

Article

PRESCRIPTIONS FOR THE CONTROL OF A CLONAL INVASIVE SPECIES USING DEMOGRAPHIC MODELS

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Abstract: Until recently, little focus has been given to determine the population dynamics of invasive species and evaluate their genetic variation. Consequently, not much is known of what drives clonal invasive species and their demography. Here we describe the population dynamics of *Kalanchoe delagoensis* (Crassulaceae), considered invasive to several countries. We quantified the demography of a population in central Mexico using integral projection models (IPM) in a population that reproduced asexually exclusively through plantlets. The effect of clonal recruitment on λ was evaluated by changing plantlet survival and simulating management scenarios that used previous data of watering and seven experimental herbicide treatments. The finite rate of population increase indicated that this *Kalanchoe delagoensis* population is growing (above one) with significant potential increases that correlated with water availability. The IPM showed that plantlet survival and recruitment were the most critical steps in the cycle for the population and simulations of different management scenarios showed that reducing plantlet survival significantly decreased λ only in two out of the seven herbicides used.

Keywords: Herbicide treatments; Integral Population Models; *Kalanchoe*; plantlet survival

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1. Introduction

Interest in alien invasive species (AIS) has grown in recent years because the impacts are widely recognized [1], and global costs are being quantified [2–4]. Critical stages of invasion involve the establishment and spread into new habitats (categories C, D, and E in [5]), which can depend on a suite of factors including habitat suitability [6], components of propagule pressure (frequency and size of introductions [7,8]), presence/absence of pollinators, dispersers or herbivores [9] and phenotypic plasticity [10,11]. The reproductive mechanisms behind the spread can vary widely, however, even though clonality seems to be quite common among alien invasive species [12], the role played by clonality during spread is context-dependent [13,14]. To our knowledge, of the 31 papers that deal with population dynamics of invasive species, six had some form of vegetative reproduction [15,16]. Even though no attempt has been made to evaluate the overall demographic importance of clonality among invasive species, it is widely recognized as an essential trait in risk assessments [17–19], invasion success [14], and is a critical component of population growth [20].

Only recently have demographic models been used to assess components of invasion and to guide management of invasive species [15,21–25] which can even include

prioritization based upon cost [26]. Population dynamics of AIS commonly have high population growth rates [15], and transient dynamics seem to play a part in invasion success [16,27,28]. Invasive species have also been shown to have demographic plasticity [29,30] and buffer environmental variation [21,31] which enables them to exploit both ends of the phenotypic plasticity spectrum [10, master of one, jack of all] and even combinations of this [32]. Targeting certain life stages (or combinations thereof) can provide insight towards identifying critical pathways [22,25,33,34] that would lead to optimal management strategies [15,27], as well as diminish the cost and overall impact of AIS [35].

Integral projection models (IPM's) have been used recently and widely for demographic analyses (e.g. [36,37]), including assessments of population viability for endangered plants (e.g. [38]) or invasive plants (e.g. [24,25,31]). Demographic modelling can then provide insight into short-term possible directions for management, and benefit from being robust to small data sets compared to matrix population models ([39] and are able to incorporate other explanatory drivers as covariates [31,38,40].

The genus *Kalanchoe* is native to the dry regions of Madagascar and Eastern Africa, and several species are now found in several countries (Mexico, Australia [listed under the noxious weed act], USA, Spain, and South Africa) where it has been introduced and spread either accidentally or through the horticultural trade [41,42]. In Mexico, several species and one hybrid have been introduced (*K. pinnata*, *K. tubiflora*, *K. blossfeldiana*, *K. fedtschenkoi*, *K. daigremontiana*, *K. calcynum*, *K. laciniata*, *K. integra* and *K. daigremontiana* × *delagoensis*, [43]); one, *Kalanchoe delagoensis*, can now be found in six states within the arid environments in Mexico and has been declared invasive [44]. *Kalanchoe delagoensis* can hybridize with *K. daigremontiana* to generate what is known as Houghton's hybrid, also introduced with no evidence of hybridization in Mexican populations even though they may grow sympatrically in some areas [45]. In addition, populations of *K. delagoensis* share a single genetic makeup suggesting a single introduction event with subsequent spread. This means that *K. delagoensis* could establish founder populations under a wide range of conditions entirely through clonality [45]. Negative impacts of *K. delagoensis* include allelopathic effects [41], harm to domestic animals [46–48] and changes in available soil carbon [34]. Even though herbicidal control has been tried, as have controlled burns, management has been difficult due to the high production of clonal plantlets from the margin of leaves. This apomictic trait is the main driver of population dynamics of its congener *K. daigremontiana* in Venezuela [49].

The aims of this study were to 1) assess the population dynamics of *K. delagoensis*, and 2) determine the management effectiveness of targeting the plantlet life stage which has been previously shown to be susceptible to some herbicides.

2. Results

2.1. Vital rates

A total of 497 individuals were followed during the study period. Models adjusted for survival, fecundity and growth to generate the kernel used a log transformation of plant size to improve fit. Of the models fitted to the data (survival with 5 models, growth 6 models, reproductive probability 8 models and fecundity 8 models), those with the lowest value of AIC were used (Figure 1). The production of plantlets was found for even small individuals that started to produce plantlets within the year and with plant size as small as 1.5 cm. The population of *K. delagoensis* studied showed no seeds and therefore the driver of population growth is entirely through the prolific production of plantlets. During the period (2010–2011), the survival probability of *K. delagoensis* and growth (regression with slope > 1; Figure 1 a and b) increased with stem size, and probability of reproduction and fecundity also increased with stem size (Figure 1 c and d). In our study site and period, the population growth rate (λ) of *K. delagoensis* with plantlet survival set for the control treatment (no water and full sunlight) was > 1 (Table 1), which would suggest the growth rate under severe natural conditions. Fecundity

Table 1: Probability of survival after water and herbicide treatments were applied and the resulting population growth rate with their confidence interval (95%) and the sub-kernels contributions.

Treatment ¹	Plantlet survival	λ (Confidence Interval)	Pmatrix	Fmatrix
Control ²	0.12	1.28 (1.094-1.640)	0.556	0.444
25% Water	0.14	1.37 (1.228-1.836)	0.545	0.455
50% Water	0.25	1.81 (1.531-2.869)	0.502	0.498
100% Water	0.84	3.51 (2.234-5.142)	0.399	0.601
G/2-4D	0	0.29 (0.282-0.415)	1.000	0.000
2-4D	0.01	0.55 (0.245-0.717)	0.776	0.224
Other herbicides	>0.33	2.08 (1.860-2.410)	0.480	0.520

¹ Survival probabilities from experiments done in Guerra-García et al 2018

² No water full sunlight

(Fmatrix) contributed 60% and 52% to the population growth rate (λ) for 100% water and other herbicides treatment, respectively. The high values of λ (3.51 and 2.08) of these models suggest the importance of vegetative reproduction in the dynamics of the population and the potential for invasion. Survival-growth (Pmatrix) contributed 100% and 78% towards λ for G/2-4D and 2-4D treatments, respectively basically due to the high plantlet mortality caused by the herbicide treatments. Herbicide treatments (G/2-4D and 2-4D) contributed to the reduction of λ and point towards an effective control of *K. delagoensis* populations that rely on clonal reproduction. Although not considered here, the effects of plantlet mortality could be offset by high water availability which suggests herbicide treatments should be avoided during rainy seasons to maximize plantlet mortality.

3. Discussion

Demographic variation at an individual level has only recently been taken into account to determine how individual traits influence population growth [22,50]. Clonality is one of those components that for invasive species seems to be a known and important driver of invasion [14,34,51–53]. However, little attention has been given to the demography of clonal invasive species, and the role played by the clonal component, even though it may be the only means of population growth for some extremely clonal species. This lack of information could be partly due to the cost and difficulty of differentiating genotypes in natural populations of clonal species or to the often overriding importance and haste of direct management options and/or eradication. Nevertheless, among alien invasive species, some examples exemplify the role played by clonality [45,52,54]. Fortunately, sexual reproduction has not been found in the studied population of *K. delagoensis* which the genetic data also suggest [45]. Adding seeds would increase genetic diversity and quite possibly generate even broader responses to environmental variation and increased invasive capacities [54]. Sexual reproduction would also very likely create seed banks such as those found for *K. daigremontiana* [55] complicating management further and increasing management costs basically because of the longer control periods needed to reduce the seed bank. Clonality may not have the potential for dormant stages nor the benefit of genetic variability, but clonal offspring can have higher survival rates over long periods and be a strategy to occupy suitable habitats in short time periods.

Almost all of the invasive species with some form of clonality have population growth rates above equilibrium [15,56–59]. This observation is consistent with the spread of invasive species [5] and is one of the reasons for highlighting the importance of clonality in risk assessments. Clonality coupled with other traits such as self-compatibility [60], resprouting [22], and no need for pollinators or dispersers makes these species more likely to invade successfully than others. There are clear benefits of clonality including

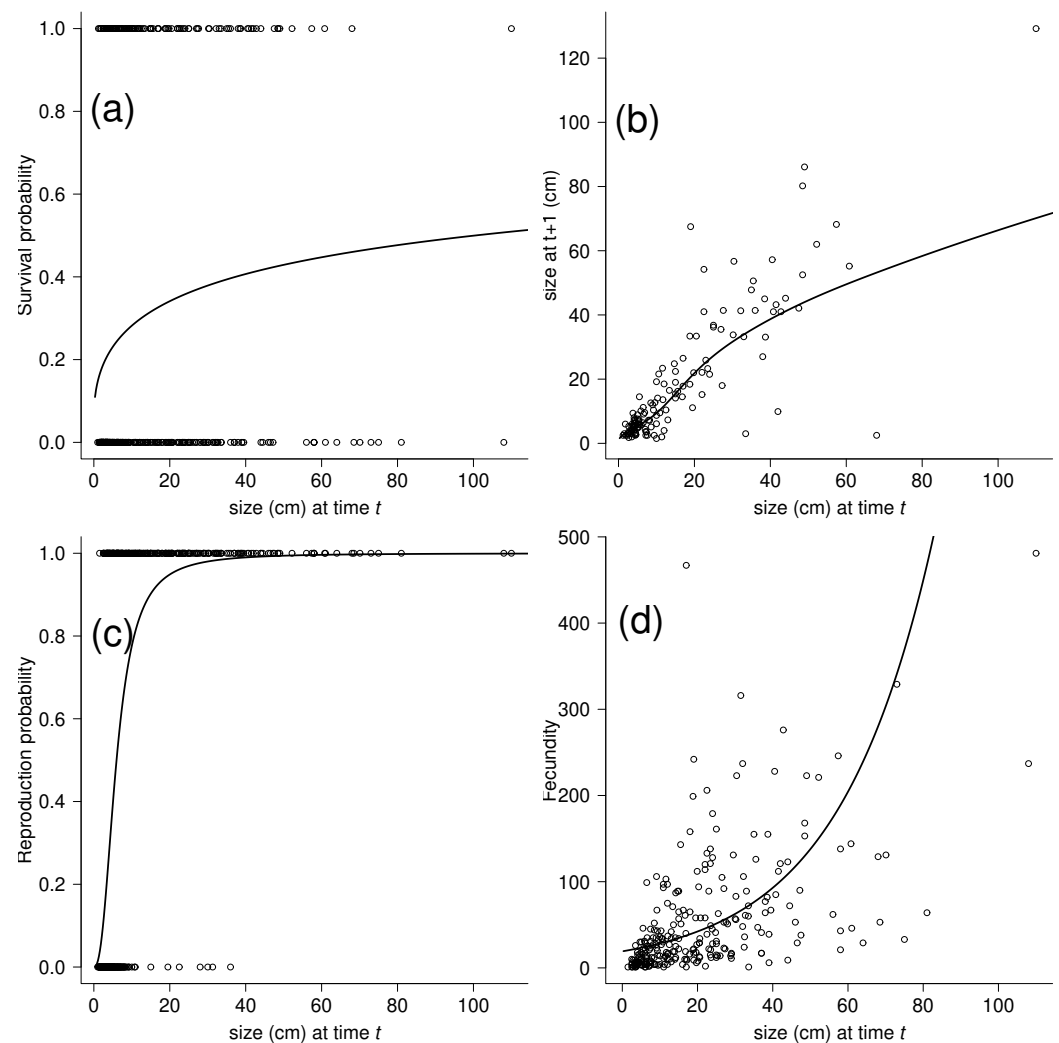


Figure 1. Fitting of the survival, growth, reproduction probability and fecundity of the *K. delagoensis* 2011 data. **(a).** The survival (s) data are plotted (0, death; 1, survival) as function of individual size x (plant height in cm), along with a logistic regression fitted to the data. The fitted curve is $\log(s/(1-s)) = -1.904 + \log(0.206)x$ ($P < 0.05$). **(b)** The data on year-to-year changes in size, along the regression fit for mean size at year $t+1$ as a function of size in year t . The fitted line have $\mu = 0.327 + \log(0.885)x$ ($P < 0.05$) and $\sigma^2 = -1.273 + \log(0.269)x$ ($P < 0.05$). **(c)** The reproductive (r) probability are plotted (0, non reproductive; 1, reproductive) as function of individual size x (plant height in cm), along with a logistic regression fitted to the data. The fitted curve is $\log(r/(1-r)) = -4.316 + \log(2.414)x$ ($P < 0.05$). **(d)** The fecundity as a function of individual size, a long with the regression for the mean number of plantlets. The fitted line is $\mu = 2.955 + \log(0.039)x$ ($P < 0.05$). The y -axis scales are different among the panels.

the spread of an already successful genotype for a determined habitat. If the traits of clonal offspring have phenotypic plasticity, the species can exhibit a “Jack and Master” strategy [10] allowing the possibility of increasing fitness in favorable environments while maintaining fitness in stressful environments. This would also compound with complex transient dynamics [16,28] and variation in vital rates [31]. Even small increases in favorable abiotic conditions has the ability to add to plantlet survival and therefore increase the invasive potential significantly.

Management scenarios

A successful management option suggested by [15] was the reduction in fecundity for short-lived invasive species, but seemingly that cannot be applied consistently across species [61]. Reducing one of two demographic processes (fecundity or stasis) was shown to be sufficient to control growing populations [15]. For the sister species *K. daigremontiana* and *K. pinnata* clonality, as well as sexual reproduction, contributed significantly to population growth [34,62]; however, the genetic identity of the individuals was not evaluated. The lack of a sexual component of fecundity in *K. delagoensis* at the site makes control easier and also highlights the danger of triggering higher growth rates if genetically dissimilar individuals are introduced. [15] also found that reducing one demographic process (namely growth or reproduction) under simulated conditions was adequate to control short-lived invasive species, while reduction of at least two was needed to control long-lived perennials. [61] simulated reduction in the sexual component of perennial invasive species and found that reducing this demographic process was not enough to curb population growth. As the plantlets of *K. delagoensis* contribute to fecundity a management scenario would necessarily involve lowering the recruitment of plantlets by using one of two herbicides that had important effects on plantlet survival. Unfortunately not all herbicides had the same effectiveness and of the seven that were tested only two induced high enough mortality in plantlets so generate falls in λ needed for adequate control. Lowering recruitment of plantlets, however, poses a problem because plantlets are produced by very young individuals and are generated year-round, such that management must be carried out continuously and would entail long-term control. The timing of herbicide applications should also consider that mortality can be offset in the seasons with higher water availability.

The populations of *K. delagoensis* in Mexico pose an interesting system in which plantlets are the drivers of population growth. This also means that management can be feasible if plantlet survival is severely limited in this population. Little is known of the demographic behavior in other populations which could potentially behave very differently and increase the invasion potential of this and the sister species. Currently, only *Kalanchoe pinnata* and *K. delagoensis* are listed as invasive species in Mexico [44], but the sister species *K. daigremontiana* and what is known as Houghton’s hybrid (*K. daigremontiana* $\times$ *K. delagoensis*) already have large populations with wide distributions and also pose a significant risk as they have very similar demographic behavior.

4. Materials and Methods

4.1. Species

Kalanchoe delagoensis Ecklon & Zeyher [63] is a succulent able to reproduce sexually as well as clonally through pseudobulbils (hence the name “mother of millions”) that arise from the margin of their leaves [64]. Clonal plantlets have accelerated growth, high survival, and a common sight in invaded areas [65]. *K. delagoensis* is considered to be an aggressive invader in Australia and the US [41]. It is included in the exotic species lists in Mexico, and risk assessments suggest a significant risk to native vegetation and soils (Guerrero-Eloisa, unpub. data).

4.2. Population Dynamics

For two years (2010-2011), a populations of *K. delagoensis* (hereafter Cadereyta 20.687 061° N –99.805 255° W) was followed. The site has 15.9°C average annual tem-

perature and 488 mm annual rainfall (data from 60 years obtained from the National Meteorological Service stations at the sites). Vegetation at the site consisted of Chihuahuan xerophytic scrub. During April 2010, 1×1 m plots (Cadereyta 7 plots) were set, and all individuals of *K. delagoensis* within the plots were tagged and measured (plant width (cm) and height (cm)). Tagged individuals were followed every two months for a year.

4.3. Population growth rate

Demographic data on *K. delagoensis* were obtained as plantlets and adults. Data were widely examined for errors and outliers. All data were used to construct informative models for vital rates (individual survival, growth and fecundity) based on plant size (height, cm). We performed model selection using AICc criteria to choose the most plausible models among a range of different models. The vital rate models support the basis for building of integral projection models [36,37,66] to model the life cycle of *K. delagoensis* ([67]). We used an integrative measure (height, cm) as the size variable and analyzed models assessing the effect of size on each vital rate using generalized linear and Generalised additive models for location scale and shape (GLM, GAMLSS).

The IPM incorporates models for individual survival, changes in size, and fecundity. The models for individual survival used a logit link function GLM and binomial distribution using the lme4 package [68]. We modelled plant growth for year $t+1$ (2011) in relation to plant size from year t (2011) with nonparametric normal models using the gamlss package [69]. We estimated size-dependent fecundity of reproductive individuals as the product of size-specific probability of successfully producing plantlets (estimated with a logit link GLM and binomial errors using the lme4 package [68]), and the size specific number of plantlets produced (with nonparametric normal model using the gamlss package [69]). This gives an estimate of number of plantlets produced by plants of different sizes as a means of reproduction. Mesh size was set to 500 bins. We numerically integrated the demographic kernel using the mid-point rule to generate the IPM [36]. The dominant with eigenvalue of the square matrix coincides to population growth rate (λ). Population growth rates = 1 show population stability, < 1 indicate a population expected to decline and rates > 1 indicate a growing population and over the long term. Confidence intervals (95%) for λ were obtained for each population by bootstrapping, such that individuals were resampled to generate 1,000 parameters or each element in the kernel [70].

Possible management scenarios were simulated by changing the survival rates of plantlets. Plantlet survival under different treatments with watering levels and the use of herbicides was used from data taken from [71]. The baseline plantlet survival was the survival of plantlets with no watering and under full sunlight, similar to what would be expected under natural conditions. To assess the contributions of changes in vital rates following management scenarios to λ we modified the probability of plantlet survival to what was found in the herbicide treatment experiments. We modelled 3 water treatment (25, 50 and 100% water field capacity) to determine the effect of water on population growth rates and seven herbicide treatments, five of which were grouped into those with more than 33% plantlet survival and those that had the highest mortality (G/2-4 Glyphosate + 2-4D amine mixture and 2-4D, see concentration details in [71]). Population growth rates and error intervals (through bootstrapping) were calculated for each treatment. We calculated the population growth rate and the vital rate elasticity and sensitivity for the additive sub-matrices of survival-growth (P) and fecundity (F) [72] based on each IPM representing a different management scenarios (elasticity and sensitivity ::popbio; [73]).

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