A Population Dynamic Model for Facultative Agamosperms

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Plants that can reproduce both sexually and agamically are called facultative apomicts. Some species, such as Taraxacum, contain both sexual diploids and triploid facultative apomicts. Triploids produce seeds without gamete fusion and recombination, and can also produce pollen and fertilize diploids. We present a population dynamic model that deals with gene flow and competition between diploids and triploids, with differing allocation towards reproductive investment in seeds and pollen. This paper examines whether diploids and triploids of plants with facultative agamospermy can coexist within a single population. We analyse the global behavior of such a dynamic system. Features of the system are significantly affected by the germination rates of diploids and triploids. Either diploids or triploids persist alone when the germination rate of diploids is sufficiently larger or smaller than that of triploids, respectively. Competitive exclusion occurs when both germination rates are sufficiently large. Coexistence is possible under certain specific conditions when: (I) the germination rates of both diploid sexuals and triploids are not sufficiently large, and (II) triploids produce sufficient pollen. When diploid sexuals and triploids coexist, triploids cannot exist alone, implying that the pollen of triploids is necessary to exploit diploid ovules.

1. Introduction

Plants that can reproduce both sexually and agamically are called facultative apomicts. Some species, such as Taraxacum, include both triploid facultative apomicts and sexual diploids. Facultative apomicts form seeds without gamete fusion and recombination. Facultative apomixis is common in plants, and is found in about 15% of angiosperm plant families, although 75% of all apomicts belong to the Poaceae, Asteraceae, and Rosaceae families (Asker & Jerling, 1992). These

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populations of *Taraxacum* (Compositae) (Den Nijs et al., 1990), *Antennaria* (Anteraceae) (Bayer et al., 1991) and *Amelanchier* (Rosaceae) (Campbell & Dickinson, 1990). Den Nijs & Sterk (1984) showed that *Taraxacum* populations may be pure triploid, pure diploid, or mixed. Thus, the ratio of diploids to polyploids varies among populations. The ecological situation that brings about the coexistence of polyploids and diploids in unknown.

Models of competition between asexual and sexual strains within a single population have been used to explain the evolution and maintenance of sexual reproduction. Asexual strains probably invade sexual populations due to the two-fold advantage of sex (Williams, 1975; Maynard Smith, 1978). Recent models show how a small competitive advantage for sex can cancel the growth advantage resulting from asexuality in a density-dependent system (Doncaster et al., 2000; Kerszberg, 2000). Most models of competition between sexual and asexual types assume that asexuality is obligate, and that no genes are exchanged between the two types. However, gene flow does exist between polyploids and diploids in plants with facultative agamospermy. In this paper, we present a mathematical model that deals with facultative agamospermy and includes gene flow between diploids and triploids, such as exists in dandelions. We examine whether diploid sexuals and triploid apomicts can coexist within a single population.

We focus on the allocation of reproductive investment in pollen and seeds. For simplicity, we assume that a plant is monocarpic, unlike dandelions. We analyse the stability properties of pure diploids, pure apomicts, and mixed populations, and discuss the conditions under which a stable equilibrium is possible. Although the germination rate may change with environmental conditions and the accumulation of deleterious mutations over the long term, we consider a constant environment and ignore genetic degradation of asexual strains, and discuss the short term.

2. Model

Our model is based on a monocarpic annual plant population that consists of sexual diploids and facultatively apomictic triploids. Diploids produce haploid pollen and ovules via meiosis in the usual fashion. However, triploids produce both haploid and diploid pollen via meiosis and triploid ovules via agamospermy. Agamosper- mous triploids of *Taraxacum* form male gametes with haploid, diploid, or triploid chromosome sets, although most gametes have incomplete sets and die (Richards, 1973). For simplicity, we ignore triploid pollen in our model. We assume that triploids produce haploid pollen with probability $r$ and diploid pollen with probability $1 - r$. Diploid seed is produced when haploid pollen fertilizes a haploid ovule. Triploid seed is produced either (1) when diploid pollen fertilizes a haploid ovule or (2) when a triploid ovule becomes a seed without pollination. The system of reproduction is summarized in Fig. 1. We describe the diploid and triploid population densities at generation $t$ by $x_t$ and $y_t$, respectively. We assumed that a diploid individual produces $a$ pollen grains and that an apomict individual produces $b$ pollen grains. Therefore, an apomict individual produces $rb$ haploid pollen and

![Fig. 1. Mating scheme used in our model with hybridization between diploids and apomicts. All facultative apomicts are apomictic and all diploids are sexual. Apomicts (left) not only cross with diploids (right), but also reproduce without pollination. A diploid individual produces $a$ haploid pollen grains. An apomict individual produces $b$ both haploid and diploid pollen grains with probability $r$ and $1 - r$, respectively.](image-url)
(1 - r)b diploid grains. We assumed that haploid ovules from diploid donors randomly cross with pollen from diploids and triploids. In intermixed populations consisting of diploids and triploids, the total number of pollen grains at generation \( t \) is \( ax_t + by_t \). Assuming random mating within the population, the probability that haploid ovules produced by diploids are fertilized by haploid pollen from diploid donors is given by \( ax_t / (ax_t + by_t) \). On the other hand, the probability of crossing a haploid ovule produced by diploids and diploid pollen from triploid donors is given by \( (1 - r)by_t / (ax_t + by_t) \). This cross produces a triploid seed. In the same way, the probability of crossing a haploid ovule produced by a diploid and haploid pollen from a triploid donor is given by \( rby_t / (ax_t + by_t) \). This cross produces a diploid seed.

We consider the cost of sexuality and impose restrictions on sexual compensation. Both diploids and triploids have limited resources available to produce pollen and ovules. Let \( K_1 \) and \( K_2 \) denote the weight of total reproductive investment per diploid and triploid, respectively. The weight of a pollen grain from diploid donors is \( k_1 \), and that from triploid donors is \( k_2 \). A diploid invests \( k_1a \) in pollen and \( K_1 - k_1a \) in seeds, while a triploid produces the weight of \( K_2 - k_2b \) seeds. We define \( g_1 \) and \( g_2 \) as the germination rate of diploids and triploids, respectively. Let \( g_3 \) be the germination rate of hybrid diploid seeds, and \( g_4 \) be the germination rate of hybrid triploid seeds. The germination rate of seeds may depend on seed size or ploidy. Note that \( K_1 - k_1a \) and \( K_2 - k_2b \) must not be negative.

The population dynamics of diploids \( x_t \) and triploids \( y_t \) is given as follows:

\[
x_{t+1} = \left[ g_1(K_1 - k_1a) \frac{ax_t}{ax_t + by_t} x_t 
+ g_3(K_1 - k_1a) \frac{rby_t}{ax_t + by_t} x_t \right] F_1,
\]

\[
y_{t+1} = \left[ g_2(K_2 - k_2b)y_t
+ g_4(K_1 - k_1a) \frac{(1 - r)by_t}{ax_t + by_t} x_t \right] F_2,
\]

where \( F_1 \) and \( F_2 \) are the rates at which diploids and triploids survive and reach maturity (to produce the next generation), respectively.

Within a population, there is competition for resources, such as light and nutrients, while germinated seeds develop to the adult stage. We assume that competition specifically occurs among seedlings. \( F_1 \) and \( F_2 \) were assumed to depend on total densities within a population. Let \( z_t \) be the total density of seedlings produced at generation \( t \), defined as

\[
z_t = \frac{(K_1 - k_1a)x_t}{ax_t + by_t} (g_1ax_t + g_3rby_t + g_4(1 - r)by_t) + g_2(K_2 - k_2b)y_t.
\]

We assume that the survival probabilities \( F_1 \) and \( F_2 \) monotonically decrease and approach 0 as the total seed population density \( z_t \) increases:

\[
F_i(z_t) = \epsilon_i e^{-\rho_i z_t} (\leq \epsilon_i) \quad (i = 1, 2),
\]

where \( \epsilon_i \), the maximal survival probability, and \( \rho_i \), the coefficient of density effect, are positive constants (Ricker, 1954). Assuming that the coefficient of density effect of diploids is equal to that for triploids, then \( \rho_1 = \rho_2 = \rho \). If the functional form of density dependence follows Michaelis–Menten \( [F_i(z) = \epsilon_i z / (m + z)] \), the stability property becomes simpler. The necessary conditions for coexistence can be demonstrated even when we use eqn (4) and the equilibrium is unstable.

From eqns (1–4), we constructed the following mathematical model:

\[
x_{t+1} = \left\{ \begin{align*}
\alpha(s_1 - a) \frac{ax_t^2}{ax_t + by_t} \\
+ \delta(s_1 - a) \frac{rby_x}{ax_t + by_t} e^{-\rho z_t}, & \text{if } s_1 - a > 0
\end{align*} \right.
\]

\[
y_{t+1} = \left\{ \begin{align*}
\gamma(s_2 - b)y_t \\
+ \beta(s_1 - a) \frac{(1 - r)by_t}{ax_t + by_t} e^{-\rho z_t}, & \text{if } s_2 - b > 0
\end{align*} \right.
\]
\[ z_t = \frac{(s_1 - a)x_t}{ax_t + by_t} \left\{ \frac{ax_t}{\varepsilon_1} + \frac{\beta(1 - r)by_t}{\varepsilon_2} + \frac{\delta rb y_t}{\varepsilon_1} \right\} + \frac{\gamma(s_2 - b)y_t}{\varepsilon_2} , \]  

(7)

where \( \alpha \equiv \varepsilon_1 g_1 k_1 \), \( \beta \equiv \varepsilon_2 g_2 k_1 \), \( \gamma \equiv \varepsilon_2 g_2 k_2 \), \( \delta \equiv \varepsilon_1 g_3 k_1 \), \( K_1 / k_1 \equiv s_1 \), \( K_2 / k_2 \equiv s_2 \), \( s_1 > a \) and \( s_2 > b \).

### 3. Analysis

#### 3.1. Density Ratio \( \psi_t \)

Let the density ratio \( \psi_t \equiv x_t / y_t \). In this section, we consider the case \( y_t > 0 \). We obtain the following one-dimensional discrete dynamic system for \( \psi_t \), from eqns (5–7):

\[ \psi_{t+1} = \frac{(s_1 - a)(ax_t \psi_t + rb \delta) \psi_t}{\{ \beta b(1 - r)(s_1 - a) + a\gamma(s_2 - b) \} \psi_t + b \gamma(s_2 - b)} \equiv f(\psi_t) . \]  

(8)

\( f(\psi_t) \) is the monotonically increasing function of \( \psi_t \), independent of \( z_t \). Let \( \psi^* \) be the non-trivial equilibrium satisfying \( \psi^* = f(\psi^*) > 0 \), which is explicitly and uniquely obtained as

\[ \psi^* = \frac{b [\gamma(s_2 - b) - r \delta (s_1 - a)]}{a [\alpha(s_1 - a) - \gamma(s_2 - b)] - \beta b(1 - r)(s_1 - a)} . \]  

(9)

Since \( s_1 > a \) and \( s_2 > b \), a positive equilibrium \( \psi^* \) exists if and only if

\[ l_1 < \gamma < l_2 \]  

(10)

or

\[ l_2 < \gamma < l_1 , \]  

(11)

where \( l_1 \) and \( l_2 \) are defined by

\[ l_1 = \frac{s_1 - a}{s_2 - b} \left\{ \frac{a - \beta b(1 - r)}{a} \right\} , \]  

(12)

\[ l_2 = \frac{r(s_1 - a)}{s_2 - b} \delta . \]  

(13)

If eqn (10) is satisfied, a positive equilibrium \( \psi^* \) given by eqn (9) is globally stable. Therefore, \( f(\psi_t) / \psi_t > 1 \) if \( \psi < \psi^* \) and \( f(\psi_t) / \psi_t < 1 \) if \( \psi > \psi^* \) [Fig. 2(a)].

In contrast, if eqn (11) is satisfied, the positive equilibrium \( \psi^* \) is always unstable, whereas the zero equilibrium is locally stable, because \( f(\psi_t) / \psi_t < 1 \) if \( \psi < \psi^* \) and \( f(\psi_t) / \psi_t > 1 \) if \( \psi > \psi^* \) [Fig. 2(b)]. The cobweb method (Mooney & Swift, 1999) clearly shows that if the initial value \( \psi_0 \) is less than \( \psi^* \), \( \psi_t \) monotonically decreases over generations (iterations) and asymptotically approaches 0. On the other hand, if \( \psi_0 \) is greater than \( \psi^* \), \( \psi_t \) monotonically increases to positive infinity. Thus, whether \( \psi_t \) converges to 0 or diverges to \( + \infty \) depends on the initial conditions. The given system has a bistable structure.

From these arguments, if \( f'(0) < 1 \) is satisfied, but eqn (10) is not, then the value of \( f(\psi) \) must always be less than \( \psi \) for any positive \( \psi \). Therefore, the cobweb method shows that \( \psi_t \rightarrow 0 \) as

![Fig. 2. The graph of function \( f(\psi) \) given by eqn (8) is shown by a solid curve. The broken line shows the iterating trajectory of eqn (8): (a) \( \psi_t \) approaches a positive equilibrium, and (b) approaches 0 or diverges to \( + \infty \). The initial condition is indicated by the dot on the \( \psi \)-axis.](image-url)
\( t \to +\infty \) for any positive initial value \( \psi_0 \). The necessary and sufficient condition for \( f'(0) < 1 \) is

\[
\gamma > l_1, l_2. \tag{14}
\]

Similarly, if \( f'(0) > 1 \) is satisfied, but eqn (11) is not, then the value of \( f(\psi) \) must always be greater than \( \psi \) for any positive \( \psi \). Therefore, the cobweb method indicates that \( \psi_t \to +\infty \) as \( t \to +\infty \) for any positive initial value \( \psi_0 \). The necessary and sufficient condition for \( f'(0) > 1 \) is

\[
\gamma < l_1, l_2. \tag{15}
\]

### 3.2. ASYMPTOTIC BEHAVIOR OF \( x_t \) AND \( y_t \)

We focus on the dynamic property of the ratio \( \psi \). In this section, we consider the dynamic properties of densities \( x_t \) and \( y_t \) for the following separate instances: (I) \( \psi_t \to 0 \), (II) \( \psi_t \to +\infty \), and (III) \( \psi_t \to \psi^* \). From eqns (5–7), \( x_t \) and \( y_t \) do not positively diverge (see below). In each case, the absolute density may either approach 0, approach a unique finite-positive equilibrium or fluctuate permanently. Since the germination rate is assumed to depend on seed size, seeds originating from the ovules of diploids should have the same germination rate, regardless of ploidy. Thus, \( g_1 = g_3 = g_4 \) and \( \alpha = \delta \). A discrete dynamic system (5–7) has four equilibria, described as \((0,0)\), \((0,\bar{y})\), \((\bar{x},0)\), and \((\bar{x},\bar{y})\). System (5–7) may not reach equilibrium. If \( \psi_t(\equiv x_t/y_t) \) reaches 0, then \( x_t \) reaches 0 and \( y_t \) reaches 0 or is kept positive. If \( \psi_t \to \psi^* \), given by eqn (9), \( x_t \) and \( y_t \) either simultaneously reach 0 or both remain positive. If \( \psi_t \to +\infty \), \((x_t,y_t)\) becomes either \((0,0)\) or \((\bar{x}, \bar{y})\), and thus \( y_t \) reaches 0 and \( x_t \) reaches 0 or is kept positive. We investigate (I) the dynamical behavior of \( y_t \) if \( x_t \equiv 0 \), (II) that of \( x_t \) if \( y_t \equiv 0 \), and (III) that of \( x_t \) if \( y_t \equiv x_t/\psi^* \).

### 3.2.1. Dynamic Behavior of Apomictic Triploids

We consider the condition \( x_t \equiv 0 \). From eqns (6) and (7), we obtain

\[
y_{t+1} = \gamma(s_2 - b) y_t e^{-\rho(y_2 - b)} y_{t+2} \equiv f_1(y_t). \tag{16}
\]

Since eqn (16) indicates a Ricker type of discrete dynamic system, \( y_t \) does not positively diverge. When eqn (14) is satisfied, equilibrium \((0, 0)\) is stable if and only if \( f_1'(0) < 1 \), i.e. \( \gamma(s_2 - b) < 1 \). Under this condition, \( y_t \) converges to 0 for all \( y_0 > 0 \). The non-trivial equilibrium satisfies \( f_1(\bar{y}) = \bar{y} \). From eqn (16), we can easily obtain the unique equilibrium \( \bar{y} = s_2/\rho(\gamma(s_2 - b)) \). The equilibrium \( \bar{y} \) exists if \( \gamma(s_2 - b) > 1 \). \( \bar{y} \) is globally stable if \( |f_1'(\bar{y})| = |1 - \ln[\gamma(s_2 - b)]| < 1 \), or if \( 0 < \ln[\gamma(s_2 - b)] < 2 \). Therefore, \( \bar{y} \) exists and is stable if

\[
1 < \gamma(s_2 - b) < e^2. \tag{17}
\]

In contrast, the equilibrium \( \bar{y} \) exists and is unstable if \( \gamma(s_2 - b) > e^2 \). Figure 3 shows the following asymptotic behaviors for the number of triploids: apomict apomicts (Ia) become extinct, (Ib) reaches a positive equilibrium, or (Ic) persist and fluctuate permanently.

### 3.2.2. Dynamic Behavior of Diploids

Next, we consider the condition \( y_t \equiv 0 \). From eqns (5) and (7), we obtain

\[
x_{t+1} = a(s_1 - a)x_t e^{-\rho(s_1 - a)x_t} \equiv f_2(x_t). \tag{18}
\]

Since \( f_2(x_t) \) also indicates a Ricker type of discrete dynamic system, \( x_t \) does not positively diverge.
either. When eqn (15) is satisfied, equilibrium (0, 0) is stable if \( f_2'(0) < 1 \), i.e. \( x(s_1 - a) < 1 \). Under this condition, \( x_t \) converges to 0 for all \( x_0 > 0 \). The non-trivial equilibrium satisfies \( f_2(\bar{x}) = \bar{x} \). From eqn (18), we can easily obtain the unique equilibrium \( \bar{x} = e_1 \ln[\alpha(s_1 - a)]/\rho x(s_1 - a) \). As used to obtain condition (17), the equilibrium \( \bar{x} \) exists and is globally stable if

\[
1 < x(s_1 - a) < e^2. \tag{19}
\]

In contrast, the equilibrium \( \bar{x} \) exists and is unstable if \( x(s_1 - a) > e^2 \). Domain II in Fig. 3 shows the following types of asymptotic behaviors for diploids: diploids (IIa) become extinct, (IIb) reach positive equilibrium, or (IIc) persist and fluctuate permanently.

### 3.2.3. Asymptotic State of Coexistence

We consider what happens when \( x_t \equiv y_t/\psi^* \) with \( \psi^* \) given by eqn (9). From eqns (5–7),

\[
x_{t+1} = x(s_1 - a) \frac{ax_t + rb y_t}{ax_t + by_t} x_t e^{-\rho z_t} < z_t e^{-\rho z_t},
\]

where

\[
\forall x_t, \forall y_t > 0,
\]

and

\[
y_{t+1} = \left\{ \beta(s_1 - a) \left( 1 - r \right) b x_t + \gamma(s_2 - b) \right\} \times y_t e^{-\rho z_t} < z_t e^{-\rho z_t} \quad \forall x_t, \forall y_t > 0. \tag{21}
\]

\( ze^{-\rho z} \) maximizes \( 1/\rho e \) at \( z = 1/\rho \). Therefore, both \( x_t \) and \( y_t \) do not positively diverge. Since \( \psi^* \) is the unique equilibrium, \( \bar{x} \) satisfies \( x = g(\bar{x}) \) for the one-dimensional discrete dynamic system (24), and obtain

\[
\bar{x} = \frac{\log A}{2 \rho A}, \tag{26}
\]

respectively. Simplifying, eqns (22) and (23) become

\[
x_{t+1} = A x_t e^{-2 \rho A x_t} \equiv g(x_t), \tag{24}
\]

where

\[
A = \frac{\alpha(s_1 - a) (a \psi^* + rb)}{a \psi^* + b}
\]

\[
= \beta(s_1 - a) \frac{(1 - r) b \psi^*}{a \psi^* + b} + \gamma(s_2 - b).
\]

From eqn (9), \( A \) becomes

\[
A = \frac{\alpha g(s_2 - b) - rb \beta(s_1 - a)}{a x - b \beta}. \tag{25}
\]

\( A \) is positive if eqn (10) is satisfied. Quantity \( A \) determines the stability property of this system. We consider the non-trivial unique equilibrium \( \bar{x} \) satisfying \( x = g(\bar{x}) \) for the one-dimensional discrete dynamic system (24), and obtain

\[
\bar{x} = \frac{\log A}{2 \rho A}. \tag{26}
\]

The function \( g(x) \) is positive and finite for all \( x \geq 0 \) and reaches a maximum at \( x = 1/(2 \rho A) \). Therefore, \( x_t \) never positively diverges. When \( \psi^* \) is stable, the dynamic behavior of \( x_t \) has three cases determined by \( A \): (IIa) \( A < 1 \), (IIb) \( 1 < A < e^2 \), and (IIc) \( A > e^2 \). In case (IIa), \( x_t \) and \( y_t(\equiv \psi^*/x_t) \) converge to 0 for all \( x_0 > 0 \) if \( A < 1 \), i.e. \( \gamma > \max(\gamma_1, l_1) \), where

\[
\gamma_1 = A + rb(s_1 - a) - rb \frac{b \beta}{a(s_2 - b)\bar{x}}. \tag{27}
\]

In case (IIb), \( x_t \) converges to the positive equilibrium \( \bar{x} \) if \( 1 < A < e^2 \), i.e. \( \max(\gamma_2, l_1) < \gamma < \min(\gamma_1, l_2) \), where

\[
\gamma_2 = \frac{ae^2 + rb(s_1 - a) - e^2 b \beta}{a(s_2 - b)\bar{x}}. \tag{28}
\]

Finally, in case (IIc), diploids and apomicts coexist with cyclic or chaotic fluctuations if \( A > e^2 \), i.e. \( l_1 < \gamma < \min(\gamma_2, l_2) \). The hatched region in Fig. 4 represents a globally stable coexisting...
FIG. 4. Stability property for (i) $0 < \beta < \frac{a}{b(1-r)(s_1-a)}$, (ii) $\frac{a}{b(1-r)(s_1-a)} < \beta < \frac{e^a}{b(1-r)(s_1-a)}$ and (iii) $\beta > \frac{e^a}{b(1-r)(s_1-a)}$. Both diploids and apomicts become extinct in Domain (IIIa). Diploids and apomicts coexist in Domain (IIIb). Domain (IIIc) shows that both diploids and apomicts persist and fluctuate stably.

equilibrium $(\hat{x}, \hat{y})$, where $\hat{y} = \hat{x}/\psi^*$. The dotted region in Fig. 4 represents persistent, but fluctuating, levels of diploids and apomicts. We investigate the dynamic behavior of $x_t$ numerically. After 10,000 generations, the system reaches periodic or chaotic oscillations. Figure 5 shows the population for the last 100 generations. Simulations starting from a population size of 100 reveal a bifurcation diagram of $x_t$. $\hat{x}$ becomes unstable and the system has periodic cycles as $A$ increases. Increasing $A$ further results in periodic doubling in the asymptotic state and finally results in a chaotic state.

When $\psi_t \to 0$ (Domain I in Fig. 3), $y_t$ has three asymptotic states: $(x_t, y_t) \to (0, 0), (0, \hat{y}), (0, \text{variable})$. The asymptotic state $\hat{y}$ depends on $\gamma$ if $\psi_t \to 0$. When $\psi_t \to +\infty$ (Domain II in Fig. 3), $x_t$ has three asymptotic states: $(x_t, y_t) \to (0, 0), (\hat{x}, 0), (\text{variable}, 0)$. The asymptotic state $\hat{x}$ depends on $A$ if $\psi \to +\infty$. When $\psi \to \psi^*$ (Domain III in Fig. 4), $(x_t, y_t)$ has asymptotic states: $(x_t, y_t) \to (0, 0), (\hat{x}, \hat{y}), (\text{variable}, \text{variable})$. The asymptotic state $(\hat{x}, \hat{y})$ depends on $A$ if $\psi \to \psi^*$. When the fate of $\psi_t$ depends on the initial value (Domain IV in Fig. 3), nine asymptotic states arise: (IVaa) $(0, 0)$ (not bistable), (IVab) $(\hat{x}, 0)$ or $(0, 0)$, (IVac) (variable, 0) or $(0, 0)$, (IVba) $(0, 0)$ or $(0, \hat{y})$, (IBbb) $(\hat{x}, 0)$ or $(0, \hat{y})$, (IVbc) (variable, 0) or $(0, \hat{y})$, (IVca) $(0, 0)$ or $(0, \text{variable})$, (IVcb) $(\hat{x}, 0)$ or $(0, \text{variable})$, and (IVcc) (variable, 0) or $(0, \text{variable})$. When $b\beta/a > 1/(s_2-a)$, Domains IIa, IVaa, IVba, and IVca disappear (see Fig. 3). I similar ways, all Domains, but Ic, IIc, IIIa, and IVcc may disappear depending on parameter values.

Figure 6 demonstrates that the stable structure changes from coexistence to extinction as $\gamma$ (the germination rate of triploid seed without
Here, \( \hat{y} \) (apomict) initially increases then decreases with increasing \( \gamma \), as shown in Fig. 6. Thus, increasing \( \gamma \) does not always support the triploid population. If the germination rate of triploid seed asexually produced by triploid apomict \( \gamma \) is sufficiently small, most triploids are reproduced by crossing. Under these conditions, diploids and triploids coexist. As \( \gamma \) increases, diploids and apomicts are affected by the density effect of the seedlings. The number of triploids offspring increases with \( \gamma \). Diploids are fertilized by triploids and become extinct. Subsequently, triploids also become extinct. When \( \gamma \) is sufficiently large, diploids become extinct. Under these conditions, the stability of the equilibrium depends on \( \gamma \).

Figure 8 shows the trajectories of \( x_t \) and \( y_t \) for Domain (IVab) in Fig. 3. Whether diploids persist depends on the initial conditions. Both diploids and apomicts become extinct when \( x_0/y_0 < \psi^* \) (shown by the dotted line); however, diploids can invade when \( x_0/y_0 > \psi^* \). For example, a small number of diploids invade at a trivial equilibrium \((0, 0)\) and \( x_0/y_0 > \psi^* \) and therefore the system moves to the other equilibrium \((\hat{x}, 0)\). We compile dynamics of this system as follows: (i) both diploids and apomicts become extinct (Domains Ia, IIa, IIIa, and IVaa), (ii) both diploids and apomicts coexist (Domains

![Diagram of population density](image)

**Fig. 6.** Change in the equilibrium density of diploids and apomicts as \( \gamma \) increases from 0 to 1. \( \alpha = 1.04, \beta = 2, \rho = 1, a = 1, b = 1, r = 0.8, s_1 = 2, \) and \( s_2 = 2. \) (---) and (---) curves, respectively, indiate diploids and apomicts.

![Diagram of trajectories](image)

**Fig. 7.** The five trajectories of \((x_t, y_t)\) for \( \gamma = 0.676, \alpha, \beta, \) and \( \rho \) are the same as in Fig. 6. Each initial value is \((x_0, y_0) = (1, 1), (0.01, 10^{-4}), (0.01, 10^{-4}), (0.03, 10^{-4}), (0.1, 10^{-4}). \) Each (---) curve presents the trajectory with each initial value. The (○○○) and (●●●) circles are unstable and stable equilibria, respectively. The slope of the broken line indicates \( \psi^* \) and the ratio \( x_t/y_t \) monotonically approaches \( \psi^* \).

When \( \gamma < l_1, \) \( x_t \) converges to a positive equilibrium and \( y_t \) converges to 0. In other words, the population becomes purely diploid. When \( l_1 < \gamma < \gamma_1, \) diploids and triploids coexist. However, as \( \gamma \) increases to \( \gamma_1, \) \( \hat{x} \) monotonically decreases, \( \hat{y} \) initially increases and subsequently decreases, and finally \( \hat{x} \) and \( \hat{y} \) approach 0, as \( \gamma \) increases from \( l_1 \) to \( \gamma_1. \) If \( \gamma_1 < \gamma < l_2, \) both diploids and triploids become extinct. Figure 7 shows the trajectories of \( x_t \) and \( y_t \) for \( \gamma_1 < \gamma < l_2. \)
IIIb, IIIc), (iii) only diploids can invade (Domains Iib, Iic, IVab, and IVac), (iv) only apomicts can invade (Domains Iib, Ic, IVab, and IVca), and (v) whether diploids or apomicts invade depends on the initial relative density (Domains IVbb, IVbc, IVcb, and IVcc).

4. Discussion

Based on our results, the coexistence of triploid apomicts and diploid sexuals does not require niche separation. However, coexistence is only possible under specific conditions, where both \(z\) (the germination rate of sexual diploid seeds) and \(\gamma\) (that of triploid seeds without crossing) are sufficiently small, as in Fig. 4. When diploids and apomicts coexist, the system has three equilibrium states: stable or periodic cycles or a chaotic state. These complex dynamics depend on the functional form of density dependence. If the functional form of density dependence conforms to a Ricker form density dependence. If the function of density dependence is Michaelis–Menten \(F(z) = \frac{a_zz}{m + z}\) in eqn (4), this system always has a stable equilibrium. The coexistence conditions shown in Fig. 3 are the same irrespective of the functional forms of density dependence. System (5–7) is bistable in conditions (IVbb), (IVbc), (IVcb), and (IVcc). In these cases, neither apomicts nor diploids invade each other’s population. Apomicts cannot increase where diploids already exist. Diploids cannot increase where apomicts already exist. This situation is thought to be unlikely in nature. In Taraxacum, which is perennial and has both sexual diploids and apomictic triploids, the latter have invaded broad areas in Japan where the native species is exclusively diploid (Morita et al., 1990b; Ogawa & Isao, 1991). If the germination rate of triploids is large, a pure triploid population would be generated as in Case (I). In contrast, if the germination rate of diploids is large, they would make a pure diploid population as in Case (II).

The maintenance of sexual diploids depends on the difference between the germination rates of diploids and apomicts, \(z - \gamma\). If apomicts do not produce pollen, that is \(b = 0\), \(s_1 = s_2\), and \(z = \gamma\), then the slope of \(l_1\) is smaller than 1, and diploids never persist. Coexistence of diploid and apomict is possible if apomicts produce pollen. If \(b = 0\), both lines \(l_1\) and \(l_2\) in eqns (12) and (13) pass on \((0, 0)\) and Domain (III) in Fig. 3 vanishes. Facultative apomicts may be forced to pay the cost of pollen production when the germination rate of triploid apomicts is very low. When apomicts produce more pollen (\(b\) becomes large), diploids and apomicts may coexist, because Domain (III) becomes larger. Apomicts become extinct when diploids produce more pollen (\(a\) becomes large). Diploids become extinct when they produce less pollen (\(a\) becomes small).

The population structure depends on the germination rates of diploids and triploids (\(z\) and \(\gamma\), respectively). However, we have little quantitative information on the germination rate or the numbers of seedlings produced by diploids and triploids. The germination rate of diploids depends on density, climate, and pollinator conditions, since diploids are considerably self-incompatible. If the population density is very low, the germination rate of diploids may be lower. Thus, the germination rate differs among habitats and between diploids and triploids owing to ecological conditions.

Crossing can alter genetic variability, but our model did not include this phenomena. Crossing may also provide variability in agamosperms by promoting recombination (Mogie, 1992). Populations in the wild may be subject to immigration, since vectors such as birds can transport seeds over considerable distances. Isozyme evidence suggests that genetic variation exists between sexual and agamospermous species (Yahara et al., 1991; Overath & Hamrick, 1998). Variation in agamosperms may be the result of crossing, immigration, or mutation. Spatial structure and genetic diversity should also be considered. Further modifications of our mathematical model are expected to contribute to the examination of the evolution of facultative agamosperms.

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