete time model:

\[
N_i(t+1) = f[N_0(t), \ldots, N_i(t), \ldots, N_m(t)].
\]

(2)

The functional dependence is specified by the age specific fertility and mortality rates. The continuous model represented by (1) was developed by Lotka (1925) and the discrete model by Leslie (1945). Both these developments assume linearity. Then for the discrete model there is a set of \( m+1 \) linear algebraic equations:

\[
N_0(t+1) = a_{00}N_0(t) + \ldots a_{0i}N_i(t) + \ldots a_{0m}N_m(t)
\]

\[
N_i(t+1) = a_{i0}N_0(t) + \ldots a_{ii}N_i(t) + \ldots a_{im}N_m(t)
\]

\[
N_m(t+1) = a_{m0}N_0(t) + \ldots a_{mi}N_i(t) + \ldots a_{mn}N_m(t)
\]

The precise meaning of the coefficients may be clarified by a human example. Let the time step involved be one year, and the categories the various age-groups starting with 0 to 1, and ending in 99 to 100. The assumption is made here that the survival beyond age 100 is negligible, and only the females are considered. Let \( t = 1970 \) and \( t + 1 = 1971 \). Then the first equation states that the number of 0–1-year-olds in 1971 equals \( a_{0i} \) times the number of \( i \)-year-olds in 1970 summed over all \( i \). Clearly, \( a_{0i} \)’s represent age-specific net reproductive rates. Similarly, consider the fifth equation. It states that the number of 4–5-year-olds in 1971 is the sum of \( a_{4i} \) times \( N_i \) for all in 1970. Since the number of 4–5-year-olds alive in 1971 is the number of 3–4-year-olds alive in the previous year times the survivorship of 3–4-year-olds, only \( a_{43} \) will have a positive value, all other \( a_{4i} \)’s being zero. In general, the coefficient \( a_{ij} \) specifies the contribution by the \( j \)th category individuals living at time \( t \) to the \( i \)th category individuals that come into existence at time \( t+1 \). These equations may be cast into the matrix form by setting:

\[
n(t) = \begin{bmatrix} N_0(t) \\ \vdots \\ N_i(t) \\ \vdots \\ N_m(t) \end{bmatrix} \quad \text{and} \quad M = \begin{bmatrix} a_{00} & \cdots & a_{0m} \\ \vdots & \ddots & \vdots \\ a_{i0} & \cdots & a_{im} \\ \vdots & \ddots & \vdots \\ a_{m0} & \cdots & a_{mn} \end{bmatrix}
\]
Thus, $n$ is a column vector and $M$ is a square matrix, which may be termed the projection matrix (Pielou 1969). Then:

$$M_n(t) = n(t+1).$$

For the human population model suggested above:

$$M = \begin{bmatrix} F_0 & F_1 & F_2 & \ldots & F_{67} & \ldots & F_{99} \\ P_0 & 0 & 0 & \ldots & 0 & \ldots & 0 \\ 0 & P_1 & 0 & \ldots & 0 & \ldots & 0 \\ 0 & 0 & P_2 & \ldots & 0 & \ldots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \ldots & 0 & \ldots & P_{99} \end{bmatrix}$$

Thus, the $F_i$'s which make up the first row are the age-specific net reproductive rates and the $P_i$'s lying along the sub-diagonal are the age-specific survivorship rates. All other elements of the projection matrix are zero (Keyfitz 1972; Williamson 1972).

This model is based on the assumption of a life-history such that all age-groups may contribute to the youngest age-group through reproduction and contribute to the next age-group via survival. This model may be easily extended to model a different kind of life-history (Usher 1973). Consider, for example, an imaginary plant population with the following categories: $0 =$ seed, $1 =$ vegetative offspring, $2 =$ non-flowering adult, $3 =$ flowering adult, and $4 =$ flowering and vegetatively reproducing adult. Further, assume that the following transitions may take place in one time-step: (1) a seed may remain a seed ($a_{00} = P_0$); (2) a seed may become a non-flowering adult through germination ($a_{20} = G$); (3) a non-flowering adult may become a flowering adult ($a_{32} = P_2$); (4) a vegetative offspring may become a flowering adult ($a_{31} = P_1$); or (5) a flowering adult may become a flowering and vegetatively reproducing adult ($a_{43} = P_3$) and (6) a flowering adult may produce seeds ($a_{03} = F_3$); a flowering and vegetatively reproducing adult may remain in that category ($a_{44} = P_4$) and (7) it may produce seeds ($a_{04} = F_4$); and it may also produce vegetative offspring ($a_{14} = V$). The projection matrix for such a system may be represented as follows:

$$\begin{bmatrix} P_0 & 0 & 0 & F_3 & F_4 \\ 0 & 0 & 0 & 0 & V \\ G & 0 & 0 & 0 & 0 \\ 0 & P_1 & P_2 & 0 & 0 \\ 0 & 0 & 0 & P_3 & P_4 \end{bmatrix}$$

The formulation may clearly be modified in any way to accommodate different categories and different types of transitions between categories.

A further sophistication may be introduced by recognizing that the projection matrix may not be the same for every transition from one time step to the next. This would be the case if the time step is shorter than the complete annual (or secular) cycle in the behaviour of the population. A projection matrix $M_i$ for $i$th season of the year may then be specified. If $n_x$ is the column vector specifying the number of individuals in the various categories at the beginning of the season $x$, then

$$n_{x+1} = M_x n_x.$$
Let \( x = 1 \), and \( s \) be the number of seasons in which the year is divided. Then the population after the lapse of a complete year may be specified by:

\[
n_1(t+1) = M_s M_{s-1} \ldots M_1 n_1(t),
\]

and that after the lapse of \( T \) years by

\[
n_1(t+T) = (M_s M_{s-1} \ldots M_1)^T n_1(t).
\]

**Computations**

Figs. 1, 2 and 3 give the details of the categories into which the life-history stages of each of the three species were separated and the seasons into which each year was divided. There are three broad life-history categories in common for all of the species: (1) the seeds in the 'seed bank' in the soil, (2) seedlings, and (3) 'matures'. The 'matures' in the case of *R. repens* were further classified into: (1) 'non-vegetative', i.e. plants which did not produce any stolons, (2) plants producing stolons which failed to root, (3) 'unsuccessful parents', i.e. plants which produced stolons that rooted but failed to leave any vegetative offspring. Along with the category of vegetative 'daughters', *R. repens* populations are thus divided into seven categories. The pertinent projection matrix is of the order \( 7 \times 7 \) for all seasons. In the *R. acris* the 'matures' were divided only into (1) flowering and (2) non-flowering categories and no differentiation was made on the basis of vegetative reproduction, since the flowering 'matures' that did not reproduce vegetatively did not differ in rates of survival from those that succeeded in reproducing vegetatively. Along with the vegetative 'daughters', the *R. acris* populations are thus distinguished into five categories. The projection matrix for the species is of the order \( 5 \times 5 \) for each season. In the case of *R. bulbosus* the seedlings have been distinguished into early and late categories, and the 'matures' in the spring into flowering and non-flowering categories. The two categories of matures merge in autumn after the plants resprout following their summer dormancy. There are then five categories into which *R. bulbosus* populations are differentiated, and the projection matrix is of the order \( 5 \times 5 \) for each season.

The present data justified the division of the year into the following five seasons: (1) spring (March or April–May); (2) early summer (June and July); (3) late summer (August and September); (4) autumn (October and November); (5) winter (December–February or March). The seasons were selected so that certain transitions could be conveniently considered to be restricted to a given season. Occasionally this involved neglecting certain events. For example, the restriction of germination of one of the buttercups to spring meant the neglect of a certain amount of germination taking place in early summer. When a decision was made to disregard such an event the numbers involved were negligible, generally less than 4%.

Figs. 1, 2 and 3 provide a detailed picture of the flux of populations of the three species. Each arrow in the figure represents a transition which will be represented by a positive number in the projection matrix. These parameters were computed separately for each of the three species on each of the one metre square permanent sites. They were also computed by pooling together all the data for each species for a given year, as well as by pooling all the data for each species for both the years (see Table 1). The estimation of the parameters follows in principle the methods described by Leslie (1945) for the estimation of survivorship and fertility. The detailed computations are presented by Sarukhán (1971).

The basic statistic obtained from a given set of parameters was the stable 'age' (or category) distribution and population growth rate per year. It is known that for a fixed
Fig. 1. Data flow diagram showing the categories and times considered for populations of *Ranunculus repens* and the transition from category to category.
Fig. 2. Data flow diagram showing the categories and times considered for populations of *Ranunculus bulbosus* and the transition from category to category.

Fig. 3. Data flow diagram showing the categories and times considered for populations of *Ranunculus acris* and the transition from category to category.
schedule of mortality and fertility rates a population generally achieves a stable age distribution irrespective of its initial state. Once this stable age distribution has been achieved the population continues to grow (or decline) at a constant rate. These statistics were computed by a simple iterative procedure.

This model assumes a constant population growth rate and hence an exponential growth of the population. For this case:

\[ N(t+1) = \lambda N(t) = N(t)e^m. \]

In the following discussion \( \lambda \) is used as an estimator of the population growth rate. Its relation to \( m \), the malthusian parameter, is evident from the expression given above. The population size is constant when \( \lambda \) equals one or \( m \) equals zero, increases when \( \lambda \) is greater than one, and declines when it is less than one.

Although this study is believed to provide one of the most accurate estimates of plant population parameters, it still suffers from three major deficiencies in the data available. These are a lack of information on migration and on senescence and a limited assessment of the effects of density-dependence. As shown below, populations of \( R. bulbosus \) in particular seem to be subjected to wide fluctuations, increasing at very rapid rates on some sites, and declining equally drastically on others. The other species show somewhat milder fluctuations. It becomes evident that a process of local extinction of some populations and recolonization of new sites must be continually going on in the sward. A major aim of further studies on buttercups designed to provide data for a truly predictive model should be to estimate the parameters of migration. In addition to migration, the fluctuations in the populations must be under control of density-dependent regulation such that the population growth tends to decline with any increase in the population density. There is evidence of this for \( R. repens \) and to a lesser extent for \( R. acrius \), but none at all for \( R. bulbosus \). Perhaps density-dependent regulation for the last species occurs on a larger spatial scale than dealt with here. In any event, the present data were found to be inadequate for a proper assessment of the density-dependence of the various demographic parameters. Deliberate manipulations of population densities, of seed output and the production of ramets will probably greatly increase our knowledge of the density-dependence of the demographic parameters. Lastly, it has not been possible to distinguish between the behaviour of mature plants of various ages. Senescence and a sharp decline in survivorship and fertility may occur beyond a certain age. Because this has not been taken into account, the present models predict, for example, that the population of \( R. bulbosus \) would persist for a very long time even if its reproduction was completely eliminated. Nevertheless, this is probably the least serious of the limitations of the data and analysis.

**RESULTS**

Table 1 gives the growth rates that would be achieved by the populations under a stable age distribution for the parameters computed separately for each of the populations for the two years. It also shows the population growth rates similarly obtained by pooling together the data for each species for each year as well as for the two years together. In addition it provides the mean, variance and coefficient of variation for the population growth rates of each species. A scrutiny of the table reveals several interesting patterns.

**Density-dependence**

It has been suggested that the rates of survival may be density-dependent in all the three
buttercups (Sarukhán & Harper 1973). The data were therefore examined for any indication of the density-dependence of the population growth rates. The number of mature individuals per unit area in early April was taken as a measure of the population density. Fig. 4a, b and c shows the population growth rates as a function of population density for the three species. A population is said to be subjected to negative density-dependent regulation if its growth rate declines with an increase in the density of the population, and to positive density-dependent regulation if the growth rate increases with an increase in the population density. The former type of regulation will tend to stabilize the population numbers, the latter will lead to an unstable situation such that the population will either tend to increase beyond limits or go to extinction depending on the initial conditions. An examination of Fig. 4 shows that the populations of *Ranunculus repens* are perhaps subject

Table 1. The population growth rates (λ) for the three *Ranunculus* species separately for the two years for all the sites, and the mean variance and coefficient of variation (values are also shown for λ pooled over all sites for each year and for the two years together)

<table>
<thead>
<tr>
<th>R. repens</th>
<th>Sites</th>
<th>A1</th>
<th>A2</th>
<th>A3</th>
<th>B1</th>
<th>B2</th>
<th>C1</th>
<th>C2</th>
<th>C3</th>
<th>All sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>1969</td>
<td></td>
<td>0.743</td>
<td>0.760</td>
<td>0.756</td>
<td>0.879</td>
<td>0.753</td>
<td>1.309</td>
<td>1.215</td>
<td>1.269</td>
<td>0.85</td>
</tr>
<tr>
<td>1970</td>
<td></td>
<td>0.809</td>
<td>1.271</td>
<td>1.022</td>
<td>1.295</td>
<td>1.801</td>
<td>1.067</td>
<td>0.851</td>
<td>0.891</td>
<td>1.02</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>1.04</td>
<td></td>
<td></td>
<td>1.04</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.926</td>
</tr>
<tr>
<td></td>
<td>Variance</td>
<td>0.089</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>C.V. 0.287</td>
</tr>
<tr>
<td>R. bulbosus</td>
<td>Sites</td>
<td>B3</td>
<td>E1</td>
<td>E2</td>
<td>E3</td>
<td>F1</td>
<td>F2</td>
<td>F3</td>
<td>G1</td>
<td>G2</td>
</tr>
<tr>
<td>1969</td>
<td></td>
<td>2.487</td>
<td>0.485</td>
<td>0.406</td>
<td>0.307</td>
<td>0.393</td>
<td>0.095</td>
<td>0.308</td>
<td>1.484</td>
<td>4.068</td>
</tr>
<tr>
<td>1970</td>
<td></td>
<td>0.804</td>
<td>0.796</td>
<td>0.926</td>
<td>0.980</td>
<td>0.093</td>
<td>0.500</td>
<td>0.898</td>
<td>0.894</td>
<td>8.170</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>1.603</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Variance</td>
<td>3.583</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R. acris</td>
<td>Sites</td>
<td>D2</td>
<td>D3</td>
<td>A2</td>
<td>B3</td>
<td>G2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1969</td>
<td></td>
<td>1.381</td>
<td>1.056</td>
<td>1.102</td>
<td>1.673</td>
<td>2.328</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1970</td>
<td></td>
<td>0.832</td>
<td>0.786</td>
<td>1.305</td>
<td>0.860</td>
<td>0.350</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>1.167</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Variance</td>
<td>0.264</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
to a negatively density-dependent regulation, and those of *R. bulbosus* to a positive density-dependent regulation while the growth rates of *R. acris* populations seem to relate to the population density in no way at all. The behaviour of *R. repens* corresponds to the negative density-dependence of survivorship and reproductive rates reported by Sarukhán & Harper (1973). None of these trends is, however, statistically significant.

The number of plants per unit area is a rather crude measure of density of a plant population, in particular for *R. acris* and *R. bulbosus* both of which have a patchy distribution. For a proper assessment of the density-dependent regulation of a species, the density needs to be related to the capacity of the environment to sustain the population, i.e. its carrying capacity, 'K'. If this carrying capacity is high relative to the numbers per unit area, the population may be expected to increase; if the carrying capacity is low relative to the numbers per unit area, the population is expected to decrease. The different sites being compared may have very different carrying capacities, so that the numbers per unit area may not serve as useful indices of density. The carrying capacity of a given site may also change from one year to the next, thus obscuring any trend when populations in different years are compared. The present data do not lend themselves to
Fig. 4. The relationships between the growth rates attained by populations at different densities of: (a) *Ranunculus repens*, (b) *R. bulbosus* and (c) *R. acris*, during 1969 and 1970. Densities are the number of plants of each species per m², recorded in April of 1969 and 1970.
Fig. 5. Rates of increase shown by populations of (a) *Ranunculus repens*, (b) *R. bulbosus* and
(c) *R. acris* in the two successive years of 1969 and 1970.
an estimation of the carrying capacities of the various sites, which would be best estimated through an experimental manipulation of the populations and the environment. However, an alternative method of analysis is available if the assumption is made that the carrying capacity of a given site does not change appreciably from one year to the next. Then, if the growth rate of a population is greater than one for a year, the population may be expected to increase beyond the carrying capacity, or at least towards it, and therefore to exhibit a population growth rate of less than one, or at least smaller than that of the previous year during the course of the following year. The opposite situation will hold if the population had a growth rate of less than one in the first year. A negative correlation would then be expected between the growth rates of a given population for two successive years. This relationship is plotted in Fig. 5 a, b and c, which shows the population growth rates of 1969 against 1970 for each site. A negative correlation is apparent for *R. repens*, there is an indication of a negative correlation for *R. acri*s, and of a positive correlation for *R. bulbosus*. The results of this analysis therefore parallel those of the first analysis, with *R. repens* showing indications of negative density-dependence, and *R. bulbosus* indications of a positive density-dependence.

![Graph](image)

**Fig. 5 (cont.)**

**Variance of growth rates**

An examination of the extent of variation in the population growth rates from locality to locality and from year to year for a given species shows a very clear relationship between the extent of such variation and the possible mode of density-dependent regulation of the population. The pertinent data are given in Table 1. The range of variation of the population growth rates is smallest for *R. repens*, namely from 0·74 to 1·8, intermediate for *R. acri*s, from 0·35 to 2·33, and largest for *R. bulbosus* from 0·09 to 8·17.
Mode of reproduction

Besides this relation between the extent of variation in the population growth rates and the mode of density-dependent regulation of the population, a relationship may also be discerned between these two attributes and the extent of reliance on vegetative propagation as opposed to seed production. *R. repens*, the species with an indication of negative density-dependence and the smallest variation in the population growth rates, also exhibits the greatest reliance on vegetative propagation, while *R. bulbosus*, the species with a possible positive density-dependence and the greatest variation in the population growth rates, is exclusively dependent on seed production. In order to document this in a more objective fashion, it is desirable to derive a measure of the extent to which the three species are dependent on sexual as opposed to vegetative reproduction. Such a measure may be obtained through a conceptual experiment. Let us consider a population of any of the three species with the various demographic parameters such as survivorship, and the rates of reproduction by seed and vegetative means fixed at an average value obtained by pooling together the data for all the sites and for the two years for that particular species. The rate of vegetative propagation may then be multiplied by a factor ranging
from 0 to 3, leaving as before all other parameters including reproduction by seed unchanged. Population growth rates for these imaginary populations may then be computed by using the modified matrix method. If a species depends mainly on seed production, its population growth rate will be very sensitive to any change in the value of seed production, but insensitive to a change in the value of vegetative reproduction and vice versa.

The results of these computations for the three species are presented in Fig. 6. The abscissa denotes the factor by which the average rates of vegetative or sexual reproduction have been multiplied (one at a time), and the ordinate the resulting population growth rates normalized by dividing by the population growth rate for the average values of the demographic parameters. As expected, *R. repens* can be seen to rely to a greater extent on vegetative than on sexual reproduction. A 0- to 3-fold change in seed production produces a change in the population growth rate only from 0·92 to 1·10, but a similar change in vegetative propagation results in a much more marked change in the population growth rate from 0·82 to 2·33. *R. bulbosus* which reproduces almost exclusively through seed production is extremely sensitive to a change in the seed output. When the seed production is reduced to zero, the population continues to decline by a factor of 0·3 per year, this rate being determined by the rate of survival of the ‘matures’. If senescence is taken into account, this rate of decrease would probably be much steeper. *R. acris* behaves in an intermediate fashion. Its population growth rate changes from 0·8 to 1·27 when the seed production is varied from 0 to 3 times its average value, and from 0·9 to 1·11 with a similar change in vegetative propagation.

Although *R. repens* relies on vegetative propagation to a greater extent, it appears to have a good alternative mode of reproduction in seed production, if the former fails. *R. acris* relies more equally on both means of propagation. Both these species appear to be well buffered against the failure of one of the two means of reproduction.

### Table 2. A summary of the major results regarding the three species

<table>
<thead>
<tr>
<th>Species</th>
<th>Mode of density-dependence</th>
<th>C. V. of population growth rates</th>
<th>Importance of vegetative in contrast to sexual reproduction</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ranunculus repens</em></td>
<td>Negative (?)</td>
<td>0·287</td>
<td>Greater</td>
</tr>
<tr>
<td><em>R. acris</em></td>
<td>—</td>
<td>0·455</td>
<td>Nearly equal</td>
</tr>
<tr>
<td><em>R. bulbosus</em></td>
<td>Positive (?)</td>
<td>1·181</td>
<td>Negligible</td>
</tr>
</tbody>
</table>

DISCUSSION

As Table 2 shows, the results of the present study fall into a very neat pattern. The lack of negative density-dependence for the population of any species may be an indication that the species is a ‘colonizing’ or ‘fugitive’ species which is found either expanding rapidly in a habitat which has become newly available, or on the way to extinction in a habitat which is rapidly deteriorating, but seldom maintains populations for long near the level of a stable ‘carrying capacity’ of the habitat to provide evidence of a negatively density-dependent population regulation. Such species are expected to live in habitats which remain available for relatively short durations at any time. In other words the carrying capacity of a given site shows great fluctuations in time. The population growth rates of any species present in such habitats will also be forced to fluctuate by the fluctuations of the carrying capacity of the environment, and will therefore exhibit great variation from
site to site and from one year to the next. Finally, fugitive species inhabit environments which cannot be relied on to remain favourable from one year to the next. There would therefore be selection favouring a high degree of dispersibility (Gadgil 1971). Vegetative propagation is, of course, the ultimate of non-dispersing and such fugitive species may be expected to rely very little on vegetative reproduction. Species inhabiting more stable environments would have populations which have grown very close to the carrying capacity and hence show good evidence of negative density-dependence. Since all the populations will be quite stable, all will have growth rates ($\lambda$'s) close to one, and will therefore exhibit little variation in the growth rates from site to site and from year to year. Finally, as such environments can be relied on to stay favourable from one year to the next, a low degree of dispersibility will be favoured, and the species will tend to invest substantially more in vegetative propagation. These two types are of course the two extremes of a continuous spectrum that one would expect to encounter in nature. It may be noted that the pattern summarized in Table 2 seems to illustrate such a series, with *Ranunculus repens* characteristic of a species inhabiting a stable environment, *R. bulbosus* exhibiting some of the attributes of a fugitive species and with *R. acris* as an intermediate in all respects. Such a theoretical interpretation must of course be scrutinized in detail on the basis of knowledge of all the aspects of the biology of the three species. This will be attempted in a later paper of this series.

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SUMMARY

This paper presents a comparative population dynamics study of three closely related species of buttercups (*Ranunculus repens*, *R. acris*, and *R. bulbosus*). The study is based on an investigation of the behaviour of the seeds in soil under field conditions and a continuous monitoring of survival and reproduction of some 9000 individual plants over a period of 2½ years in a coastal grassland in North Wales. The data were analysed with the help of an extension of Leslie's matrix method which makes possible a simultaneous treatment of vegetative and sexual reproduction. It was found that *R. repens* (a) depends more heavily on vegetative as compared with sexual reproduction, (b) shows indications of negatively density-dependent population regulation, and (c) exhibits little variation in population growth rates from site to site and from one year to the next. In contrast, *R. bulbosus* (a) depends exclusively on sexual reproduction, (b) shows indications of a positively density-dependent population behaviour, and (c) exhibits great variation in population growth rates from site to site and from one year to the next. *R. acris* exhibits an intermediate behaviour in all these respects. It is suggested that the attributes of *R. repens* are those expected of a species inhabiting a stable environment, while *R. bulbosus* exhibits some of the characteristics of a fugitive species.
REFERENCES


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