Title: Genet dynamics and its variation among genets of a clonal plant *Convallaria keiskei*

Abstract

In clonal plant populations, a number of genetically identical ramets form a genet. While coexisting ramets potentially perform independently, their behaviours not only depend on ages and sizes but are also constrained by genetic background. In this study, genet dynamics and its variability among neighbouring genets were investigated based on the ramet demography of each genet in *Convallaria keiskei*. Genet dynamics were first formulated as a matrix model with the two components of clonal growth (clonal reproduction) and survival-transitions between ramet size classes. Then, a statistical estimation of the matrix elements was established using three datasets: aboveground demographic censuses, belowground directional rhizome connections and genetic identification of ramets. Finally, genet growth rates reflecting both the changes of clonal growth and ramet size growth were estimated and compared for fundamental demographic elements among genets. Over three years of aboveground annual censuses of a 28 × 2 m plot, 2021 ramets were identified as belonging to 28 genotypes. Belowground excavation detected 515 clonal fragments. Genet growth rate of three dominant genets varied with medians of 1.13, 1.02 and 1.05; 95% credible intervals of the posterior distributions did not overlap between the genet with the largest median and the others. The variation was caused primarily by differences in clonal growth rather than survival-transitions between size classes. Clonal growth by branching was rarer than at the tips but contributed to the maintenance of the genet. Therefore, both clonal growth frequencies and connecting patterns of ramets caused the variation of genet dynamics and established genets persist for a long time through the positive growth rates, which would contribute to maintain a population. We also conclude that fundamental demographic elements relating to clonal growth traits (the features of individual genets) strongly impact genet dynamics.

Introduction

Plants with the ability to produce offspring via clonal organs, such as rhizomes, stolons and tubers, are called clonal plants (Klimeš et al. 1997, Whigham 2004, Silvertown 2008). A remarkable characteristic of clonal plants is horizontal expansion and multiplication by developing clonal organs (Klimeš et al. 1997, Herben and Klimešová 2020). This ability generates interesting and complex life-histories with two life cycles – seedling recruitment and clonally recruited offspring (Jackson et al. 1985, van Groenendael and de Kroon 1990). A number of genetically identical sub-units (ramets) exist simultaneously and have the potential to perform independently from each other; these constitute a genetic individual called a genet (Abrahamson 1980, Tuomi and Vuorisalo 1989, Eriksson 1993, Tanner 2001). A clonal plant thus possesses a hierarchical structure of ramets, genets and populations.

Demographic analysis is an effective approach to understanding the population dynamics and life-history of organisms (Abrahamson 1980, Silvertown et al. 1993, Franklin et al. 2021). A basic approach is to determine three fundamental demographic elements of individuals in a population: reproduction, survival and growth. Many mathematical modelling approaches set the individual as the basic unit (e.g. Caswell 2001 and references therein). In the case of clonal plants, both ramets and genets can be treated as individuals; the formation of clonal ramets is sometimes treated as reproduction of ramets (clonal reproduction) and sometimes as growth of a genet (clonal growth) (Hartnett and Bazzaz 1985, Fair et al. 1999, Eriksson and Bremer 1993). Many studies have mainly analysed ramet demography by using ramet-based data, and have offered useful predictions for changes in dynamics such as biomass, ground cover and population expansion (e.g. Cain and Damman 1997, Ehrlén and Lehtilä 2002, Decruyenaere and Holt

2005). Genet-based studies, on the other hand, treat genet recruitment as reproduction by seeds, and genet growth as the incrementation of the ramet number and/or occupied area (e.g. Fair et al. 1999, Suzuki et al. 2006, Kouassi et al. 2014). However, the origin of clonal offspring ramets has so far not been considered in studies. If demographic characteristics differ from one genet to another, considering the variations among genets may improve understanding of population dynamics of clonal plants (Barsoum et al. 2004, Franklin et al. 2021). In addition, the demographic variation among ramet ages and sizes may differently impact on the dynamics of each genet. Thus, determining the fundamental demographic elements for ramets with considering clonal growth as well as growth, survival and transition of each ramet per genet and comparing them among genets, would shed light on understanding the life-history strategy of clonal plants.

It is sometimes hard to determine demographic traits such as reproduction (seed and clonal growth), growth and survival of ramets per genet because of ecological and genetic features of clonal plants. First, in order to deal with genets, we have to know which genet each ramet belongs to. Although genet distribution can be distinguished by the clumping structure for plants forming genet patches (Kouassi et al. 2014, Kawai and Kudo 2018), it is impossible to identify genets at a glance for plants spreading via structures that intermingle with each other. DNA analysis is an alternative tool now available for identifying genetic relations between ramets (e.g. Reusch 2006, Suzuki et al. 2006, Matsuo et al. 2018). Second, in order to explore features of ramets producing offspring, it is necessary to detect which ramets perform clonal growth and produce offspring ramets. Clonal growth can be treated as reproduction by the mother ramet and largely depends on the situation of the mother ramet and the reproductive ability of the genets in such plants as the stoloniferous herb *Rubus* (Lambrecht-McDowell and

Radosevich 2005) and the pseudo-annual herb *Uvularia perfoliata* (Huber et al. 2004). However, the mother ramet of newly emerged offspring may not be identifiable from aboveground plant structures, especially in clonal plant species that use underground organs for clonal growth and have long life spans. Ease and required approach of observation largely depend on the architecture of the clonal organs and on expansion frequency (Franklin et al. 2021). If the directional connection of mother to daughter is directly observable, exact information about mother-daughter pairs can be obtained and variability in clonal recruitment from mother ramets may be analysed in addition to such demographic traits as survival and growth (e.g. leaf area incrementation and stem height expansion) of mother ramets.

Convallaria keiskei is a perennial clonal herb species that can expand widely on the forest floor (Ohara et al. 2006, Araki et al. 2007). It has stoloniform rhizomes, i.e. underground stems (Bell 2008), elongating during the growing season. The distal end of the rhizome containing the apical meristem becomes erect and grows vertically forming a new ramet, while rhizomes gradually die from the basal end (Supporting information). The resulting linear structure is thus oriented from an older to the youngest end in a rhizome fragment (Araki and Ohara 2008, Logofet 2016). Since most rhizomes are maintained for several years and older ones often persist as more fragmented pieces in soil, destructive excavation provides not only a snap-shot of belowground connections but also a record of growth history; that is, the directional connections of the belowground rhizome may be used as a source of information for reconstructing the expanding state of a genet over the previous few years. On the other hand, ramets usually live for years and produce new ramets repeatedly even if they are disconnected from each other (Supporting information; Araki and Ohara 2008). However, as identifying all ramet members of an

expanding and fragmented genet is impossible because of vigorous clonal expansion, statistical estimation from sampled data is inevitable.

In this study, we aimed to reveal the life-history strategy of herbaceous clonal plants having stoloniform rhizomes by investigating the variation of genet dynamics in a population, based on the ramet demography of clonal recruitment and survival-transition. We addressed the following questions: 1) do genet growth rates, composed of clonal growth and ramet size growth, vary among genets?; 2) what demographic traits of ramets cause any variation?; 3) do less frequent clonal growth patterns such as branching contribute to the genet dynamics, and if so, to which degree compared with frequent expansion at a clonal fragment tip?

To this end, we first formulated genet dynamics as a matrix model. After establishing a statistical estimation of the elements of the matrix using three datasets (aboveground behaviour, belowground directional rhizome connection and genetic identification of ramets), we quantitatively estimated genet growth rates and compared these between genets for a *C. keiskei* population. In particular, we estimated the consecutive clonal growth probability over years, which also indicates how long it takes for a *C. keiskei* genet to expand over a given distance. Finally, we discuss the belowground ecology of this plant, an aspect that has repeatedly been highlighted in the population ecology of clonal plants (Janovský et al. 2017, Klimešová et al. 2021).

Methods

Study species

Convallaria keiskei (Asparagaceae) is a perennial herb, distributed across Japan (Hokkaido, Honshu and Kyushu), Sakhalin Island, Korea, China and eastern Siberia

(Utech and Kawano 1976). An aerial shoot of sheath leaves is elongated aboveground and develops one or two leaves in late April to May. An inflorescence also develops and flowering takes place in late May to June (Ohara et al. 2006). The aerial shoots die down during September and October, leaving only belowground organs over winter (Supporting information). In the following season the aerial shoots grow again from the basal organs that persist for years, thus ramets of *C. keiskei* emerge at almost the same position (Supporting information). *Convallaria keiskei* propagates clonally by growing stoloniform rhizomes belowground. A rhizome starts to elongate in spring and forms a new ramet that expands a shoot at the tip next season in autumn. Rhizomes gradually decay and are usually maintained for several years in the soil. Therefore, ramets are separated physically every year, resulting in an average of 1.86 ramets connected in a clonal fragment. This indicates that the rhizomes primarily function to produce new ramets rather than provide physiological integration to transport resources. This configuration has been described as 'developmentally-programmed division of labour' (*sensu* Alpert and Stuefer 1997) or 'division of labour in time' (Jonsdottir and Watson 1997), based on the type and degree of functional specialization.

Study site

The study was carried out in a windbreak forest (143° 10' N, 42° 40' E) in Nakasatsunai, eastern Hokkaido, Japan. The forest is several kilometres long and fragmented by roads and agricultural fields. Planted *Larix leptolepis* is the most dominant tree, followed by naturally established *Quercus dentata* and *Betula platyphylla*. In 2001, a study plot (100 × 90 m) with grid points plotted every 5 m (total 21× 19 = 399 points) and characterized by *x* and *y* coordinates, was established on the forest floor. Genotypes of the ramets

147 nearest to each grid point were identified using allozyme analysis over the whole plot
148 (Araki et al. 2007). In 2005, a new, long rectangular plot (28 × 2 m) was established for
149 the present study within the original plot (coordinates x = 20–48, y = 50–52). Fifty-six 1
150 × 1 m subplots were also laid out in the plot.
151
152 **Aboveground demographic census**
153 Aboveground demographic censuses were performed in June and July from 2005 to 2007.
154 In the first year, all aerial shoots observed in the 28 × 2 m plot were carefully marked and
155 mapped. For each shoot, the number of leaves was counted and the length of the longest
156 leaf (leaf size) was measured. The fate of leaves and successive changes in leaf number
157 and size at marked shoots were recorded and re-measured until 2007. Newly emerged
158 shoots (NEW) within the plots were additionally marked and measured. Marked shoots
159 that did not emerge aboveground in following years might be either 1) dead or 2) living;
160 in the latter case they were recorded as ‘unemerged (UEM)’ for that year (Araki et al.
161 2009).
162
163 **Genetic identification**
164 Leaf tissues of all ramets appearing in 2005 and newly emerging in 2006 and 2007 within
165 the 28 × 2 m plot were collected after they were measured. Collected leaves were frozen
166 until analysis. To minimize the damage to plants, we collected only ~1 cm^2 of tissue from
167 each leaf. DNA was extracted using CTAB methods, and 5 ng of the extracted DNA was
168 then amplified using a set of six labelled primer pairs targeting highly polymorphic DNA
169 microsatellite loci according to previously reported protocols (GeneBank accession
170 numbers AB251398, AB251399, AB251400 and AB251401; Araki et al. 2006). Size

171 separation of the PCR products was carried out using capillary electrophoresis on an ABI
172 3100 genetic analyzer (Applied Biosystems, Thermo Fisher Scientific). Size scoring of
173 banding patterns and genotyping were performed using a semi-automated method and the
174 program GENESCAN (Applied Biosystems). Identical genotypes were classified as
175 members of the same clone if the probability of a particular multilocus genotype occurring
176 by free recombination was very small. The error likelihood of falsely ascribing genotypes
177 to the same genet, P_{gen}, was calculated according to Parks and Werth (1993). Since the
178 chance of obtaining the same multilocus genotypes by recombination was smaller than
179 1%, the results (all $P_{gen} < 0.001$) overall affirmed that the used primers were highly
180 polymorphic microsatellite markers and that all identical genotypes could be considered
181 members of the same clone.
182
183 **Belowground rhizome connection**
184 In order to explore rhizome connections between ramets in the soil, all subterranean
185 organs in fourteen of the 1 × 1 m subplots (coordinates x = 30–42, y = 50–52) within the
186 28 × 2 m plot were completely dug up in September 2007. Only the area where ramets
187 and underground organs could be stably excavated was used in this experiment. All plant
188 organs of elongating or senescent rhizomes with established aboveground shoots, new
189 apical buds and remaining old tissues were carefully taken out, so as to maintain rhizome
190 connections between ramets for direct observation. When a rhizome extended beyond the
191 plot, the subterranean organs were excavated as far as possible towards the end of the
192 rhizome connections. Some rhizomes ended or started with decayed or interrupted tips
193 and were classified as ‘interrupted rhizomes’.
194 We defined a set of connected subterranean organs and shoots as a ‘fragment’

unit. Observing rhizome connections in a fragment enabled us to identify pairwise connections and the direction of rhizomes elongating from mother to daughter ramets (Araki and Ohara 2008). These observations were first sketched and then digitized in the form of a table in which each row corresponded to one pairwise connection from a mother to a daughter ramet.

In *C. keiskei*, rhizome elongation takes place during the spring to autumn growing season and daughter ramets emerge in the subsequent year. Thus, new buds found in September 2007 indicate clonal growth in 2007 and newly emerged shoots in June 2007 reflect the clonal growth in 2006. A further eight of the 1 × 1 m subplots in 2008 and three in 2009 were similarly excavated. The remaining areas in the plot proved impractical to dig up because of heavy grass cover and typhoon damage.

Modelling genet dynamics

In order to examine the genet dynamics of *C. keiskei*, we applied a matrix model which has been widely applied in population dynamics studies of perennial plant species (Caswell 2001, Salguero-Gómez et al. 2015). In this model, individuals are categorized into 'growth stages'. Let i and j denote the stages (i, j = 1, …, I where I indicates the number of stages). The model consists of a diagonal matrix of survival, $\mathbf{S} = (S_j)$, a transition matrix, $\mathbf{T} = (T_{ij})$ and a reproductive matrix, $\mathbf{R} = (R_{ij})$. The diagonal element S_j indicates the survival probability per year of an individual that belongs to stage j. T_{ij} indicates the transition probability that an individual in stage j is transmitted to stage i conditionally for survival at stage j. R_{ij} indicates the expected number of offspring in stage i produced by an individual of stage j. The population matrix $\mathbf{A}$ is then defined as $\mathbf{A} = \mathbf{TS} + \mathbf{R}$

Supposing that in year $t-1$, there are n_j individuals in stage j. Denoting them by vector $\mathbf{n}_{t\text{-}1} = (n_1, \ldots, n_I)^T$ (^{T} indicating transposition), the expected number of individuals in year t can be written as:

$\mathbf{n}_t = \mathbf{A}\mathbf{n}_{t\text{-}1} = (\mathbf{TS} + \mathbf{R})\,\mathbf{n}_{t\text{-}1}$.

Applying this population dynamics modelling framework, we developed a genet dynamics model in which the population was replaced by a genet, individuals by ramets in the genet, and reproduction was obtained from clonal growth. When a matrix model is applied in population ecology under the stationary assumption (i.e. matrix **A** is invariant across years), the largest real eigenvalue of **TS** + **R**, which is often denoted by λ, is generally interpreted as the intrinsic growth rate of the population. Thus, in the case of genet dynamics, it expresses the genet growth rate.

The partial derivative of λ with respect to each matrix element is called sensitivity and has been commonly applied in population ecology in order to examine effects of a small change in each matrix element on the largest eigenvalue λ. There is a convenient formula (Caswell 2001);

$$\frac{\partial \lambda}{a_{ij}} = \frac{v_i u_j}{\sum_k v_k u_k}$$

in which **u** and **v** respectively indicate the right and left eigenvector of the largest eigenvalue λ.

Growth stage

A new rhizome regularly extends from the internode that is the nearest to a shoot, which finally develops a new bud at the tip (Fig. 1a, 2, Supporting information). In terms of ramet behaviour this mean that a new ramet is produced from a ramet at the tip of a clonal fragment (Araki and Ohara, 2008). Rhizomes also occasionally extend to shoots from

internodes other than the nearest, resulting in rhizome ‘branching’. Thus, if a new ramet is formed from a non-tip ramet, it was treated as ‘branching’ clonal growth in this study. It was hypothesized that clonal growth occurred at different rates between tip and non-tip ramets and between newly born and older ramets. We therefore classified ramets according to I) age and position, followed by II) size.

I) Three classes were defined for age-position in a fragment:

1-y-tip: ramet at the tip of a fragment and appearing in that year, age = 1.

2-y-tip: at the tip of a fragment and appearing before that year, age ≥ 2.

Non-tip: at an intermediate position of a fragment and appearing before that year, age ≥ 2.

II) Ramets were first grouped into two size categories according to the number of leaves: (1) one-leaf (1L), and (2) two or more (rarely three or four) leaves (2L). Ramets in the 2L category were then further divided according to leaf length: < 10, 10–15, 15–20 and ≥ 20 cm. Ramets in 1L were not subdivided by leaf length because of a smaller variance in leaf length (Araki et al. 2009). Ramets were thus categorized into a total of 15 stages (1-y-tip 1L, 2L- < 10, …, 2L- ≥ 20; 2-y-tip 1L, 2L- < 10, …, 2L- ≥ 20; non-tip 1L, 2L- < 10, …, 2L- ≥ 20). Hereafter, the age-position is denoted by h and the size class by k (k = 1, …, K = 5) as ${}_k{}^h$.

Structure of the matrix model

Examples of the transition patterns of surviving ramets and those of recruiting new ramets by clonal growth are shown in Fig. 1a. If a ramet at the 1-y-tip age-position performs clonal growth, it transitions to non-tip (ramet A in pattern 1-1); otherwise, it transitions to 2-y-tip (ramet A in pattern 1-2). If a ramet at the 2-y-tip age-position conducts clonal

growth, it transitions to non-tip (ramet B in pattern 2-1); otherwise, it stays at the 2-y-tip (ramet B in pattern 2-2). A ramet at the non-tip remains in this position (ramet C in pattern 3) regardless of its clonal growth (branching). These transitions are illustratively summarized as blue arrows in Fig. 1b. The position of a daughter ramet is always at the 1-y-tip (red arrows in Fig. 1b).

For simplicity, it was assumed that the size of a daughter ramet was not affected by the stage, i.e. either by the age-position or size category, of the mother. Let N_k be the probability that a daughter belongs to size class k. Let E_l^h and C_l^h be the expected number of daughters and the probability that a mother recruited a new ramet via clonal growth (clonal reproduction), when the mother belongs to age-position h and size class l, respectively. The expected number of daughters in size class k produced by a ramet in age-position h and size class l, R_{kl}^h, can then be written as $R_{kl}^h = N_k E_l^h C_l^h$ (right matrix in Fig. 1c).

When a ramet in size class l survives with the probability S_l, it transitions to size class k with probability T_{kl} (left matrix in Fig. 1c). Genet dynamics of *C. keiskei* are thus modelled in the matrix model framework as illustrated in Fig. 1c. In the following, the left blue 15 × 15 matrix is referred to as $\mathbf{T}_{SC}$ (this matrix is formed by not only T_{kl} but also S_l and C_l^h) and the red right matrix as **R**. The largest real eigenvalue of the matrix $\mathbf{T}_{SC}$ + **R** is referred to as 'genet growth rate' that integrates clonal growth and ramet size growth.

Statistical estimation of matrix elements

Statistical estimation of C_l^h, N_k, E_l^h, S_l and T_{kl} was carried out separately for each genet. In the following we therefore do not explicitly indicate genet identity. Because we applied

291 the matrix model that assumes stationarity, all data were pooled across years. The
292 estimations were conducted in a Bayesian modelling framework separately for the five
293 parameter sets. Some additional technical details are described in the Supporting
294 information.

295 Information regarding whether a ramet in age-position h and size class l in year
296 t produced a daughter ramet was obtained from three annual censuses of shoots, as well
297 as from the belowground information such as the rhizome connections between ramets
298 from excavated fragments. Focusing on the tip parts, how a series of shoots were observed
299 during the censuses, and on the fragments excavated in 2007, we classified connection
300 patterns incorporating above- and belowground information into eight groups (Fig. 2).
301 For example, if a ramet newly born in 2007 (defined as year t) was positioned in front of
302 a ramet born in 2006 (year $t - 1$), this indicated that the latter ramet performed clonal
303 growth in the summer of 2006 (year $t - 1$) at the 1-y-tip position. If an apical bud was
304 observed in front of the former, this showed that a 1-y-tip ramet performed clonal growth
305 in the 2007 summer (pattern-1). If the ramet did not have a bud, it belonged to pattern-2.
306 This classification was performed for every branch in a fragment (when branching clonal
307 growth was performed, a new 'branch' appeared in the fragment; throughout the paper,
308 'branching' is used to represent a clonal growth while a "branch" indicates a part of one
309 fragment). We then counted the numbers of branches of the eight patterns. Fragments
310 excavated in 2008 and 2009 were similarly classified (in these cases, the excavated year
311 was defined as year t and the longest series begins with year $t - 3$).

312 For branching clonal growth ($C^{\text{non-tip}}$), the numbers of triplets consisting of a
313 mother ramet, an old daughter and a new bud (or new ramet) and those of potential non-
314 tip ramets of branching clonal growth were counted (these were not classified into size

315 classes). When we counted new daughter ramets belonging to the size class k, if some
316 newly emerged shoots connected to dead ramets or to interrupted rhizomes, they were
317 excluded because such ramets were probably not newly born (Supporting information).
318 The numbers of new buds were counted if a ramet produced a bud.

319 Following Araki et al. (2007), if a ramet observed in 2005 appeared neither in
320 2006 nor 2007, it was classified as dead from 2005 to 2006. Subsequently, some of these
321 ramets were excavated and found to be alive. They were re-labelled as surviving ramets.
322 Mortality from 2006 to 2007 and later was not considered. We counted the numbers of
323 surviving and dead ramets for each size class. We also counted the numbers of ramets that
324 were transmitted from size class l to k, conditional on survival.

325 To evaluate uncertainty caused by these limited count data, we applied a
326 Bayesian approach. This was done separately for C_l^h, N_k, S_l and T_{kl}, while for E the
327 average number of new buds was used, because most of the existing ramets produced just
328 one daughter ramet and two or more were rare (Supporting information). For $C_l^{1\text{-y-tip}}$ and
329 $C_l^{2\text{-y-tip}}$, a generalized linear model (GLM) was applied. Using flat prior distributions, we
330 produced random samples from the posterior distributions of the coefficients in the GLM
331 by Markov chain Monte Carlo (MCMC) simulation and transformed them to those of $C_l^{1\text{-}}$
332 $^{\text{y-tip}}$ and $C_l^{2\text{-y-tip}}$ (further details are provided in the Supporting information). For $C^{non\text{-}tip}$,
333 N_k, S_l and T_{kl}, flat conjugate prior distributions were applied. Random samples were drawn
334 from the (binomial or multinomial) posterior distributions (details are provided the
335 Supporting information).

336

337 **Matrices and genet growth rate**

338 By randomly combining random samples from the posterior distributions of $\{C_l^h\}$, $\{N_k\}$,

339 $\{S_l\}$, $\{T_{kl}\}$ and the fixed value for E, we produced 10000 matrices ($\mathbf{T}_{SC}$ + $\mathbf{R}$) and for each
340 computed the largest real eigenvalues showing the genet growth rate.

341 In order to examine which component ($\mathbf{T}_{SC}$ or $\mathbf{R}$) contributed to determining the
342 differences in the growth rates between the genets, if any, we produced another two
343 matrices: in matrix (1), let clonal growth ($\{C_l^h\}$, $\{N_k\}$, E) be common to the genets; in
344 matrix (2), let the survival and transition ($\{S_l\}$, $\{T_{kl}\}$) be common to the genets. For (1),
345 by pooling the three genets' data on clonal growth, random samples from the posterior
346 distribution for $\{C_l^h\}$ and $\{N_k\}$ were produced by respectively MCMC and by using the
347 conjugate prior. The mean numbers of buds for the three genets were used for E.
348 Combining this with the random samples of $\{S_l\}$ and $\{T_{kl}\}$ for each genet, we then
349 produced 10,000 matrices and computed eigenvalues for the three genets. For (2), by
350 pooling the three genets' data on survival and transition, we produced 2000 random
351 samples of $\{S_l\}$ and $\{T_{kl}\}$. We then combined them with the random samples from clonal
352 growth ($\{C_l^h\}$, $\{N_k\}$) for each genet to produce 10000 matrices, and computed
353 eigenvalues for the three genets. If the posterior distributions of eigenvalues vary from
354 the original ones only for (1), it implies that inter-genet differences had effects on clonal
355 growth but little influence on survival and transition, and vice versa.

356 To examine the contribution of branching, we set the branching probability to 0
357 for the 10000 matrices and calculated the eigenvalues for each genet. If the posterior
358 distribution decreases, it indicates a contribution of branching to the maintenance of that
359 genet.

360 Finally, we conducted a sensitivity analysis. In this case, the commonly used
361 formula was considered insufficient due to the need to know the partial derivatives of λ
362 with respect to C_l^h and the others. We derived suitable formulae (Supporting information)

and calculated sensitivity for each of the 10,000 matrices.

Results

Genet identification

Of 2114 ramets in the 28 × 2 m plot, 2021 were identified and grouped into 28 genotypes. There were four dominant genotypes with respectively 809, 152, 648 and 367 ramets; hereafter genets e-1, e-2, e-3 and e-4, respectively. Nineteen genotypes were represented by only one ramet, and the other five were represented by 2–13 ramets. The four dominant genets were also found in the 5 m lattice of the original 100 × 90 m plot (Araki et al., 2007).

Aboveground shoot demography

A total of 1525, 1868 and 2113 ramets were found in the 28 × 2 m plot in 2005, 2006 and 2007, respectively. The numbers of ramets counted during the three annual censuses of aboveground shoots are summarized for the four dominant genets in Table 1. In the four genets, 108 to 701 ramets emerged every growing season. More new ramets (NEW) were found in 2006 than in 2007 and the number of ramets increased from 2005 to 2006 for all the genets (Table 1). New ramets mostly emerged clonally with two leaves 15–20 cm in length in genets e-1 and e-3, and with two leaves 10–15 cm in length for genet e-2 (Supporting information). Recruitment rates of ramets per genet were calculated as 8–20% based on ramet numbers existing in the previous year and newly emerged in the current year. The four genets were distributed to form clonal patches except in a section of intermingled parts where the range of genet e-2 overlapped with genets e-1 and e-3 (Supporting information).

Belowground rhizome connection and fragments

The *C. keiskei* parts dug up from 2007 to 2009 contained 943 living ramets (including 638 censused ramets and ramets connecting to a fragment but located outside the plot) and 139 buds. Old tissues of 58 remains from dead ramets were also found in fragments. These were also separated into 515 fragments. The numbers of branches varied from 2 (56 fragments) or 3 (19 fragments) to more (the maximum was 9 followed by 8, one fragment for each), while 431 fragments had no branches. The biggest fragment, in genet e-2, contained 34 living or dead ramets and buds with 9 branches (Supporting information). This fragment also contained the longest series of 11 ramets and a new bud at the tip, indicating that this genet was born at least 10 years ago. The average was 2.21 ramets per fragment. The dominant genets, e-1, e-2 and e-3, had 307, 57 and 125 fragments, respectively (Table S1b), with a total of 478, 152 and 279 living ramets (genet e-4 was not found in this area).

Among 210 newly emerged ramets in 2006 and 2007, 46.2% were connected to dead tissues or not connected to anything (isolated), implying that these were not newly born but had not emerged in the previous censuses and that the recruitment rates of 8–20% were overestimated.

Features of clonal growth in each genet

Table 2 shows the number of fragments associated with each connection pattern which informs the occurrence of clonal growth in certain ages and positions in the 2006 and 2007 growing seasons. Pattern-4 and -6 in Fig. 2 were dominant connection patterns in genets e-1 and e-3, while pattern-6 was less frequent in genet e-2. Most fragments

belonged to pattern-8. Based on these data combined with those of fragments excavated in 2008 and 2009, we classified all fragments, separately for every branch, and counted the number of successful and unsuccessful clonal growth occurrences for each stage (Supporting information). Ramets at the 1-y-tip position exhibited higher clonal growth frequencies than those at the 2-y-tip, especially in genet e-2 with 38.5% versus 11.3% and marginally in genet e-1 with 38.8% versus 32.2% and in genet e-3 20.4% versus 20.3% (these were further examined with Bayesian modelling, below). The average branching frequency was 3.4, 3.1 and 1.4% for genets e-1, e-2 and e-3, respectively (Supporting information). The numbers of buds per mother ramet ranged from one (91.9%) to three (1.6%), with a mean of 1.10, 1.00 and 1.12 for genets e-1, e-2 and e-3, respectively (Supporting information).

Survival and transitions of ramets between size classes

The observed numbers of ramets that did or did not change size class, the numbers of surviving and dead ramets from 2005 to 2007 and the numbers of new ramets for each size class are summarized in the Supporting information. In the 2L category, most ramets remained in the same size class or transitioned to a larger size class, whereas more than half of the 1L ramets grew to the 2L size classes. This tendency did not differ between the three genets (Supporting information). Surviving and newly born ramets from genets e-1 and e-3 were mostly within the 2L 15–20 cm size class and those from genet e-2 were within the 2L 10–15 cm size class (Supporting information).

Matrix and genet growth rate

By randomly combining 2000 samples from the posterior distributions of C_l^h (Supporting

information; some of 95% credible intervals of C_l^h overlapped between genets and between 1-y-tip and 2-y-tip), N_k (Supporting information), S_l (Supporting information), T_{kl} (Supporting information) and the fixed value of E, we produced 10000 matrices for each genet. Intrinsic growth rates (the largest real eigenvalues) for the three genets, derived from the largest real eigenvalues, were differently distributed (Fig. 3a). Genet e-1 tended to show higher growth rates (99.8% across 10000 matrices were highest, median = 1.13) and genet e-2 was the lowest for 77.7% (median = 1.02). The 95% credible interval of genet e-1 did not overlap with those of genets e-2 and e-3 (median = 1.05). The interval of genet e-2 was relatively wide, presumably because of the smaller sample size, and overlapped even to include the median of e-3. These patterns suggest that genet growth rates varied among genets. It is also noteworthy to point out that the tendency of these growth rates were consistent with changes of observed numbers of ramets from 2006 to 2007 (Table 1): 1.00 (genet e-1), 0.96 (genet e-2) and 0.98 (genet e-3).

Figure 3b–c compares how the posterior distributions of eigenvalues were affected when either clonal growth (C_l^h, N_k, E) or survival and transition (S_l, T_{kl}**)** of ramets was unified over genets. The difference between genets e-1 and e-3 was reduced when the clonal growth data were pooled (Fig. 3b). On the other hand, when the survival and transition data were pooled, the difference between genets e-1 and e-3 was largely unaffected (Fig. 3c), and the differences to genet e-2 were reduced. This implies the effects of clonal growth and suggests much weaker influences of survival-transition on the genet growth rates.

If no branching was assumed, the medians of posterior distributions of eigenvalues declined in all three genets by 4.7‑9.0% (Fig. 4), among which genet e-1 showed the largest decline. This result suggests that branching ramet recruitment

459 significantly contributes to maintaining genet dynamics despite the clonal growth
460 probabilities being lower than those at fragment tips. The sensitivity of $C^{non\text{-}tip}$ also
461 exhibited much higher values than $C^{1\text{-}y\text{-}tip}$ and $C^{2\text{-}y\text{-}tip}$ (Supporting information). While Fig.
462 4 shows an extreme case when the branching never occurs, the sensitivity expresses
463 changes of the largest eigenvalue by a (infinitesimally) small change of the branching
464 probability. The consistent results between the two support the definite contribution of
465 branching to the maintenance of the genets.
466
467 **Discussion**
468 **Variation of genet dynamics**
469 We here proposed a 'genet dynamics' approach, exploring the fundamental elements for
470 ramet demography of genets in a clonal plant species by deriving demographic
471 information from ramet connections in clonal fragments. To this end, we defined the
472 intrinsic growth rate of a genet using the maximum real eigenvalue of a matrix model
473 reflecting clonal growth and survival-transitions depending on age-position and size of
474 each ramet in the genet (Fig. 1). It was quantitatively detected that genet growth rates
475 varied between dominant genets with closely adjacent locations in a natural population
476 (Fig. 3, Supporting information). The differences resulted from the different probabilities
477 and contributions of such demographic traits as clonal growth, ramet size growth and
478 branching to the genet growth rates depending on genets (Fig. 3b‑c, 4).
479 Demographic variations between genets have been reported within experimental
480 populations (Geber et al. 1992, Cheplick 1997, Prati and Schmid 2000), between genet
481 patches in a population (Falinska 1995, Kawai and Kudo 2018) and between populations
482 of clonal plant species (Nantel and Gagnon 1999, Barsoum et al. 2004). Differences in

genet performance are caused by such factors as genetic variation, age of establishment and environmental heterogeneity (Prati and Schmid 2000, Pan and Price 2002, Timerman and Barrett 2019). Investigation of genet dynamics after simultaneous death in dwarf bamboo, a monocarpic clonal plant, revealed that more productive genets survived and spread initially, replacing less productive ones (Matsuo et al. 2018, Tomimatsu et al. 2020). Kawai and Kudo (2018) detected different ramet productivity between genets located in different snow melt habitats. In the present study, we investigated already established adjacent genets and the area where ramets of some genets were intermingled (Supporting information). The assumption was that genetic variation would sometimes interact with environmental conditions and/or differences of ages to contribute to genet dynamics variations. Indeed, genet e-1 was found distributed over a large area of about 15 × 25 m (see Araki et al. 2009), implying a relatively long time since establishment, and showed the highest genet growth rate (Fig. 3).

Ramet demography for population and genet dynamics

To understand population dynamics, demographic traits of individuals in a population are generally investigated (Silvertown et al. 1993, Menges and Dolan 1998, Logofet 2016). As for clonal plant populations, recruitment, mortality and growth of ramets were explored based on ramet census, from which annual variations of ramet numbers and biomass, frequencies of clonal recruitment per ramet and contributions to a population were estimated (Tanner 2001). In the case of *Rubus*, clonal growth has the greatest impact on population growth rates, suggesting a significant contribution of clonal growth to population development (Lambrecht-McDowell and Radosevich 2005). Guàrdia et al. (2000) used a matrix model to conclude that clonal growth contributed less population

507 growth in *Achnatherum calamagrostis* while the population growth rate was higher than
508 1.0. Growth and survival of ramets in the certain size class caused the different dynamics
509 between populations in *Helianthus divaricatus* (Nantel and Gagnon 1999).

510 Genet growth rates were also observable as an increase in numbers and area
511 occupied by ramets of a certain genet. For example, de Witte and Stöcklin (2010)
512 measured changes in genet sizes from plant morphology. Reusch (2006) monitored
513 changes in the lattice point numbers for each genet to assess genet growth in a seagrass
514 population. If not all ramet members are identifiable and multiple genets are intermingled
515 with one another, statistical inference of genet growth rates from sampled data is required;
516 the present study established a statistical method for this purpose (Fig. 1, 2). In this study,
517 we found that ramets located at the tip of a fragment more frequently produced offspring
518 (Supporting information). This clonal growth seems to support genet maintenance rather
519 than contribute to genet expansion, because the rhizomes expanded in all directions,
520 forming a complex clonal structure. Moreover, clonal growth of non-tip ramets showed
521 higher sensitivity (Supporting information), suggesting that clonal growth of older ramets
522 was also important to maintain genets. This implies that in genets containing older ramets,
523 e.g. larger genets, branching clonal growth has a greater impact on genet growth and
524 longevity. Thus, once a genet occupies a certain area, it would be able to survive for a
525 long time.

526

527 **Applications of belowground information**

528 Estimation of the elements in the matrix model was achieved using both data from
529 aboveground censuses and information from belowground directional connection of
530 ramets (Fig. 2). We were able to classify excavated fragments into eight patterns, although

531 belowground organs exhibited very complex structures. Belowground information is as
532 important as aboveground data for advancing studies on plant species (Klimešová et al.
533 2018, Ott et al. 2019), and integrating both types of data demands novel approaches suited
534 to particular data and species characteristics. For example, Wildová et al. (2007)
535 excavated to parameterize the architecture of belowground clonal organs as well as
536 aboveground performances, which showed different impact on population and
537 community structure between aboveground and underground traits among species. From
538 belowground excavation after two annual censuses, Araki and Ohara (2008) also derived
539 preliminary insight of ramet reproductive demography that ramets perform clonal growth
540 before repeated flowering. In contrast to these approaches, the present study investigated
541 directional rhizome connections of ramets (Fig. 2) and estimated consecutive clonal
542 growth rates at tips (Fig. S3) to understand clonal growth strategy of genet as well as
543 ramet. This growth rate also enables prediction of genet distribution and thus sizes for a
544 given period. In fact, genet e-1 covered a 15 × 25 m area (see Araki et al. 2007) and
545 occupied over more than half the area of the 28 × 2 m plot (Fig. S1). Based on the distance
546 between ramets (average 22.7 cm in Araki and Ohara 2008), combining the distributions
547 of rhizome lengths and turning angles enables calculation of the number of years needed
548 to attain the expansion of a given genet size as it fits the reality.
549
550 **From genet demography to population dynamics**
551 Population dynamics can also be estimated from demographic traits of genets. If a genet
552 growth rate was smaller than 1.0, we could predict the reduction of ramets in that genet
553 and its disappearance, using the stationary assumption in the matrix model. All studied
554 genets of *C. keiskei* showed growth rates greater than 1.0, and few dead ramets were found

during the experimental period. In our study plot, nine of 19 seedlings with one leaf shorter than 10 cm found in 2005 did not emerge in 2006 and 2007. These findings can provide evidence of birth and death of genets, but there were no observations of genets with two or more ramets disappearing. The employed statistical analysis incorporated only growth but not the birth and death of genets. Suzuki et al. (2006) estimated genet mortality in *Festuca rubra* from ramet demographic data and genet identification by applying spatial theory using the probabilities of genet identity of ramets, as described in Harada et al. (1997).

Conclusion

Fundamental demographic elements are important in understanding life-history characteristics of species. This study formulated genet growth rates in terms of both clonal growth and ramet size growth per genet in a population. Genet dynamics and associated variability between genets were statistically investigated using a matrix model of ramet demography within each genet. The structure and growth pattern of the rhizome of *C. keiskei* include continuous clonal growth at the tip end of the rhizome and spatial spread. However, once a genet was established, clonal growth at the tip as well as growth of non-tip ramets contributed to genet maintenance rather than expansion. Consequently, dominant genets with positive genet growth rates would tend to persist for a long period, contributing to population maintenance in this herbaceous clonal plant.

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Figure legends

Figure 1. Schematic representation of the life-history transition of ramets in a genet in a clonal perennial plant species, *Convallaria keiskei*.

(a) Examples of transition patterns of mother ramets from year $t - 1$ to t. (b) All transition patterns of ramets. Blue components show the position and age transitions of ramets, red components indicate ramet recruitment through clonal growth. The survivals are not shown for simplicity. (c) Matrix for genet dynamics. Details of the symbols in the matrix elements are described in the text.

Figure 2. Eight clonal fragment patterns found in *Convallaria keiskei* and obtained information about clonal growth occurring in year $t - 1$ and t in each fragment.

Years of aboveground growth were obtained from the 2005 (correspond to year $t - 2$) to 2007 (correspond to year t) censuses and rhizome connections were derived from belowground excavation in 2007. The two right columns show the transition probability of clonal growth by focal (mother) ramets. Years and arrows in parentheses indicate birth years of offspring (right side of the arrow) and connections between the focal ramets (left side of the arrow). In case of year $t - 1$ season of the column, year t at the right side of the arrow means clonal growth and no number is no clonal growth. In case of year t season, year $t + 1$ at the right side of the arrow means clonal growth and no number is no clonal growth.

Figure 3. Posterior distributions of growth rates of the three dominant genets.

(a) When clonal growth and the survival-transition data were separated according to genets, (b) when clonal growth data were pooled and the survival-transition data were separated according to genets, and (c) when the survival-transition data were pooled and clonal growth data were separated by genet.

Figure 4. Posterior distributions of growth rates of the three dominant genets, with and without branching. Genets (a) e-1, (b) e-2 and (c) e-3.

Supplemental information

Appendix I: Technical details in the statistical estimation of matrix elements in Methods

Appendix II: Summary of data

Table S1a. The number of tip ramets performing clonal growth or not, in each age-position and size class in the three dominant genets.

Table S1b. The number of clonal fragments of each fragment size (number of ramets in a fragment) in the three dominant genets.

Table S1c. The number of triplets consisting of one mother and one older daughter ramets and one new bud (Branching) and of non-tip ramets potentially branching clonal growth (Non-tip) in the three dominant genets.

Table S1d. The number of ramets having one, two or three new buds in the three dominant genets.

Table S1e. The number of ramets transmitted from size class *k* (rows) to *l* (columns) in the three dominant genets. Genets (1) e-1, (2) e-2 and (3) e-3.

Table S1f. The number of survival and dead ramets in each size class in three dominant genets from 2005 to 2006 in the three dominant genets.

Table S1g. The numbers of new ramets in each size class in three dominant genets.

Appendix III: Supporting results

Table S2a. Medians and 95% credible intervals (in parentheses) of the posterior distributions of the coefficients in the logistic regression (GLM) for the clonal growth probabilities in the three dominant genets.

779 **Table S2b**. Medians and 95% credible intervals (in parentheses) of the posterior
780 distributions of the probabilities of branching via non-tip ramets for the three dominant
781 genets.
782 **Table S2c**. Medians and 95% credible intervals (in parentheses) of the posterior
783 distributions of new ramets in each size class for the three dominant genets.
784 **Table S2d**. Medians and 95% credible intervals (in parentheses) of the posterior
785 distributions of the probabilities that ramets survive in each size class in the three
786 dominant genets.
787 **Table S2e**. Medians and 95% credible intervals (in parentheses) of the posterior
788 distributions of the probabilities that ramets moved between size classes in the three
789 dominant genets. Genets (1) e-1, (2) e-2 and (3) e-3.
790 **Table S2f**. Medians and 95% credible intervals (in parentheses) of the sensitivity for
791 the clonal growth probabilities in each size class in the three dominant genets.

Figure S1. Morphological characteristics of underground organs and state of the field survey of *Convallaria keiskei*. A rhizome fragment connecting ramets and elongating at the tip (b) and the underground organ of a shoot (a); aboveground shoots in the study plot in the following year of making ramets (c, d). Sheath leaves start to expand aboveground (c) and fully expanded leaves of the existing ramets with pink tag and newly appearing one with orange tag (d).

Figure S2. A map of ramet distribution in a 28 × 2 m plot for a *Convallaria keiskei* population. The X axis of X = 0−28 corresponds to X = 20−48 and Y axis of Y = 0−2 is Y = 50−52 in the text. The ramets appeared at least once for the study periods were plotted.

Figure S3. The clonal growth probability of 1-y-tip and 2-y-tip ramets in each size class for the three dominant genets. Medians (solid line) and 95% credible intervals (dashed line) of the posterior distributions are shown. Genets (a) e-1, (b) e-2 and (c) e-3.

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Table 1. Summary of census data of ramets in four genets in 2005, 2006 and 2007. The total number and number of surviving (SUR), newly emerged (NEW) and unemerged (UEM) ramets were calculated for each genet. Dashes indicate that data were neither calculated nor estimated. *Numbers in parentheses represent recovering ramets that did not emerge in the previous year. †Numbers in parentheses represent unemerged ramets in the second successive year.

Genet ID	Year	No. of ramets			
		Total	SUR	NEW*	UEM†
e-1	2005	600	—	—	—
	2006	701	581	120	19
	2007	700	603	97 (8)	98 (11)
e-2	2005	108	—	—	–
	2006	137	104	33	4
	2007	131	119	12 (1)	18 (3)
e-3	2005	477	—	—	–
	2006	550	451	99	26
	2007	538	448	90 (16)	102 (10)
e-4	2005	236	—	—	–
	2006	297	227	70	9
	2007	319	255	64 (3)	42 (6)

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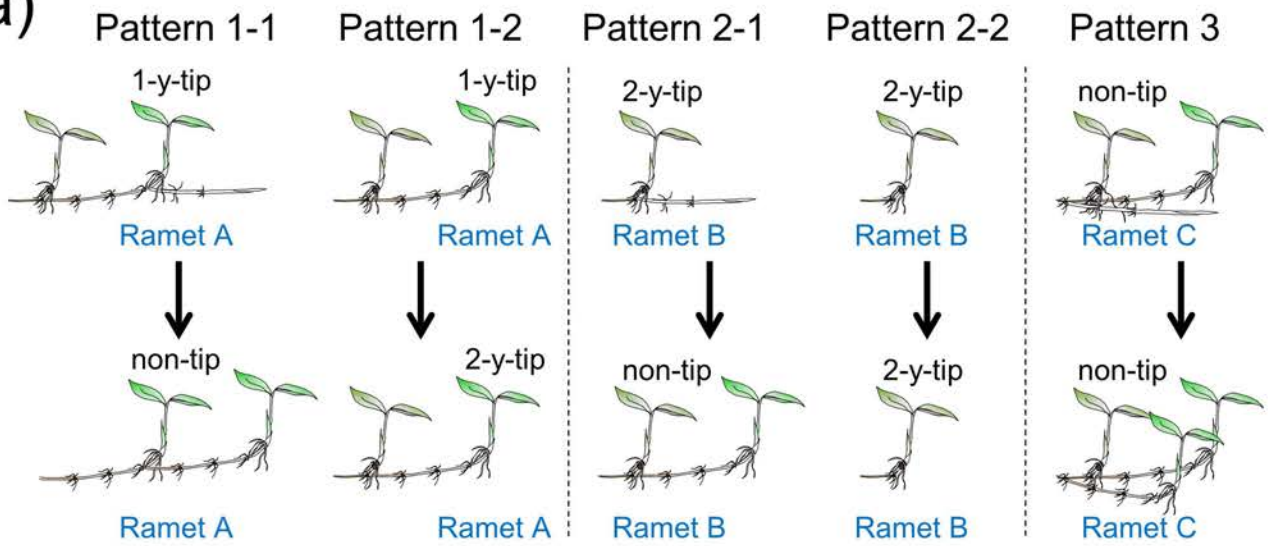
808

Table 2. Number of fragments observed in the three genets and the total of each clonal fragment pattern. Patterns correspond to those illustrated in Figure 2.

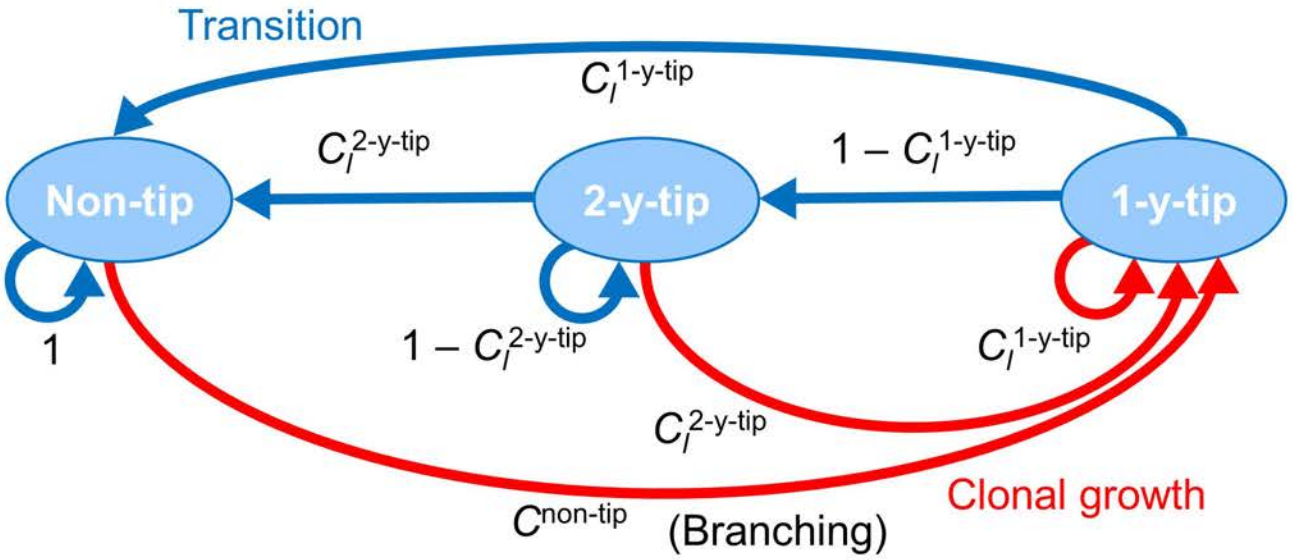
Pattern*	Genet			Total
	e-1	e-2	e-3	
1	5	3	2	10
2	8	4	4	16
3	4	3	0	7
4	18	6	9	33
5	7	1	2	10
6	21	2	12	35
7	5	0	0	5
8	32	16	39	87

809

(a)



(b)



(c)

Survival and transition **Tsc**

year t - 1, size class l

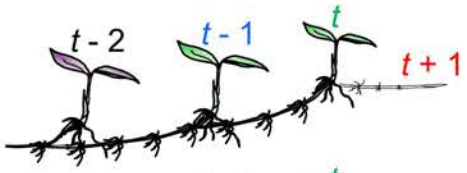
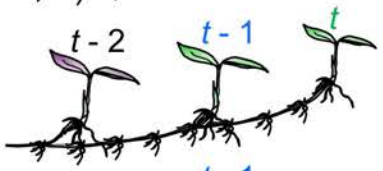
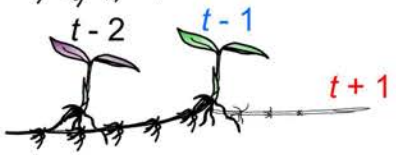
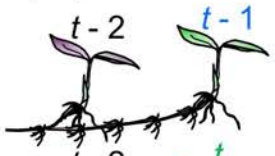
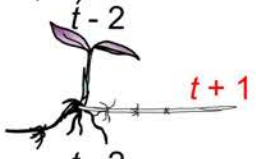
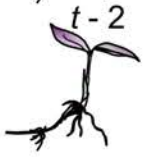
year t, size class k	1-y-tip	2-y-tip	Non-tip
1-y-tip	0	0	0
2-y-tip	$T_{kl}S_l$ $(1 - C_l^{1\text{-y-tip}})$	$T_{kl}S_l$ $(1 - C_l^{2\text{-y-tip}})$	0
Non-tip	$T_{kl}S_lC_l^{1\text{-y-tip}}$	$T_{kl}S_lC_l^{2\text{-y-tip}}$	$T_{kl}S_l$

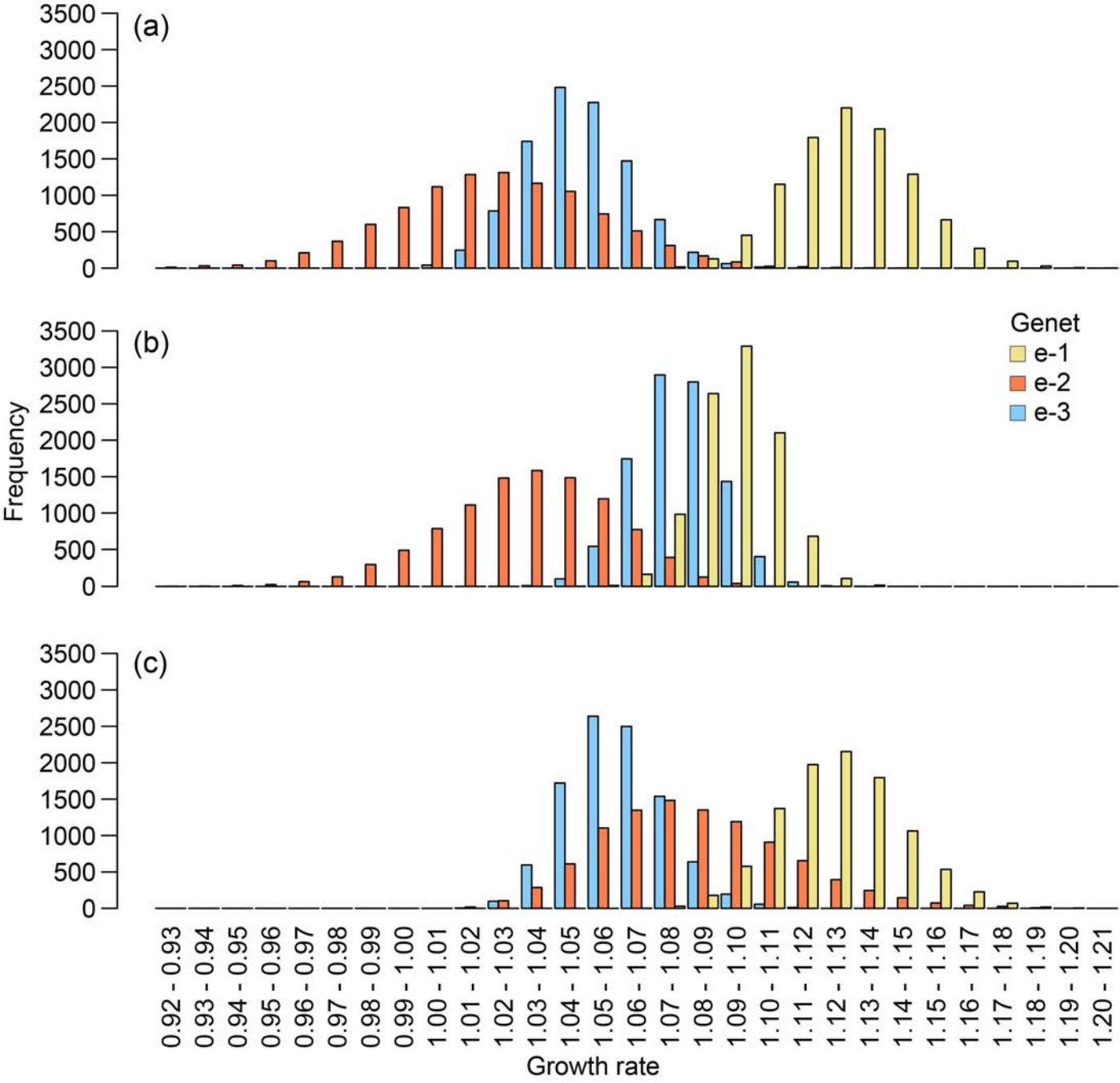
+

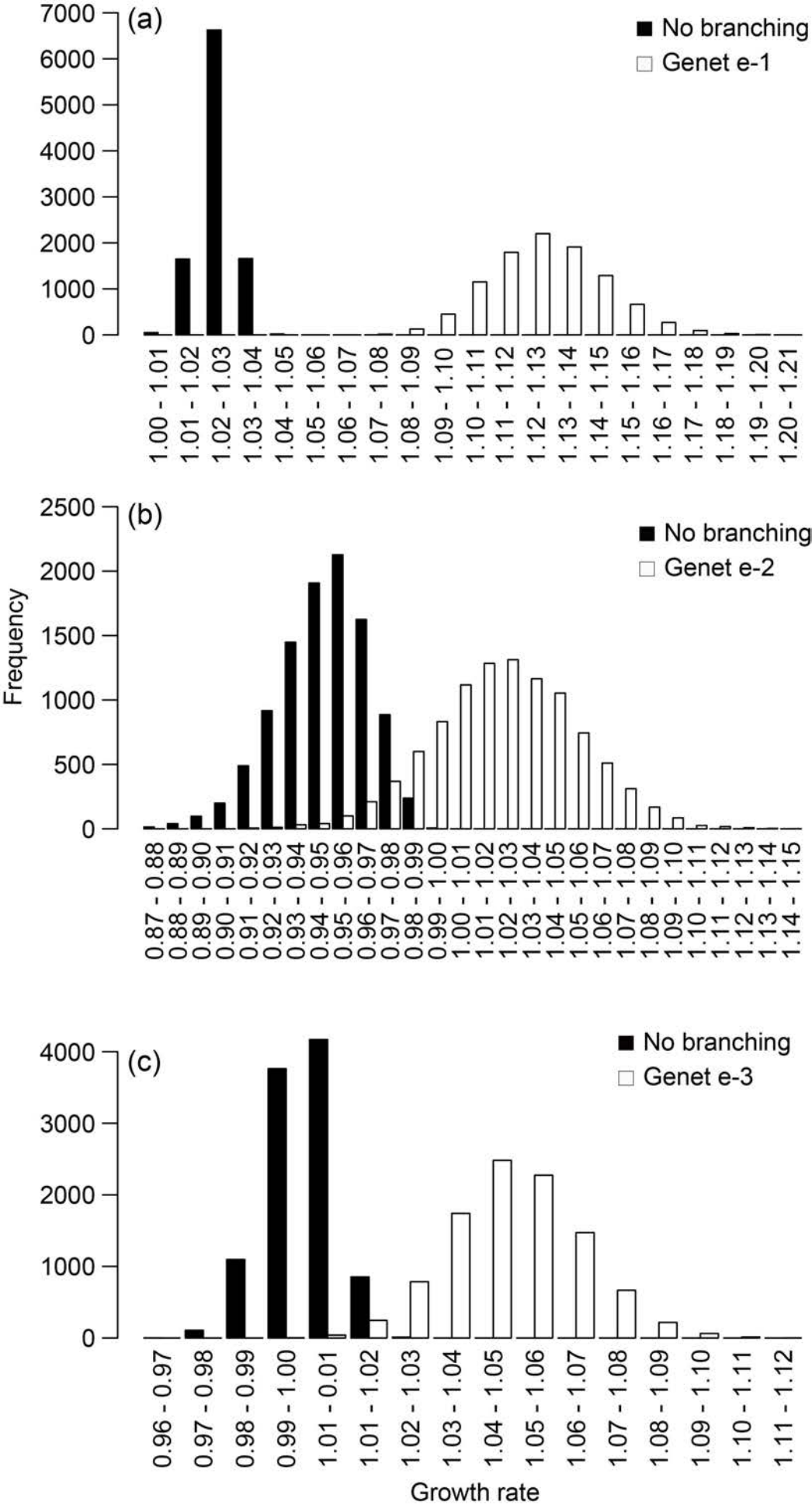
Clonal growth (reproduction) **R**

year t - 1, size class l

	1-y-tip	2-y-tip	Non-tip
1-y-tip	$N_kE_l^{1\text{-y-tip}}$ $C_l^{1\text{-y-tip}}$	$N_kE_l^{2\text{-y-tip}}$ $C_l^{2\text{-y-tip}}$	$N_kE_l^{\text{non-tip}}$ $C^{\text{non-tip}}$
2-y-tip	0	0	0
Non-tip	0	0	0

Pattern	Clonal growth	
	year t - 1	year t
1. 	$C_j^{\text{1-y-tip}}$ (t - 1 → t)	$C_j^{\text{1-y-tip}}$ (t → t + 1)
2. 	$C_j^{\text{1-y-tip}}$ (t - 1 → t)	$1 - C_j^{\text{1-y-tip}}$ (t →)
3. 	$1 - C_j^{\text{1-y-tip}}$ (t - 1 →)	$C_j^{\text{2-y-tip}}$ (t - 1 → t + 1)
4. 	$1 - C_j^{\text{1-y-tip}}$ (t - 1 →)	$1 - C_j^{\text{2-y-tip}}$ (t - 1 →)
5. 	$C_j^{\text{2-y-tip}}$ (t - 2 → t)	$C_j^{\text{1-y-tip}}$ (t → t + 1)
6. 	$C_j^{\text{2-y-tip}}$ (t - 2 → t)	$1 - C_j^{\text{1-y-tip}}$ (t →)
7. 	$1 - C_j^{\text{2-y-tip}}$ (t - 2 →)	$C_j^{\text{2-y-tip}}$ (t - 2 → t + 1)
8. 	$1 - C_j^{\text{2-y-tip}}$	$1 - C_j^{\text{2-y-tip}}$


(a)
(b)
(c)
Frequency
Genet
e-1
e-2
e-3
0
500
1000
1500
2000
2500
3000
3500
0.92 - 0.93
0.93 - 0.94
0.94 - 0.95
0.95 - 0.96
0.96 - 0.97
0.97 - 0.98
0.98 - 0.99
0.99 - 1.00
1.00 - 1.01
1.01 - 1.02
1.02 - 1.03
1.03 - 1.04
1.04 - 1.05
1.05 - 1.06
1.06 - 1.07
1.07 - 1.08
1.08 - 1.09
1.09 - 1.10
1.10 - 1.11
1.11 - 1.12
1.12 - 1.13
1.13 - 1.14
1.14 - 1.15
1.15 - 1.16
1.16 - 1.17
1.17 - 1.18
1.18 - 1.19
1.19 - 1.20
1.20 - 1.21
Growth rate


(a)
No branching
Genet e-1
7000
6000
5000
4000
3000
2000
1000
0
1.00 - 1.01
1.01 - 1.02
1.02 - 1.03
1.03 - 1.04
1.04 - 1.05
1.05 - 1.06
1.06 - 1.07
1.07 - 1.08
1.08 - 1.09
1.09 - 1.10
1.10 - 1.11
1.11 - 1.12
1.12 - 1.13
1.13 - 1.14
1.14 - 1.15
1.15 - 1.16
1.16 - 1.17
1.17 - 1.18
1.18 - 1.19
1.19 - 1.20
1.20 - 1.21
(b)
No branching
Genet e-2
Frequency
2500
2000
1500
1000
500
0
0.87 - 0.88
0.88 - 0.89
0.89 - 0.90
0.90 - 0.91
0.91 - 0.92
0.92 - 0.93
0.93 - 0.94
0.94 - 0.95
0.95 - 0.96
0.96 - 0.97
0.97 - 0.98
0.98 - 0.99
0.99 - 1.00
1.00 - 1.01
1.01 - 1.02
1.02 - 1.03
1.03 - 1.04
1.04 - 1.05
1.05 - 1.06
1.06 - 1.07
1.07 - 1.08
1.08 - 1.09
1.09 - 1.10
1.10 - 1.11
1.11 - 1.12
1.12 - 1.13
1.13 - 1.14
1.14 - 1.15
(c)
No branching
Genet e-3
4000
3000
2000
1000
0
0.96 - 0.97
0.97 - 0.98
0.98 - 0.99
0.99 - 1.00
1.01 - 0.01
1.01 - 1.02
1.02 - 1.03
1.03 - 1.04
1.04 - 1.05
1.05 - 1.06
1.06 - 1.07
1.07 - 1.08
1.08 - 1.09
1.09 - 1.10
1.10 - 1.11
1.11 - 1.12
Growth rate