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Landscape-scale population dynamics: field observations and modelling of *Puya hamata*, a flagship plant from the Andes

by

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Landscape-scale population dynamics: field observations and modelling of *Puya hamata*, a flagship plant from the Andes

Abstract

Important ecological processes happen over long periods of time and at the landscape scale. Effective conservation of biodiversity and management of natural resources and ecosystem services requires an understanding of these processes. Unfortunately, it is often impractical to conduct appropriate long-term, landscape-scale studies. Modelling offers an alternative approach.

Complete ecosystems are too complex to model practically, but simulations of simplified systems provide useful insights of practical value. LandBaSE-P is an individual-based model for *Puya hamata* that provides information about impacts of fire on ecological processes in the páramo of the Reserva Ecológica El Ángel, Ecuador. *Puya hamata* is a flagship plant affected by fires and plays a key role in a number of ecological processes.

This research found *Puya hamata* germinated much more frequently after fires, can form large aggregations of single recruitment cohorts, suffers very low mortality (with and without fires) once established, and lives up to 28 years. The spatial aggregation of *Puya hamata* plants reduced effective reproductive output, consistent with the theory that pollinator behaviour around large groups of *Puya* plants reduces cross-pollination, leading to inbreeding depression and poorer seed viability and germination. *Puya hamata's* population structure can be an indicator of recent fire regime.

LandBaSE-P simulations showed that population size is not affected by rare, long-distance seed dispersal. However, in the simulations of páramo grasslands, *Puya* relative germination is maintained in high numbers by burning. *Puya hamata* has an important role in ecology and biodiversity. The model LandBaSE-P is a complementary tool for conservation and sustainable land management. This thesis shows how fieldwork combined with laboratory studies and modelling, can provide a good understanding of complex dynamics of real-world populations, and generate ideas for management and future research.

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Dedication

Esta tesis está dedicada a mis papás: Norma y Néctar. Los extraño cada instante pero siempre están conmigo.

A mis abuelas: Aura, Laura y Nelly. Las amo, abues.

A mi pareja y amigo, Salomón.

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Author's declaration

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Demografía y fenología floral de *Puya hamata* en el páramo de la Reserva El Ángel, Ecuador. Información para modelar su dinámica poblacional a escala del paisaje.	Paramundi. Segundo Congreso Mundial de Páramos. La vida en las Alturas. Universidad Técnica de Loja, Ecuador.	Oral paper	22 June 2009
Modelaje a largo plazo utilizando especies clave e interacciones a escala de paisaje: nuevos acercamientos con evidencia basada en el manejo sustentable	Seminar to Randi, Randi NGO Quito, Ecuador	Seminar presentation	13 November 2008
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1 Introduction to the thesis

Evidence-based sustainable management in the face of climate change and increasing exploitation of natural resources is one of the world's greatest challenges (Chapin Iii *et al.*, 2010; Pullin *et al.*, 2009; Turner *et al.*, 2010). However, ecological studies are often constrained by the temporal and spatial scales that can be studied, or the availability of a wide enough range of replicate (semi-)natural ecosystems in which to collect the evidence (Grace *et al.*, 2009). Modelling provides an alternative, by examining the outcomes of different management scenarios in a virtual environment, where large spatial scales can be examined over long time scales, and can be repeated many times over (Grace *et al.*, 2009).

The full complexity of ecosystem-level interactions limits the application of detailed studies in informing management at larger scales, since complete ecosystems are too complex to model practically (Bengtsson *et al.*, 2002; Schneider & Kay, 1994). Therefore, some kind of simplification is necessary (Schneider, 2009). Nevertheless, models of simplified systems can provide useful support for management and also help to develop more realistic models with greater complexity.

Grasslands are relatively tractable ecosystems, yet provide important ecosystem services (Daily, 1997; Lavorel *et al.*, 2011; Rhymer *et al.*, 2010; Van Eekeren *et al.*, 2010) and support significant biodiversity (Bai *et al.*, 2004; Hutchinson, 1959). Despite their tractability, modelling grasslands is still difficult. The study of specific populations reduces the complexity even further (Elzinga *et al.*, 1998) and, if these populations act as indicator species, or other species with particular functional significance, they offer a more pragmatic choice for providing information of management value (Caro & Girling, 2010).

Using flagship species is useful in the modelling task because they have particular ecological importance or aesthetic appeal (Lorimer, 2007) and thus are attractive and memorable. Flagship species are selected for their charisma, to enhance public awareness of conservation issues and bring support for the protection of that species' habitat. By protecting flagship species, other species are also afforded protection via the "umbrella effect" of the flagship species (Caro & Girling, 2010; Favreau *et al.*, 2006; Heywood *et al.*, 1995; Meffe & Carroll, 1997; Simberloff, 1998). Indicator species are significant in ecology and environmental planning as a component or a measure of relevant phenomena used to evaluate environmental conditions or changes (Heink & Kowarik, 2010). Keystone species play an essential role because of their properties and profound far-reaching consequences in the web of interactions (Begon *et al.*, 1996) and keep the integrity of the overall structure and functioning of an ecosystem (Garibaldi & Turner, 2004).

In the high Andean grasslands (known as páramos), plants from the *Puya* genus can act as flagship, indicator, and possibly keystone species. They are potential indicators of fire regimes (Cochrane, 2009; Miller & Silander, 1991). They are also considered flagship species—"botanical big game" (Hedberg, 1964; Hedberg, 1969).

Puya hamata is an important species in páramos because of its close relationship as a source of food and habitat for other species. For example, *Puya hamata* is a food source for hummingbirds that keeps the relative balance between species of bird and their pollination strategies (trap lining versus territoriality) (Woods & Ramsay, 2001). *Puya hamata* is pollinated by eight species of hummingbird each with different behaviours (Woods & Ramsay, 2001): *Aglaeactis cupripennis* (Shining Sunbeam), *Pterophanes cyanopterus* (Great Sapphirewing), *Patagona gigas* (Giant hummingbird), *Chalcostigma herrani* (Rainbow-bearded Thornbill), *Lesbia victoria* (Black-tailed Trainbearer), *Oreotrochilus estella* (Chimborazo Hillstar), *Eriocnemis vestitus* (Glowing Puffleg) and *Ericnemis mosquera* (Golden-breasted Puffleg) (Woods & Ramsay, 2001). Woods *et al.,* (1998) observed a close relationship between *Patagona gigas* and *Puya* populations. He recognized that hummingbird populations are extending because of the expansion of populations of *Puya hamata*. Changes to the distribution of resources could have profound effects on the strategies adopted by different species and their abundance (Woods & Ramsay, 2001). Therefore, *Puya hamata* populations' dynamics could affect several species of hummingbirds.

Puya hamata is also a food source for bears. Peyton (1980) reported spectacle bears (*Tremarctos ornatus*) occurs in three ranges of the Andes of Peru: "ceja andina" (eyebrow of the jungle), the humid forest and high altitude grasslands. A similar distribution was reported for equivalent ranges in the northeaster Ecuadorian Andes (montane cloud forest, high evergreen upper montane forest and humid páramo) (Peralvo *et al.*, 2005). Peyton reported bears fed from 83 foods that compounded their diet, including insects, rodents, livestock, corn, berries, wood, bamboo hearts, palm frond petioles, and species of Bromeliaceaes. He also found that 76% of their food consisted of plants. Spectacle bears feed predominately on bromeliad hearts, particularly during the months when fruits are not ripe (Peyton, 1980; Troya *et al.*, 2004). Bromeliaceae constituted most of the bears' food, making up 46.8%, including 22 species of the genus *Puya*, *Tillandsia* and *Pitcarnia. It is likely that* at higher elevations like páramo grasslands the bromeliad consumption increases.

Apart from being food for bears, *Puya hamata* is food for invertebrates. These consume flowers, seeds and nectar. Larvae of Nitidulid beetle (Family Nitidulidae: *Carpophilinae*) was found by Miller in *Puya clava-herculis* fruits. Adult beetles feed on pollen, nectar and flower parts, and oviposit in the developing capsules. In his study a single larva was developed per carpel. Capsule damage and seed predation was over 50%. Miller (1988) reported this beetles were not observed on *Puya hamata* inflorescences in REEA, but we observed them and they behaved similarly than they did in *Puya clava-herculis*.

Moreover, *Puya hamata* is habitat for other important pollinator invertebrates. Once *Puya hamata* flowers and spreads it seeds, decomposition of the rosette tissues begins. Several organisms take advantage of these resources. One of them is a fly's larva *Eristalis tenax* (pers. obs.). They live inside pools formed by the rotten *Puya* rosettes where a high amount of organic matter is produced. Adults are common visitors of flowers, and can be significant pollinators (Jarlan *et al.*, 1997).

Puya hamata interacts with a wide range of organisms—at least eleven species. Surely, there are other interactions with plant species. According to Begon *et al.*, (1996) definition, *Puya hamata* could be considered a keystone species.

Modelling is achievable when is focused on individuals from a single species, in simple ecosystems at large spatio-temporal scales, but input data is needed for this task (Werner *et al.*, 2001). The reliability of the model depends on the fieldwork data, and good quality data of this type are preferable to educated guesses, but are often very difficult to get (Grimm & Railsback, 2005).

The aims of the research presented in this thesis are:

- to develop a model of the ecological dynamics of *Puya hamata* in páramo grasslands subjected to different fire regimes, operating at the landscape scale over long periods of time.
- to provide good-quality information from field and laboratory studies to support the model.
- to use simulation modelling to determine the relative significance of different ecological processes affecting the model system.
- to investigate the impact of different fire regimes on *Puya hamata* populations through simulation modelling.
- to assess the value of individual-based simulation modelling at landscape scales for ecological understanding and conservation management.

This project uses sophisticated ecological modelling to examine ecological processes, as an illustration of the capabilities of individual-based models for improving ecological understanding and sustainable management of biodiversity and ecosystem services.

Thesis outline

The rest of this thesis covers four crucial topics over nine chapters:

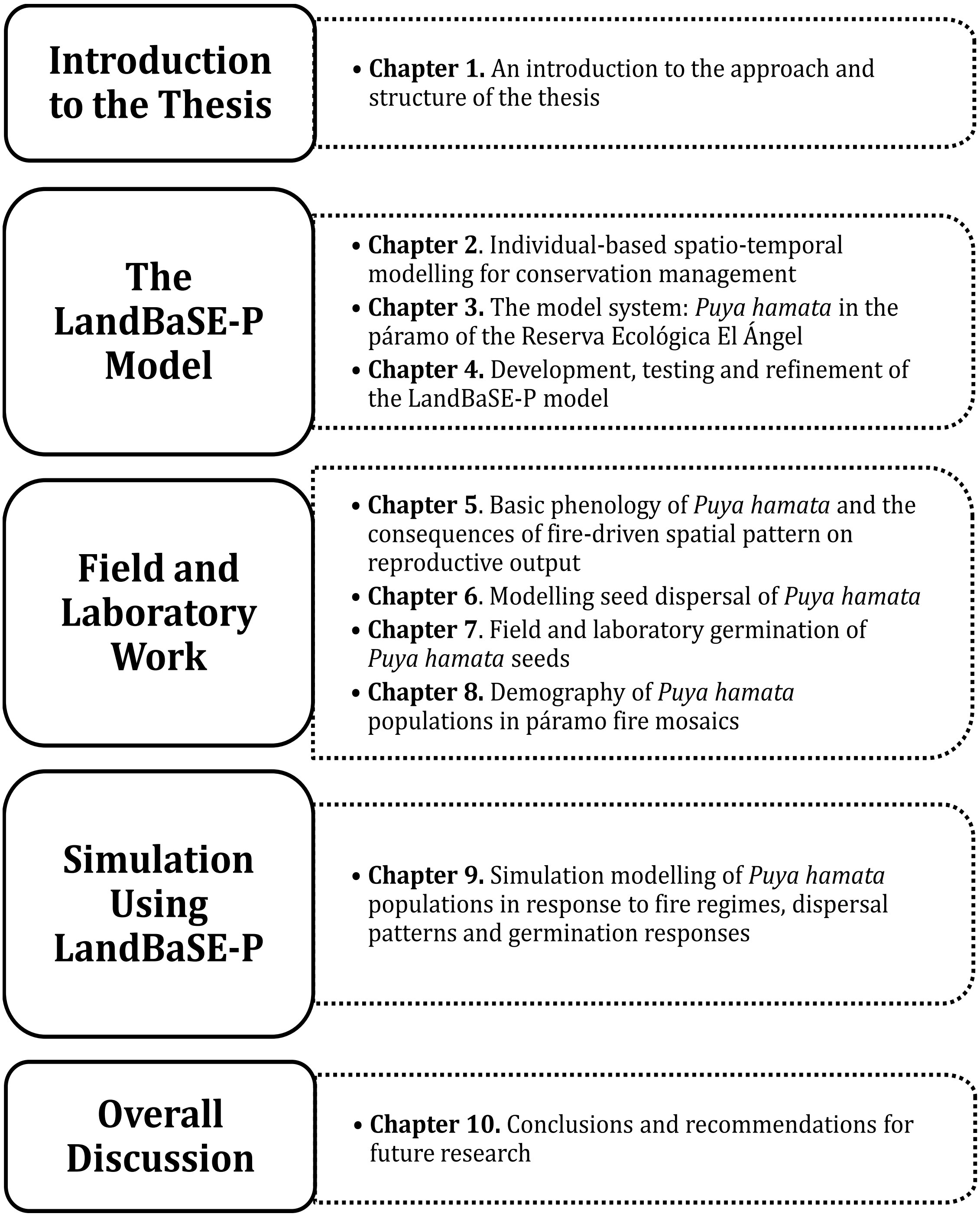
- **the development of an individual-based model, LandBaSE-P, for the simulation of *Puya hamata* populations through time at the landscape scale**
  - Chapter 2 discusses the value of spatio-temporal modelling in ecology. This chapter provides a general introduction to the evolution of modelling in ecology and it explains why individual-based models are a good tool to generate recommendations for conservation and management in the context of other modelling approaches in ecology.
  - Chapter 3 introduces the model system: *Puya hamata* in the páramo of the Reserva Ecológica El Ángel (REEA).
  - Chapter 4 describes the development of LandBaSE-P, a spatio-temporal, individual-based model. It explains how LandBaSE-P works and the sources of information used to determine the input values for the model parameters. Furthermore, the chapter presents some early testing of the model, to show how model development works and to give simple examples of the model outputs.
- **the collection of key information about the model system in detailed field and laboratory studies for ecological understanding and use in the LandBaSE-P model**

  - Chapter 5 describes the basic floral phenology of *Puya hamata*, and explores the effect of aggregation on the reproductive output of *Puya hamata* plants.
  - Chapter 6 provides a general description of seed dispersal processes at short distances for *Puya hamata* and explores the commonest approaches for seed dispersal modelling for consideration for LandBaSE-P.
  - Chapter 7 estimates germination rates of *Puya hamata* in vegetated and unvegetated páramo in the field, and presents detailed studies of controlled laboratory germination trials to investigate the effects of temperature and light.
  - Chapter 8 describes aspects of the demography of *Puya hamata*, such as rosette size-class structure of populations within the burned landscape mosaic of the REEA and its buffer zone. It also provides information about *Puya hamata* recruitment, growth and mortality rates (including the impact of páramo burning at different intensities).
- **the simulation of *Puya hamata* populations using LandBaSE-P**
  - Chapter 9 illustrates the use of the model, with simulations of *Puya hamata* populations in páramos subject to different fire regimes at landscape scale and over long periods of time. It explores the impact of uncertain parameters in the model, evaluates the suitability of LandBaSE-P for research.
- **an evaluation of the overall approach**

- Chapter 10 completes the thesis with a brief overview of the most important conclusions of the work, and recommendations for future research.

An outline of the thesis is presented in Figure 1.1.

Figure 1.1. The organisational structure of the thesis.



Introduction to the Thesis	• **Chapter 1.** An introduction to the approach and structure of the thesis
The LandBaSE-P Model	• **Chapter 2**. Individual-based spatio-temporal modelling for conservation management • **Chapter 3.** The model system: *Puya hamata* in the páramo of the Reserva Ecológica El Ángel • **Chapter 4.** Development, testing and refinement of the LandBaSE-P model
Field and Laboratory Work	• **Chapter 5**. Basic phenology of *Puya hamata* and the consequences of fire-driven spatial pattern on reproductive output • **Chapter 6**. Modelling seed dispersal of *Puya hamata* • **Chapter 7**. Field and laboratory germination of *Puya hamata* seeds • **Chapter 8.** Demography of *Puya hamata* populations in páramo fire mosaics
Simulation Using LandBaSE-P	• **Chapter 9.** Simulation modelling of *Puya hamata* populations in response to fire regimes, dispersal patterns and germination responses
Overall Discussion	• **Chapter 10.** Conclusions and recommendations for future research

2 Individual-based spatio-temporal modelling for conservation management

Introduction

Management of ecosystems, the conservation of biodiversity and the provision of ecosystem services are essential because of threats to natural resources and ecological processes from human activities (Global Environment Outlook, 2007; Millennium Ecosystem Assessment, 2005). According to the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment, 2005) between 10 and 50% of species in well-studied taxonomic groups (mammals, birds, amphibians and conifers) are currently threatened with extinction.

Conservation practice has often been based on anecdotal information rather than on systematic consideration of evidence or the experiences of others who have faced the same problem (Sutherland *et al.*, 2004). This failure is a key problem for conservationists and demands that the way in which conservation and management operate is reconsidered. Both conservation managers and research ecologists need to work together to produce sound evidence-based practice that addresses priority issues facing the sustainable management of biodiversity and ecosystem services (Grumbine, 1994; Salomon *et al.*, 2011).

Good evidence-based practice must reflect appropriate spatial and temporal scales that reflect the most relevant ecological mechanisms (Soulé *et al.*, 2005; Suding & Hobbs, 2009). However, observational or experimental research is difficult to accomplish at large-scales (Grimm & Railsback, 2005; He, 2008), especially given real-world constraints of time and money, and is usually based on 4–10 years of research (He, 2008). This shows the dilemma for conservationists who must balance the need for quick information with the greater reliability of evidence collected over larger scales of time and space.

One option for overcoming this dilemma is the use of ecological modelling, which can deliver relatively quick results based on simulations over long periods of time at large spatial scales. However, to achieve this, the model is an abstraction or simplification of the real system of interest (Hall & Day, 1977). Nevertheless, modelling can be extremely complex at these scales, and provide additional understanding and predictive potential (Gertsev & Gertseva, 2004; Larocque *et al.*, 2006).

Predictions can be made more accurate by developing models that integrate landscape scales with demographic processes that take into account ecological processes that happen at large scales like disturbance and competition (Legendre & Fortin, 1989; Maschinski *et al.*, 2006; Saltz *et al.*, 2006). For population models to be realistic, they should be based on the key ecological processes, using appropriate units of study, and calibrated using as much relevant information from real-world study as possible (Bravo de la Parra & Poggiale, 2005).

Given the wide range of applications of modelling to population ecology, there are a number of different approaches, each suited to particular kinds of study. This chapter reviews those approaches and considers their advantages and disadvantages.

A comparison of models used for modelling populations

Simple analytical models of unstructured populations

Analytical models are basic models used in classical mathematical ecology. For example,

$N_{t+1} = N_t - (d + e) + (b + i)$

where N_t is the number of individuals in a population in year t, N_{t+1} is number in year t+1, d is the number of deaths, e is the number of emigrants, b is the number of births, and i is the number of immigrants. This model is of an unstructured population, where all individuals are treated equally regardless of age or size.

The population size, N, after x years is given by:

$N_{t+x} = N_t \mathrm{e}^{rx}$

Where e is the base of natural logarithms, and r is the intrinsic rate of natural increase of the population. This kind of approach has been used extensively in population ecology (Silvertown & Charlesworth, 2001).

The strengths of simple analytical models are that they provide a basic insight into certain aspects of population dynamics, they are relatively quick to calculate, and the single solution is easy to interpret (Fenton *et al.*, 2006).

However, the extreme simplicity of this kind of analytical model can lead to inaccurate predictions for many real-world situations. In particular, real populations contain structure—organisms in different categories (perhaps according to age or size) which experience different rates of reproductive output, mortality, *etc.*

Matrix models for structured populations

Matrix population models acknowledge some of the structural complexity of real populations and have long been used in ecology and for making management recommendations (Caswell, 2001; Getz & Haight, 1989; Lefkovitch, 1965; Leslie, 1945; Leslie, 1948). Matrices have mathematical properties that can accommodate the differences between individuals of different age or size, and they are straightforward for analysis with computers. They can be used to indicate population characteristics such as the distribution of individuals in different age classes, or the reproductive contribution of each age class to subsequent generations (Caswell, 2000; McDonald & Caswell, 1993).

Matrix models are more complex than unstructured models, reflecting more of the population structure of real populations, and therefore tend to produce more accurate predictions. Matrix analyses are easy to carry out using commercially available software like MATLAB, MATHEMATICA, R, and MATHCAD (Caswell, 2001; Morris & Doak, 2002). Furthermore, there is an extensive literature on the use, development of key matrix statistics (*e.g.,* sensitivity analysis, elasticity), and interpretation of matrix models (Bucharova *et al.*, 2010; Caswell, 2001; Caswell & Trevisan, 1994; Freckleton & Watkinson, 2002; Hoffmann, 1999; McDonald & Caswell, 1993; Neubert & Caswell, 2000; Ramula, 2008; Stott *et al.*, 2010).

However, a key assumption of matrix models is that long-term averages for the vital rates experience little change, limiting their appropriate use since this is often not true (Caswell, 2000; McDonald & Caswell, 1993). Matrix population models are simple descriptions of population dynamics, using overall rates with little regard for the mechanisms that produce uncertainties in parameter estimation (Wisdom *et al.*, 2000), variation between vital rates (Van Tienderen, 2000), stochasticity (De Kroon *et al.*, 2000) and density dependence (Grant & Benton, 2000). Therefore, although matrix population models are often employed to recommend management strategies, the results need to be interpreted cautiously. Furthermore, the use of matrix population models can become extremely complicated with highly structured populations, or with variable dynamics from time to time or place to place (Caswell & Trevisan, 1994).

Metapopulation models

Metapopulation models are systems based on local populations connected by dispersing individuals (Hanski & Gilpin, 1991; Levins, 1969). Levins' metapopulation model was the first model of population dynamics for the study of population processes in a heterogeneous environment (Fahrig, 2007; Levins, 1969). These models incorporate spatial characteristics of local populations, and provide ways of analysing and predicting the response of individual species to habitat fragmentation and other landscape features (Akçakaya *et al.*, 2004; Hokit *et al.*, 2001). Metapopulation models are tools for understanding relationships between landscape structure and population dynamics in time and space (Fagan, 2002; Turner, 2005).

These models are mathematically and conceptually straightforward but modellers must have good knowledge about population and landscape-dependent processes

(Beissinger *et al.*, 2006; Hanski, 2002; Harrison & Ray, 2002). Metapopulation models are useful for evaluating actions at large spatial scales, at which experiments may not be feasible (Akçakaya *et al.*, 2007). They also provide a degree of realism because of the potential exploratory capabilities, appealing to managers and researchers alike (Akçakaya & Sjögren-Gulve, 2000; Breininger *et al.*, 2002; Brook *et al.*, 2002; Van Nouhuys, 2009). Moreover, metapopulation concepts have had positive effects in conservation research, particularly as interest in metapopulation dynamics has driven research relating to dispersal capacities that is extremely valuable in understanding population structure (Yuttham *et al.*, 2003).

However, metapopulations models do have some disadvantages. They usually assume habitat patches are of equal size and are equally isolated (Hanski, 1999). Also metapopulation models can only answer a limited number of questions because they ignore so many variables (Yuttham *et al.*, 2003). Even though metapopulation concepts are not strictly suited to real world conditions, the relevance and applicability of metapopulation models to particular problems in conservation means that they have contributed valuable insights into conservation and have encouraged field studies focused on collecting key data on demography and dispersal in the landscape (Akçakaya *et al.*, 2007; Caswell & Cohen, 1995; Fagan, 2002; Yuttham *et al.*, 2003).

Spatially explicit models

During most of the 19th Century quantitative ecological studies assumed a uniform distribution of living organisms throughout their geographic range (Darwin, 1881;

Darwin, 2009; Hensen, 1884). But now it is well known that spatial heterogeneity of populations plays an essential role in several ecological processes, such as adaptation, succession, maintenance of diversity, community stability, disturbance processes, competition, parasitism and epidemics (Legendre & Fortin, 1989). As a result, a different approach to modelling was devised in order to account for spatial heterogeneity: spatially explicit models.

Spatially explicit models (SEMs), in general, incorporate organism coordinates into the model, although these do not necessarily have to be real geographic coordinates (He, 2008). SEMs require the spatial references to create relationships between model objects and variables (He, 2008). Spatially explicit models have been used to study a variety of large scale ecological patterns and processes and there is a wide range of models that work at different scales and with a variety of units (Beissinger *et al.*, 2009; Beissinger *et al.*, 2006; Dunning *et al.*, 1995; Hanski, 1998). Spatially explicit models have a structure that specifies the location of each represented object (organism, population, habitat patch or entire metapopulation) within a heterogeneous landscape, and therefore the spatial relationships between habitat patches and other features can be defined (Beissinger *et al.*, 2006; Dunning *et al.*, 1995; Hanski, 1998).

Depending of study unit, more specific types of SEMs have been defined:

Spatially explicit population models

Spatially explicit population models (SEPMs) provide a method for determining the relationship of species population dynamics with spatial pattern in landscapes (Dunning *et al.*, 1995; Turner *et al.*, 1995). These models have been developed mainly around the processes that rule these dynamics (Bravo de la Parra & Poggiale, 2005). A few population-based SEPMs also have been constructed, where each cell contains its own population (Hassell *et al.*, 1991; Palmer, 1992; Satoh, 1990).

Individual-based models

SEPMs are often individual-based models (IBMs). Individual-based models are those which describe autonomous individual organisms (Grimm *et al.*, 2006). In individual-based models, the location of each individual within the landscape is monitored (Dunning *et al.*, 1995), and individuals' fitness characteristics depend on the cell type they occupy. Each individual is considered unique and autonomous, even though they belong to the same species, and they are able to modify their environment (Grimm & Railsback, 2005). Modelling individuals is valuable and provides detailed information about how complex systems work. Crowder *et al.* (1992) emphasized that it is the individual that survives to reproduce—the unique characteristics of individuals, and not population averages, determine which individuals produce the next generation.

In models with an annual time step, individuals go through an annual cycle of breeding, dispersal, and mortality (Pulliam *et al.*, 1992). Outputs of these models are population characteristics and processes. Population parameters in individual-based models are derived from the life cycle of every individual through time and produce estimates of total population size or extinction probability.

These kinds of models can describe the spatial pattern of population traits like demography, explicitly represent individual development and incorporate local interactions between individuals (DeAngelis & Rose, 1992; Scheffer *et al.*, 1995). Also, some researchers suggest individual-based modelling is gaining in popularity because high-performance in computers are present on almost every desk, so that individual-based modelling is now open to everyone (Grimm & Railsback, 2005; Uchmanski & Grimm, 1996).

On the other hand, IBMs present some disadvantages. They are challenging because the design of the model structure and its resolution is a more time-consuming, complex task than developing classical models, which are constrained to a coarser representation of reality (Grimm & Railsback, 2005).

IBMs have essential characteristics that cannot be described by equations and parameters. Moreover, many IBMs are too complex to describe completely in publications, and are often not available in full detail (*i.e.,* the computer code) to the scientific community, which threatens the credibility of the whole approach (Lorek and Sonnenschein 1999; Grimm 1999, 2002; Ford 2000). IBMs also require significant amounts of information: they are “data hungry”(Grimm & Railsback, 2005).

But still, despite these challenges, a large number of authors have recognized that individual-based models are not only interesting, but are perhaps the only logical way to model ecological processes (Batchelder *et al.*, 2002; Grimm & Railsback, 2005; Shanahan *et al.*, 2011; Uchmanski & Grimm, 1996; Werner *et al.*, 2001). However, these models can become even more powerful if individuals are tracked in real time in high resolution landscapes (Crowder *et al.*, 1992).

Spatially explicit models in high resolution landscapes

The development of Geographic Information System (GIS) computer software and remote sensing for conservation has allowed the incorporation of real world landscapes into spatial models. When a GIS includes the distribution of habitat patches, a landscape grid can be created by overlaying a grid of cells on top of the original map and then passing on habitat characteristics from the original map to each cell (Berry, 2007).

Spatially explicit modelling can connect a population model to a landscape map (Akçakaya, 2000). The map can be a set of patches. More complex maps can include habitat variables that contribute to classifying habitat suitability for each location.

Spatially explicit modelling with GIS is widely used and has been employed in studies of terrestrial, freshwater, and marine ecosystems. Some examples include predicting forest composition and structure (Ohman & Gregory, 2002), mapping benthic habitats (Urbanski & Szymelfenig, 2003), and the analysis of nutrient loads in rivers and streams (Pieterse *et al.*, 2003). Modelling plus GIS also plays an important role in understanding disturbance ecology (Breininger *et al.*, 1991; Hoctor *et al.*, 2000; Kautz & Cox, 2001; Knight *et al.*, 2000).

While the advantages of using GIS for ecological studies cannot be ignored, there are definitely drawbacks as well. The quality of data output from GIS is highly dependent on the quality of the data input. Also these kinds of models frequently require the coordinates of populations or individuals, and demand massive outputs and subsequent analysis. Not surprisingly, these kinds of models are put together and analysed by teams of specialists that each contribute to different aspects of the work.

One of the main advantages of SEMs-GIS is the inclusion of real coordinates of individuals (Berry, 2007). SEMs are used in different branches of ecological research, such as animal tracking and monitoring, land use, and fire control. A few more detailed examples help to illustrate this range.

Turner *et al.*(1993) used an SEMs to track movements, foraging activity, and mortality of individuals and small groups of wintering bison (*Bison bison*) and elk (*Cervus elaphus*) in Yellowstone National Park. Using their model, they found that the resource patchwork changes through time as resources in occupied patches are consumed. The model revealed how habitat-specific demography and foraging behaviour defines resource heterogeneity in the landscape.

Pulliam *et al.* (1992) used an SEMs of Bachman's Sparrow (*Aimophila aestivalis*) to determine the management and conservation importance of a rare habitat type, Longleaf Pine forest, for the sparrow's population dynamics. This approach provides a good example of how SEMs can use artificially generated landscapes to determine population responses to a general change in landscape structure.

SEMs also are used to monitor changes in land use. These models have the ability to examine—with the help of virtual scenarios— how a proposed management action in an actual landscape might affect a given population. SEMPs added to GIS are very popular to evaluate changes in land use.

Perry and Enright (2007) employed both spatially explicit and spatially-implicit models to examine forest-shrub successional dynamics in relation to fire spread in

New Caledonia. They concluded that their spatially explicit model produced outcomes closer to those documented historically, and inferred from the palaeoecological record, than those obtained with their matrix (spatially-implicit) model.

As further evidence for the range of models and their value in understanding ecological processes in a variety of ecosystems, a list of specific case studies is provided in Table 2.1.

Table 2.1. Examples of population models in ecology. SEMs = Spatially explicit Models, IBMs = Individual-based models. Multiple models combine several different approaches at once and cannot be classified into only one category.

Use	Type	Model name	Author
Climate change	IBMs	FOREL	(Busing & Solomon, 2006)
Conservation	SEMs	RMLANDS	(McGarigal *et al.*, 2003)
	Multiple	CELSS	(Costanza *et al.*, 1990; Sklar *et al.*, 1985)
	Multiple	CENTURY	(Peng *et al.*, 2002)
	Multiple	FETM	(CH_2MHill, 1998; Schaaf & Carlton, 1998)
	SEMs	FIREPAT	(Keane & Long, 1997)
	SEMs	MOSAIC	(Green, 1989)
	Multiple	REFIRES	(Davis & Burrows, 1994)
	Multiple	ZELIG-B	(Cumming *et al.*, 1995; Cumming *et al.*, 1994)
	Multiple	ZELIG-L	(Miller, 1994; Miller & Urban, 1999)
	Multiple	FFE-FVS	(Reinhardt & Crookston, 2003)
	Multiple	LADS	(Wimberly, 2002; Wimberly *et al.*, 2000)
	Cellular Automata	LANDSUM	(Keane *et al.*, 2004; Keane & Long, 1997; Keane, 2002)
	Multiple	MC-FIRE	(Lenihan *et al.*, 1998)
	Multiple	SEM-LAND	(Li, 2000; Li, 2001)
	Multiple	SUFF-1	(Suffling, 1995)
	Multiple	SUFF2	(Suffling, 1993)
Ecosystem management	Multiple	TELSA	(Klenner *et al.*, 2000; Kurz *et al.*, 2000)
	Multiple	Biome-BGC	(Thornton, 1998; Thornton *et al.*, 2002)
	Multiple	GLOB-FIR	(Thonicke *et al.*, 2001)
	Multiple	REG-FIRM	(Venevsky *et al.*, 2002)
Forest Planning	SEMs	SIMPPLLE	(Chew, 1997)
	SEMs	LAMOS	(Lavorel *et al.*, 2000)
Land use and management	SEMs	ALFRESCO	(Rupp *et al.*, 2000)
	Multiple	ANTON	(Antonovski *et al.*, 1992)
	Cellular Automata	BANKSIA	(Groeneveld *et al.*, 2002)
	Multiple	BFOLDS	(Perera *et al.*, 2002)
	SEMs	DISPATCH	(Baker, 1999; Baker *et al.*, 1991)
	Markov Chains	EMBYR	(Gardner *et al.*, 1996; Hargrove *et al.*, 2000)
	SEMs	FIRESCAPE	(Cary, 1998)
	SEMs	LANDIS	(Mladenoff & He, 1999; Mladenoff *et al.*, 1996); (He & Mladenoff, 1999) ,(Mladenoff, 2004)
	SEMs	Q-LAND	(Pennanen *et al.*, 2001)
	Multiple	QTIP	(Plant *et al.*, 1999)
	Cellular Automata	RATZ	(Ratz, 1995)
	Stochastic	SAFE FORESTS	(Sessions *et al.*, 1997; Sessions *et al.*, 1999)
	Multiple	DISPATCH	(Baker, 1995; Baker, 1999; Baker *et al.*, 1991)
	SEMs	DRYADES	(Mailly *et al.*, 2000)
	Multiple	FLAP-X	(Boychuk & Perera, 1997; Boychuk *et al.*, 1997)
	Multiple	INTERLAND	(Gauthier *et al.*, 1994)
	Multiple	LANDSIM	(Roberts & Betz, 1999)
	Multiple	MAQUIS	(Perry & Enright, 2002)
	Multiple	ON-FIRE	(Li, 1997)
	Multiple	REFIRES	(Burrows, 1988)
	Multiple	SELES	(Fall & Fall, 1996)
	SEMs	FIN-LANDIS	(Pennanen & Kuuluvainen, 2002)
	Multiple	FIRE GRADIENT MODEL	(Kessell, 1976; Kessell & Cattelino, 1978)
Landscape change	SEMs	FIRE-BGC	(Keane *et al.*, 1996b)
	SEMs	SIERRA	(Mouillot *et al.*, 2001)
Population dynamics	SEMs	CAFÉ	(Bradstock *et al.*, 1996)
	Analytical	LOTKA VOLTERRA MODEL	(Lotka, 1925)

Discussion

Some trends in model development in recent times are evident from this review, and these are summarised in Figure 2.1. Early ecological models were simple and explained a single parameter, whereas modern models are complex and involve many simultaneous calculations (Yue *et al.*, 2011). Representations of summaries or parts of a process by means of equations that could be solved manually have been replaced by computer models that simulate many complex processes simultaneously, perhaps using hundreds of parameters. At the same time, the amount of data generated by the models has increased too.

One of the reasons for the increase in computational complexity is the move over the last decade from a focus on populations to one dealing with individuals (Grimm & Railsback, 2005). The individual approach can examine questions that cannot be addressed with classical models. Already, much has been learned about the ecological significance of local interactions, individual variability, *etc.* by using IBMs to represent real and hypothetical systems (Grimm & Railsback, 2005).

Alongside the increase in detail associated with the organisms, the representation of the environment in models has become more detailed and more extensive, changing from local or stand scale to landscape scale (Akçakaya *et al.*, 2004). Today, some modelling is carried out with high-resolution representations of real landscapes.

Additional information is often associated with the individuals in contemporary ecological modelling. Three ecological factors receive particular attention: age or stage structure of the population, its spatial structure, and the individual–population interaction (Bravo de la Parra & Poggiale, 2005).

There is a trade-off between the generality of simple models and the realism complex models (Levins, 1969). As Bravo de la Parra and Poggiale (2005) highlight, the realistic representation of natural processes often leads to intractable mathematical models. An important task for theoretical ecology concerns the development of models that balance the tensions between biological complexity and mathematical tractability.

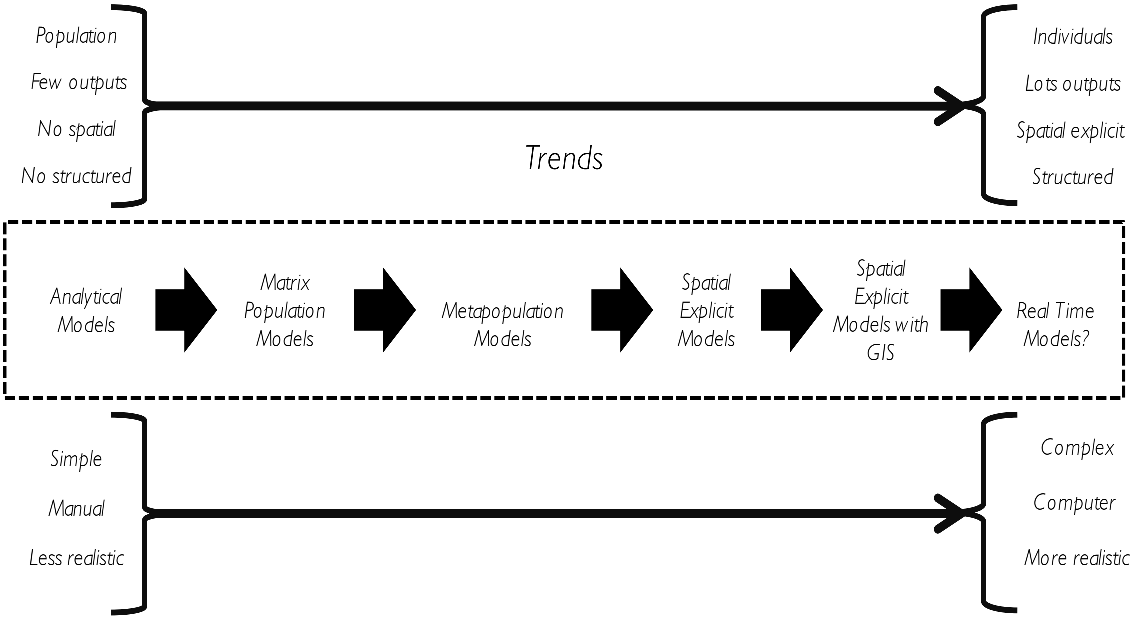
Another consequence of the increase in model complexity is the difficulty in understanding it and interpreting the outcomes. An increase in complexity often reduces the potential of a model to aid understanding. Some critics of IBMs have even argued that complex models are as hard to understand as the real world and therefore are of little use (Grimm & Railsback, 2005).

Computational time increases with complexity, as does the programming task. Additionally, managing the data requirements of complex simulations can be a problem (Scheffer & Beets, 1994): some of the data required for application of certain spatial models may not be available (Perry & Enright, 2007). The reliability of a model depends on the accuracy of the data used.

Above all, ecological models should be testable (Forbes *et al.*, 2009). Hypotheses about how a system operates must make predictions that can be tested by experiment or observation over both the short and the long term. For conservation purposes, this requires model output in the form of variables whose values can be measured in the field. Does the real-world response correspond to the model's prediction? Of course, it is difficult to test a model when it is being used to make predictions over long time periods and at over wide areas. In some cases, the only opportunity to test models is at small scale using field experiments that capture some elements of the simulation model.

It is important that models should explore system uncertainty (Burgman *et al.*, 2005; Possingham *et al.*, 2001). Of course, models should be based on biologically realistic assumptions (Soberón, 2010), and their outputs must be relevant and meaningful to conservation managers. However, conservation decisions are usually made with an incomplete understanding of system dynamics. It is the responsibility of the modeller and researcher to explore deeply the model's uncertainty and provide this knowledge to decision makers. In the case of ecological models, the risks of specific management decisions must be made open to the public.

Figure 2.1. Trends in ecological models.



Models can be classified according to use, such as those for wildlife populations, watersheds, natural or managed forests. However, classification of ecological models can be much more meaningful when based on some biologically important attributes. For example, Uchmanski & Grimm (1996) proposed a classification based on four principal criteria: the degree to which the complexity of the individual's life cycle is reflected in the model; whether or not dynamics of the resources is explicitly taken into account; the use of real data to represent the size of a population; and the extent to which variability of individuals of the same age is considered.

Usually, ecological modelling uses concepts from mathematics, systems analysis and computer programming to simulate population dynamics. Ecological modelling itself is evolving as a scientific discipline, and in recent decades has been developed to make full use of advances in computer processing power. Furthermore, ecological models are considered as powerful research tools (Johnsen *et al.*, 2001; Jørgensen, 2001) and their use is growing in importance for the management of natural resources (Johnsen *et al.*, 2001; Walters & Martell, 2004) and making predictions about the effects of disturbances, such as global change, land use, fire control and fragmentation (Luckai & Larocque, 2002; Peng & Apps, 1998; Rose *et al.*, 2010; Yue *et al.*, 2011).

Spatially explicit models, in particular individual-based models, are powerful tools to explore and understand population processes from the point of view of individual parameters at the landscape scale over the long term. Although models are useful, they have several important disadvantages and limitations, and the interpretation of the simulations needs deep understanding of the model and appropriate caution.

Individuals are usually the most appropriate ecological units for understanding how different processes interact in complex systems, and a well-designed model, primed with good-quality information, can guide conservationists in their efforts to manage the biodiversity within landscapes. For this reason, management of ecosystems effectively founded on individual-based spatial-temporal modelling—supported by field and laboratory observations—is a valuable approach.

3

The model system: *Puya hamata* in the páramo of the Reserva Ecológica El Ángel

Introduction

Terrestrial ecosystems dominated by grassland, such as steppes, prairies, savannas, and grasslands, cover about a quarter of the Earth's surface (Bardgett & Cook, 1998). Grasslands cover 41–56×10^6 km^2 of the Earth's land surface and are found on every continent except Antarctica (Gibson, 2009). Grasslands vary in composition and physiognomy according to regional and local variation in controlling factors such as climate, geology, type of soil and disturbance regime.

Grasslands are biodiverse and offer ecosystem services that sustain large numbers of people (Daily, 1997; Lavorel *et al.*, 2011; Rhymer *et al.*, 2010; Van Eekeren *et al.*, 2010). Gibson (2009) categorized four services and functions of grasslands:

1. supportive functions and structures such as pollinator services, primary production, nutrient cycling
2. regulating services like the maintenance of soil fertility, sequestration of CO_2
3. provisioning services as plant material for human use
4. cultural services as such as scenery, ecotourism and religious value.

Demand for food, fibre, timber and fuel has promoted the intensification of land use (Millennium Ecosystem Assessment, 2005; Vitousek *et al.*, 1986) and terrestrial ecosystems, like grasslands, are facing mounting pressures around the world (Carvalho & Batello, 2009). These ecosystems are affected in a variety of ways by land-use change, intensive and extensive agriculture (Lewis *et al.*, 2010;

Walker *et al.*, 2004), invasion of alien plants (Petryna *et al.*, 2002), loss of habitat area (Partel *et al.*, 2005) and the impacts of fire (Gibson, 2009).

Mountain grasslands have been influenced by humans for about 5000 years (Batzing, 2003). Gnecco (2003) and Rodríguez (2005) discusses evidence suggesting human occupation up to 8000 years BP during the Holocene in South America. It is recognized that most grasslands below the treeline in mountains are man-made (Maurer *et al.*, 2006). Over thousands of years, a dependent relationship of human populations on the ecosystem services of mountain grasslands has developed through exploitation of important natural resources (Maurer *et al.*, 2006).

One example of such mountain grasslands is the high-altitude vegetation, or páramo, found above the limits of continuous forest, from 3000–4800 m, in the Andes from Colombia and Venezuela (with outliers in the mountains of Costa Rica) to northern Perú (Hofstede *et al.*, 2003). The country with the highest proportion of páramo cover in relation to its size is Ecuador: approximately 250,000 km^2, or 5.1% of the country's territory (Hofstede *et al.*, 2003). This ecosystem is very sensitive to land-use changes, but is under significant pressures from local human populations for direct benefits (*e.g.,* agriculture) and indirect ecosystem services (*e.g.*, water supply) (Vásconez & Hofstede, 2006).

Although poorly understood in ecological terms, páramo ecosystems are important for several reasons (Hofstede *et al.*, 2003):

- Their relatively high biological diversity for grasslands, together with high endemicity, gives them high conservation interest.

- They provide various ecosystem services to a high number of Andean people both directly within the páramos themselves and indirectly to people in ecological zones at lower altitudes. Agricultural activity is mostly extensive grazing, and is almost always accompanied by regular burning of the vegetation.
- Increasingly, the páramos provide interest to tourists, and in some areas ecotourism already provides significant additional income to rural communities.
- They are fragile ecosystems and particularly threatened by poor management and climate change.

One of the most common disturbances in the páramos are fires (Cochrane *et al.*, 2009). Several authors consider that páramo below 4100–4300 m represents, secondary vegetation in previously forested areas (Ellenberg, 1979; Lægaard, 1992) that has been shaped and maintained by man fire (Lægaard, 1992). Cochrane *et al.,* (2009) recognised that human activity seems to be responsible for the majority of current páramo fires but this supposition is still debated.

There is little evidence that shows natural fire from lightning or volcanism is possible in páramos. For example, the northern Andes (Venezuela and Colombia) and Costa Rica and Panama experience a high frequency of storms with lightning. But most researchers consider the probability of lightning igniting fires in páramo to be low, because the vegetation is often moist when storms with lightning occur (Keating, 2000; Keating, 2007). However, in Neotropical páramos lightning strikes may occur even without rain and therefore there are some probabilities of this to occur (Keane & Finney, 2002). On the other hand, volcanoes are widely arranged and eruptions are infrequent in páramo areas (Cochrane *et al.*, 2009). That is why volcanism has been dismissed as a source of páramo fires. Verweij (1995) speculated that volcanism or lightning may only set one fire per 1000 years in Colombian páramos of Los Nevados National Park.

In the northern páramos of Ecuador, experiments on soil profiles showed the presence of charcoal (Di Pasquale *et al.*, 2008). This result indicates that fires have occurred in this area at least since the beginning of the Holocene (Di Pasquale *et al.*, 2008). During early Holocene, Andean climate seems to have been drier than today (Vélez *et al.*, 2003). This may have resulted in a higher frequency of natural fires. This interpretation applies until the middle Holocene. It is in pollen records where the first direct evidence of anthropogenic fire disturbance was found (Bush *et al.*, 2005).

South American first occupants did not practice agriculture, but they could have left traces of fire (Piperno *et al.*, 1990). Humans were collectors-hunters and mountain grasslands may have been burned to facilitate hunting (Wesche *et al.*, 2000). Early human populations possibly influenced high-altitude vegetation in the beginning of the Holocene. Di Pasquale *et al.,* (2008) recognized, that the difference between natural and anthropogenic fires cannot be made, this is restricted to suppositions as to the origin of the palaeo-fires, and therefore as to the 'naturalness' of the lower parts of the modern páramo. There is insufficient data supporting quantitative estimates of natural fires, as opposed to anthropogenic, in the Neotropical páramos. However, the idea that nature sets considerably fewer fires in tropical highlands than do humans these days is likely correct for the neotropical páramos, and is the accepted knowledge for tropical highlands worldwide (Wesche *et al.*, 2000).

Fire history is complicated by agricultural burning, by far the most common cause of páramo fire (Lægaard, 1992; Mena & Hofstede, 2006). A long history of modification of vegetation by fire makes it difficult to determine the ecological effects of burning by observation of existing patterns. Frequently the destructive nature of fires is considered, but the diversity-enhancing effects of disturbances are also worth attention (Carcaillet, 1998). Fire often provides opportunities for competitively inferior species to persist in communities. Where a significant shift in community structure results from fire disturbance, the effects can be much greater than what might be expected. Generally, fires have often been implicated in a shift to grassland at the expense of woodland (Hobbs & Huenneke, 1992), and this is also true in the páramo zone (Lægaard, 1992).

For all these reason, páramos offer an ideal opportunity to investigate the effects of fires on ecological processes and relationships.

Miller & Silander (1991) identified *Puya* species as beneficiaries of burning in the páramos. One species, *Puya hamata* L.B. Sm.*,* abundant in many Ecuadorian páramos, has potential as an indicator of the fire regime. Moreover, this species can be considered important —because of important interactions with hummingbirds and spectacled bears—and a flagships species in the form of "botanical big game" (Hedberg, 1964).

Therefore, *Puya hamata* presents an opportunity to evaluate some of the ecological impacts of páramo fires, and to act as an indicator of fire regime. This chapter provides more information about *Puya hamata* and identifies a suitable study area for detailed ecological investigation.

Puya hamata **L.B. Sm.**

The genus *Puya* Molina (Bromeliaceae) comprises approximately 200 species, mostly from South America, with two taxa in Costa Rica (Jabaily & Sytsma, 2010; Luther 2004). The genus has been divided into two subgenera (Hornung-Leoni & Sosa, 2008): *Puyopsis* (most of the species) and *Puya* (containing only eight species, distributed mainly in the southern part of the Andes). *Puya* plants are relatively long-lived, semelparous giant rosettes, varying in size from 10 m (*P. raimondii*) to 20 cm (*e.g., P. exigua*) when in flower. They attract bird and bat pollinators with nectar supplied by large numbers of flowers on a single inflorescence (Kessler, 2002). Some species are able to reproduce vegetatively—new plants appear from the base—but many are restricted to reproduction by seed alone.

The genus *Puya* is tropical in origin and species typical of cooler, high-altitude zones have evolved only relatively recently (Van der Hammen & Cleef, 1986). Interestingly, convergent evolution has produced plants similar in appearance and ecological function at high-altitudes in other tropical mountains, such as the giant *Lobelia* rosettes in the East African mountains (Smith, 1994).

Puya hamata occurs at altitudes from 2850–4100 m from southern Colombia, through Ecuador, to northern Peru (Jørgensen & Ulloa Ulloa, 1994). Its rosette reaches up to 3.5 m in diameter, and the pubescent inflorescence reaches up to 5 m in height (Figure 3.1), emerging from February to April, producing flowers from May to July, and dispersing seeds from August to October (Miller, 1988), though phenology varies throughout its range. *Puya* (or “achupalla”) is one of the few species from the páramo that the general public in Ecuador recognise (pers. obs.).

The flowers are pollinated by a variety of different hummingbird species, some of which can be territorial (Woods & Ramsay, 2001). The heart of the rosette is a favourite food of spectacled bears, *Tremarctos ornatus* (Peyton, 1980; Rivadeneira-Canedo, 2008), and the bears completely destroy rosettes to reach the moist, sugary centres of the plants. Once flowers are fertilized and fruits are mature, *Puya hamata* seed dispersal begins. The seeds are dispersed passively in the wind, but have small wings to aid dispersal. It has been reported seeds reach no further than 10 m from the parent plant (Miller, 1988), but there have been no direct studies to support this.

Commonly, *Puya hamata* is often found in wetter areas, where competition from grassland plants is reduced. It survives fires well: the apical meristem is protected from lethal temperatures by the outer leaves of the rosette (Lægaard, 1992; Ramsay & Oxley, 1997). The upper altitudinal limit of *Puya hamata* is regulated by low temperatures and water stress (Miller & Silander, 1991).

Therefore, *Puya hamata* is a flagship species (known by the general public), a potential keystone species (because of its interactions with hummingbirds and bears), and an indicator species for burning (because it thrives in fire-dominated páramos). For these reasons, *Puya hamata* is a good choice as the focus for a spatially explicit, individual-based population model of conservation importance.

Figure 3.1. Rosette and inflorescence of *Puya hamata* in the REEA.

Study site: the Reserva Ecológica El Ángel

As previously mentioned, páramos are fragile, biodiverse grasslands offering important ecosystem services, such as water supply and tourism—but are often threatened by agricultural burning. Although there are many páramos in Ecuador, only a few offer an appropriate combination of characteristics for a study of *Puya hamata* in relation to fire disturbance: accessibility, a suitable range of burning regimes, existing scientific research to support the study, and clear provision of ecosystem services such as water and tourism.

One area that satisfies all of these criteria is the Reserva Ecológica El Ángel (REEA), which is near the border between Colombia and Ecuador, and contiguous with the páramo of Volcán Chiles (Figure 3.2). Access is straightforward, since a maintained road runs through the páramo zone from El Ángel to Tulcán, and past reserve accommodation where visiting scientists may stay.

The reserve has a history of agricultural burning, especially since the El Ángel-Tulcán road was built. The reserve and its buffer zone often experience annual burning (Moscol Olivera & Cleef, 2009), despite protection in law. In addition, some fires are started by tourists rather than farmers, and the landscape consists of a mosaic of patches in different stages of recovery after burning (Bustos-Insuasti, 2008; Ramsay, 1998; Valdospinos-Navas, 2008).

The páramo of the REEA is linked to that of Volcán Chiles and La Esperanza, which extends across the border into Colombia. This region was the subject of some detailed ecological investigations in 1997 and 1999 (Ramsay, 2001a). More recently, scientific research in this páramo has been promoted by its inclusion as one of 14 intervention sites for Proyecto Páramo Andino, along with others in Venezuela, Colombia, Ecuador and Perú (Proyecto Páramo Andino, 2011). These sites were selected to conserve ecosystems and ecosystem services, as well as a variety of land use and human cultural diversity. In addition, Randi-Randi, a Non-Governmental Organization, has been carrying out research in the REEA since it was decreed as an Ecological Reserve in 1992, including fire monitoring (Bustos-Insuasti, 2008; Valdospinos-Navas, 2008).

Local people continue to benefit from the ecosystem services from the REEA, despite some conflicts over management practices, and a large part of the work of the REEA, Randi Randi and others involves engagement of local people with sustainable environmental management policy.

The study site for this thesis was located within the REEA and its buffer zone, over an altitudinal range of 3450–3800 m, within an area defined by UTM 18N 177826 71266 to 18 N 177990 71391. The vegetation consisted of páramo grassland, wetlands and small forests of *Polylepis*. The páramo grassland in this area is dominated by tussock grasses (*e.g., Calamagrostis, Festuca*), giant rosette plants (*Espeletia pycnophylla, Puya hamata*), shrubs (*e.g., Hypericum, Loricaria, Brachyotum*) and herbs (*e.g., Geranium, Castilleja*); a full species list is provided by Balslev (2001).

Figure 3.2. The Reserva Ecológica El Ángel is located on the north of Ecuador.

4 Development, testing and refinement of the LandBaSE-P model

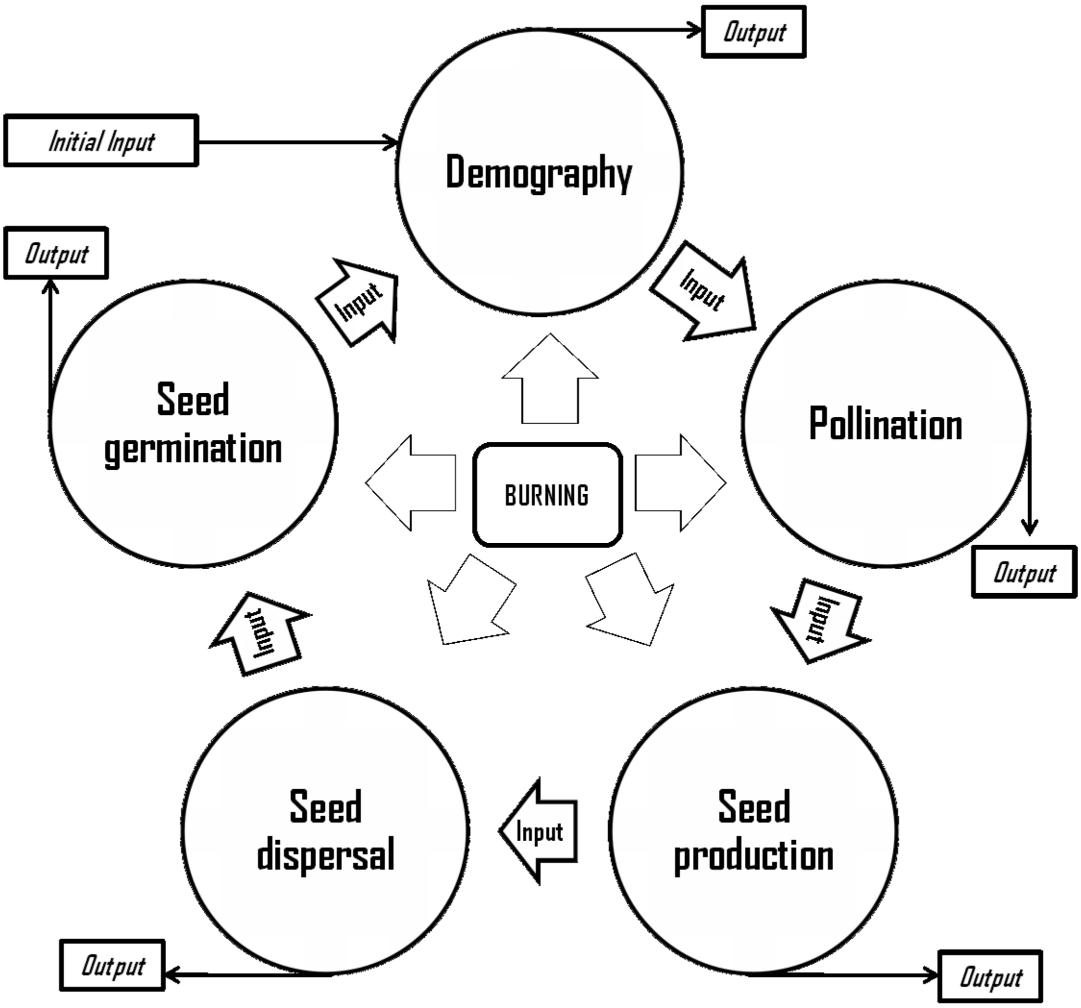
Introduction

The development of an appropriate model to explore *Puya* populations was started in 2004 by Dr Paul M. Ramsay and M. Sc. Nicholas Humphries. The aim of the programme is to model the effects of fires on *Puya* population dynamics and to simulate the ecological processes involved. It is called LandBaSE-P (*Land*scape *B*urning *a*nd *S*patially *E*xplicit *P*opulations), and as the name suggests, it is an individual-based spatially explicit model at the landscape scale. The model allows users to explore alternative fire regime scenarios and its effects on *Puya* population dynamics.

LandBaSE-P is highly complex, combining spatial and temporal processes such as pollination, seed production, seed dispersal, germination, growth and mortality, all potentially modified by fires occurring through time within the landscape (Figure 4.1).

This chapter presents an overview of some technical considerations needed to understand the model, including user-defined inputs and the outputs. The early development testing of the model, and its refinement, are also described, and some illustrative outputs are shown.

Figure 4.1. Conceptual model of LandBaSE-P. Inputs and outputs of each major process are shown and all are affected by the fire regime, which can be specified in the model.



Technical details

LandBaSE-P was written in Java (Sun Microsystems) by Nicholas Humphries (initially at the University of Plymouth, and later at the Marine Biological Association, Plymouth) using a modular approach, where each organizational level implemented in the model was developed as separate components. The potential spatial scale of the model ranges from 10 m × 10 m to 100,000 m ×100,000 m, and can be run at any spatial scale between these intervals.

LandBaSE-P cycles go from demography through pollination, seed production, seed germination and seed dispersal back to demography, all of them modified by fire. A significant number of input parameters are required in order to run the model, and outputs are available in several formats for further analysis (Table 4.1).

Input screens are illustrated in Figure 4.2.

The reporting intervals for different modules within the model can be set independently, such that demographic data could be reported annually whereas seed production data could be reported daily. The interactions of different time intervals, however, needs careful consideration, since it can affect the results if timings are poorly synchronised from one process to the next.

There is an option to display a visual representation of the landscape while the model is running (Figure 4.3, Table 4.2). Non-reproductive plants and seedlings are shown as green dots, reproductive plants by blue dots. Fires are represented by red squares and cells with insufficient fuel to burn are represented by yellow squares. This visual interface can be useful as a check that several processes are indeed running as expected, but this part of the model is very demanding of computer resources. With landscapes greater than 25 km^2, the model slows considerably as the computer struggles to plot each cell and millions of *Puya* plants in the landscape. Therefore, the model is mostly run with this option turned off.

Biological considerations

LandBaSE-P is a simplified model that employs the most important aspects of *Puya* life cycle. When the conceptual model was designed some important considerations were taken into account to make it as simplest but as realistic as possible. For example, burning processes do not consider seasonality because páramos have not seasons like other regions. Tropical climates differ sharply from middle—and high latitude climates in having very reduced month to month variation in both, mean temperature and day length (Sarmiento, 1986). Summer and winter are employed to mean the six month periods when the sun is over the opposite hemisphere (Sarmiento, 1986).

The simulated pollination process in LandBaSE-P considers the probability of pollination, the length and season of flowering (its main components)(Wright & Calderon, 1995). Other finer processes like the effect of quality and quantity of reward (pollen or nectar) are not considered.

The simulated seed production process considers that all seeds have the same size. Chapter 6 presents seed characteristics showing that they do not vary significantly between them.

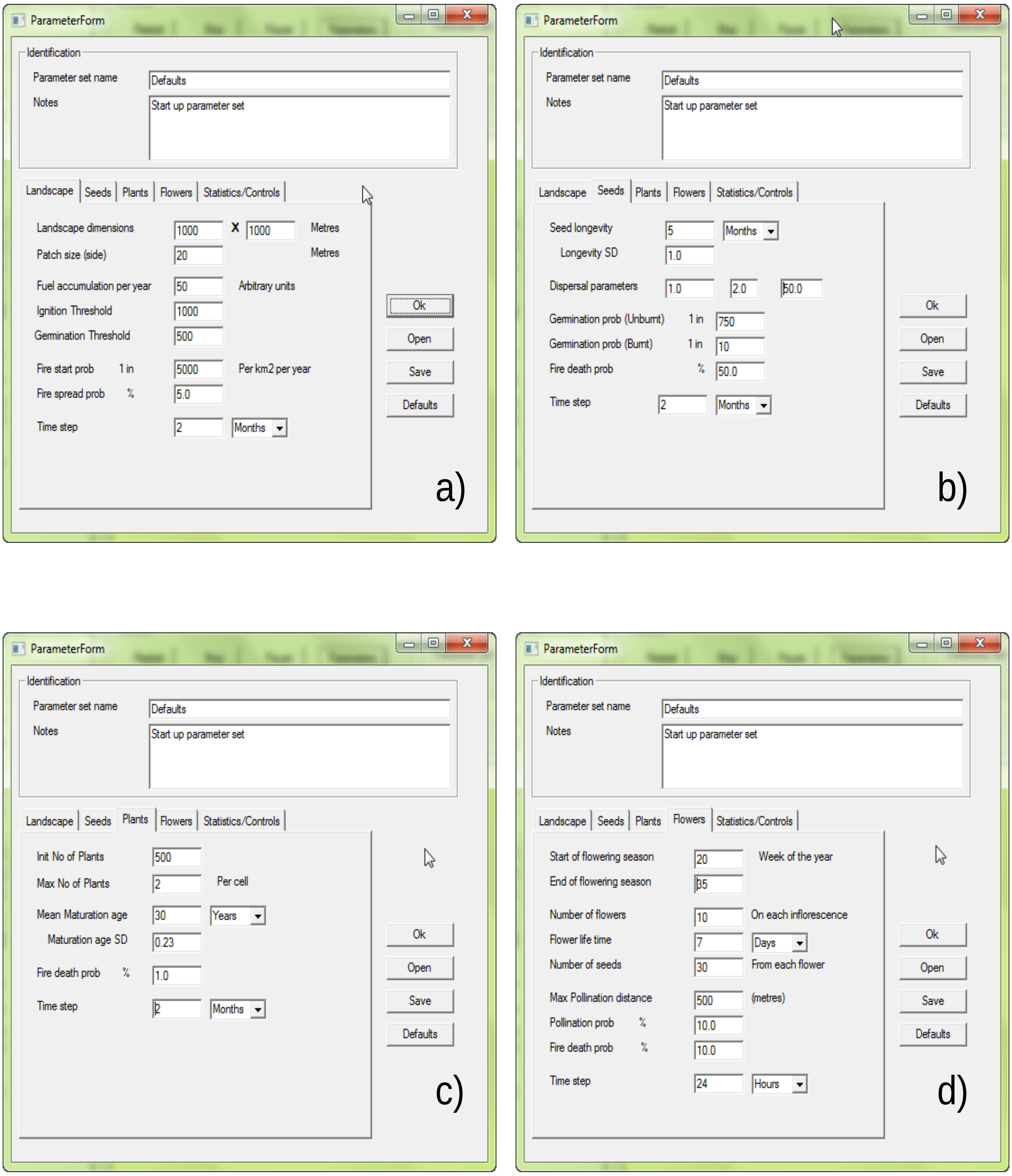
Other process that LandBaSE-P does not consider is predation after dispersal. In upper regions like páramos the number of animals is reduced (Rahbek, 1995). But still there are some potential seed predators like a large range of rodents, birds and some species of ants (Mena Vásconez, 2001). For *Puya hamata* it is not reported any important loss of seeds by post dispersal granivory.

Germination processes modelled by LandBaSE-P only consists in values based on probability of germination in open or close areas. These two values can be modified and adjusted to fieldwork observations. Factors like smoke or ash are not considered because there is no previous information about their relation to germination of *Puya hamata* seeds or any association with mycorrhizae (Mora *et al.*, 2007; Vadillo *et al.*, 2004). It seems *Puya* is not dependant on fires to complete its life cycle but that it uses the spaces provided by them very well (Miller & Silander, 1991).

Table 4.1. Inputs and outputs of LandBaSE-P pertaining to the key ecological processes affecting *Puya hamata* population dymanics at the landscape scale and potentially subject to fires.

Processes	Inputs	Outputs
Landscape	Landscape dimensions Cell size	
Burning	Fuel accumulation per year Fuel ignition threshold Fire start probability Fire spread probability Time interval for calculation and reporting	Number of cells burned Number of cells in categories of fuel accumulation
Demography	Initial number of plants Initial age of plants Age at death (± *s*) Mortality rate (with fire) Mortality rate (without fire) Time interval for reporting	Number of plants in each age category at each time interval Coordinates of each plant in the landscape Coordinates of each flowering plant in the landscape
Pollination	Initial number of inflorescences Flowering season (start and end dates) Number of inflorescences Number of flowers per inflorescence Flower longevity Flower pollination probability Maximum pollination distance Flower mortality rate (with fire)	Number of inflorescences
Seed production	Number of seeds produced per flower Proportion of flowers producing seeds Seed longevity (± s) Time interval for calculation and reporting	Number of seeds at each time interval
Seed dispersal	Initial number of seeds for dispersal Seed dispersal kernel descriptors (x_{max}, x_{min} and α) Mortality of seeds (with fire) Time interval for calculation	
Seed germination	Fuel threshold defining “open” v “closed” vegetation Germination probability (“closed” vegetation) Germination probability (“open” vegetation) Time interval for calculation and reporting	

Figure 4.2. Input parameter entry screens for LandBaSE-P. Top left, landscape and fire regime parameters. Top right, seed and germination parameters. Bottom left, aspects of plant demography. Bottom right, aspects of flowering.



a)

Parameter set name: Defaults
Notes: Start up parameter set
Landscape dimensions: 1000 X 1000 Metres
Patch size (side): 20 Metres
Fuel accumulation per year: 50 Arbitrary units
Ignition Threshold: 1000
Germination Threshold: 500
Fire start prob 1 in: 5000 Per km2 per year
Fire spread prob %: 5.0
Time step: 2 Months

b)

Parameter set name: Defaults
Notes: Start up parameter set
Seed longevity: 5 Months
Longevity SD: 1.0
Dispersal parameters: 1.0 2.0 50.0
Germination prob (Unburnt) 1 in: 750
Germination prob (Burnt) 1 in: 10
Fire death prob %: 50.0
Time step: 2 Months

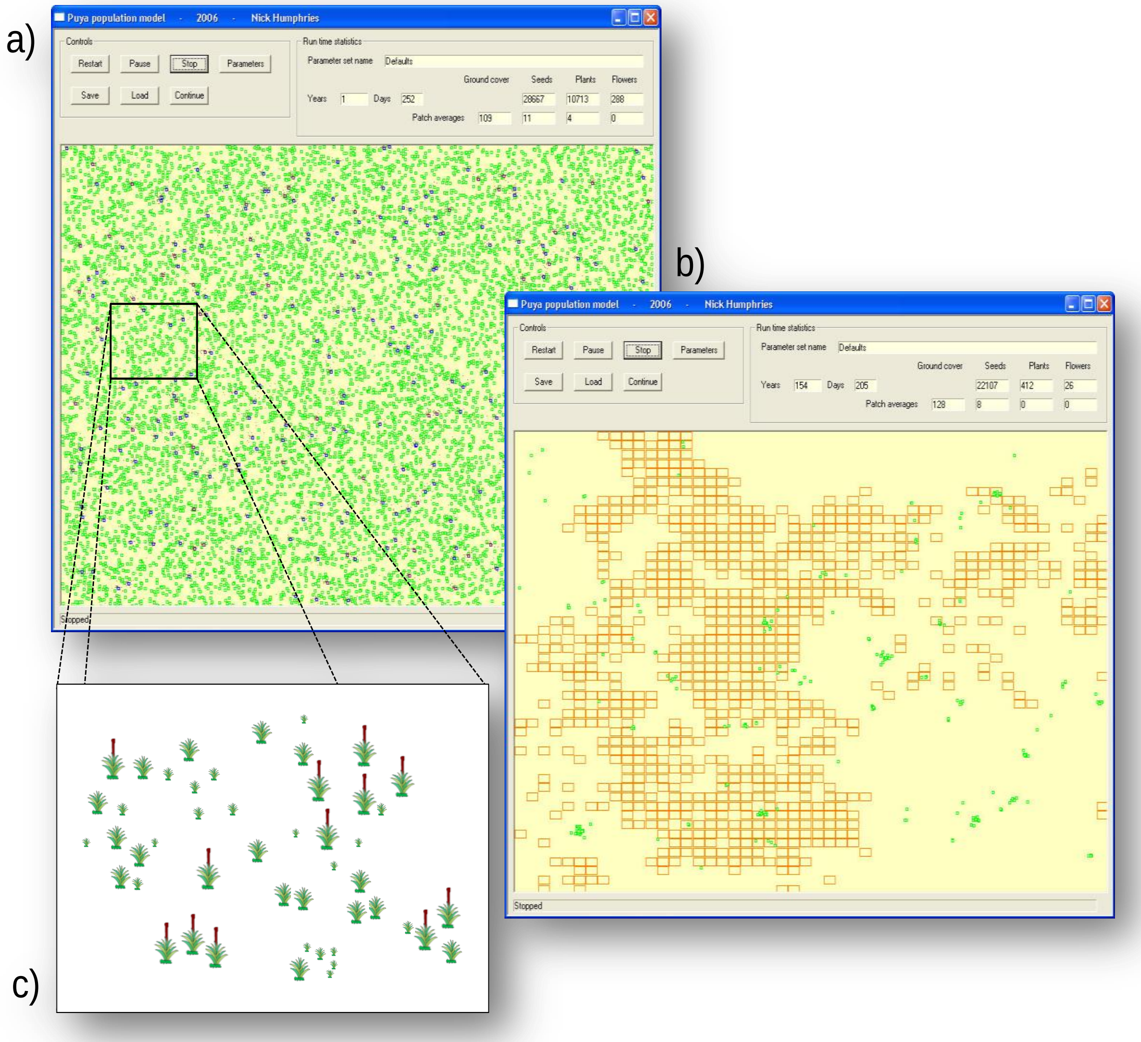
c)

Parameter set name: Defaults
Notes: Start up parameter set
Init No of Plants: 500
Max No of Plants: 2 Per cell
Mean Maturation age: 30 Years
Maturation age SD: 0.23
Fire death prob %: 1.0
Time step: 2 Months

d)

Parameter set name: Defaults
Notes: Start up parameter set
Start of flowering season: 20 Week of the year
End of flowering season: 35
Number of flowers: 10 On each inflorescence
Flower life time: 7 Days
Number of seeds: 30 From each flower
Max Pollination distance: 500 (metres)
Pollination prob %: 10.0
Fire death prob %: 10.0
Time step: 24 Hours

Figure 4.3. Optional LandBaSE-P graphical interface during simulation. a) The representation of *Puya hamata* plants as small squares: green (non-reproductive individuals) or blue (reproductive individuals). b) Cells subject to recent fire are shown in red, and these cells switch to yellow until the canopy closes and a fire could burn again. c) Although each plant is shown identically on this screen, the model tracks each plant's size through time, as illustrated here (but not in the visual interface itself).



a)

Parameter set name: Defaults

Years: 1 Days: 252

	Ground cover	Seeds	Plants	Flowers
		28667	10713	288
Patch averages	109	11	4	0

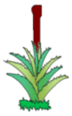
b)

Parameter set name: Defaults

Years: 154 Days: 205

	Ground cover	Seeds	Plants	Flowers
		22107	412	26
Patch averages	128	8	0	0

Table 4.2. Depiction of *Puya hamata* plants, fuel accumulation and fire spread in the LandBaSE-P model.

Plants	Stage	Representation in the program
	Reproductive plant	□
	Non-reproductive adult	□
	Young plant	□
	Seedling	□
	Seed	▪
	Cell subject to recent fire	□
	Cell with insufficient fuel to burn	□

Testing the early model

The systematic testing of models is an intensive process (Loehle, 1997), but it can be made more efficient by careful selection of test cases. Faults that would have most critical implications for the system or those that would occur most frequently can be targeted. Defects can be removed with less effort at an early stage than those found later (McGregor, 1997; McGregor, 1998; McGregor, 1999) and the model will ultimately reach a higher standard for a given effort (=cost). In addition, testing the programme guides future development by tackling practical issues such as memory management.

This section illustrates the testing and refinement of the LandBaSE-P model. It outlines some of the procedures that were used to ensure the correctness, completeness and consistency of the model, as well as explaining the balance between model complexity and practical expediency, given the computational power available.

Methods

Three evaluation criteria from McGregor (1999), plus an additional one (efficiency), were used to assess the model:

- Correctness

  A model is correct if it is judged to be equivalent to some reference standard that is assumed to be an infallible source of truth (an “oracle” in testing jargon). The standard is often a human expert and the judgement based on personal knowledge (Sargent, 2003; Suwa et al., 1984). Correctness was assessed by running the model with particular sets of parameters and evaluating the results against experience and expectation from literature and fieldwork.

- Completeness

  A model is complete if no required elements are missing. Completeness was evaluated by defining each parameter carefully, considering inter-relationships of parameters and reassessing the ecological processes incorporated into the model.

- Consistency

  A model is consistent if there are no contradictions among the elements within the model. This may be judged by searching for concepts that are represented in more than one way in the model.

- Efficiency

  The ability of the model to complete complex runs on standard PCs within acceptable time frames. In this case, about 5 h was determined to be the maximum acceptable run time.

Initially, 300 simulations were run across a range of parameters, with and without fires, and for 100 or 500 years. Initial input data were taken from available published sources, particularly Miller (1988), or from educated guesswork where published information did not exist.

Results

Although the fire spread probability worked well from the start, the fire start probability did not work correctly. This was clear from the virtual interface during simulation and from the burning summary data outputs. Once discovered, the errors in the fire module were identified and corrected. Once this part of the model had been rectified, simulated patterns of burning at the landscape scale showed the key characteristics of real-world páramo fires, such as patchiness at a variety of spatial scales, and the simulations developed the spatio-temporal burning mosaic structure that is typical in most páramo landscapes. The response of *Puya hamata* to fire within the model also matched the aggregation seen in the field (Figures 4.4–4.6).

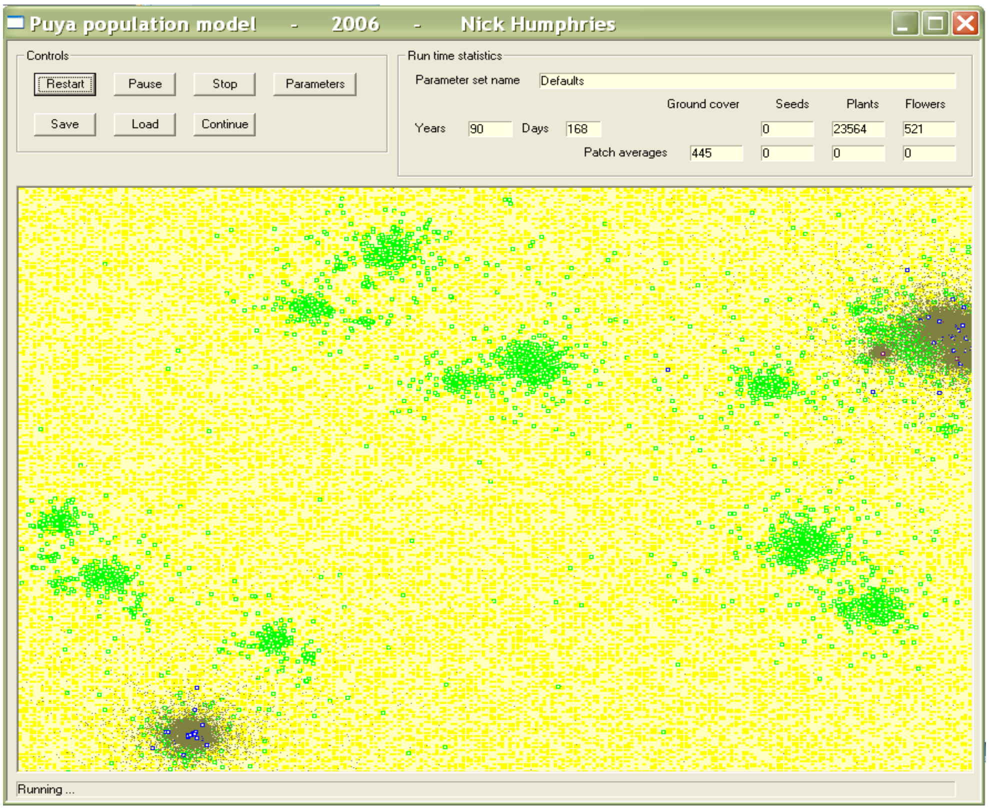
Seed dispersal was initially programmed to follow a simple decay function, with seed rain density falling quickly with distance from the parent plant. After testing, this approach was considered too unrealistic and, in its place, the truncated Pareto distribution function was inserted.

It is important to note that this testing used estimates rather than field-derived data to determine many of the parameters used. This limited the ability of the correctness testing process, and further issues became evident later (described in Chapter 9).

Only a few issues with completeness emerged from the testing. Although the model asked for a mortality rate associated with burned páramo, it assumed the mortality rate associated with densely vegetated páramo was zero. An additional parameter for the mortality rate associated with densely vegetated páramo was added.

Originally, the model kept running until it was stopped. Several stopping rules were added to the model, including a user input for a time period for the simulation. If the *Puya* population became extinct in the simulation landscape before this time, the model would also stop.

Figure 4.4. Example of the simulated pattern of *Puya hamata* plants in an unburned landscape.

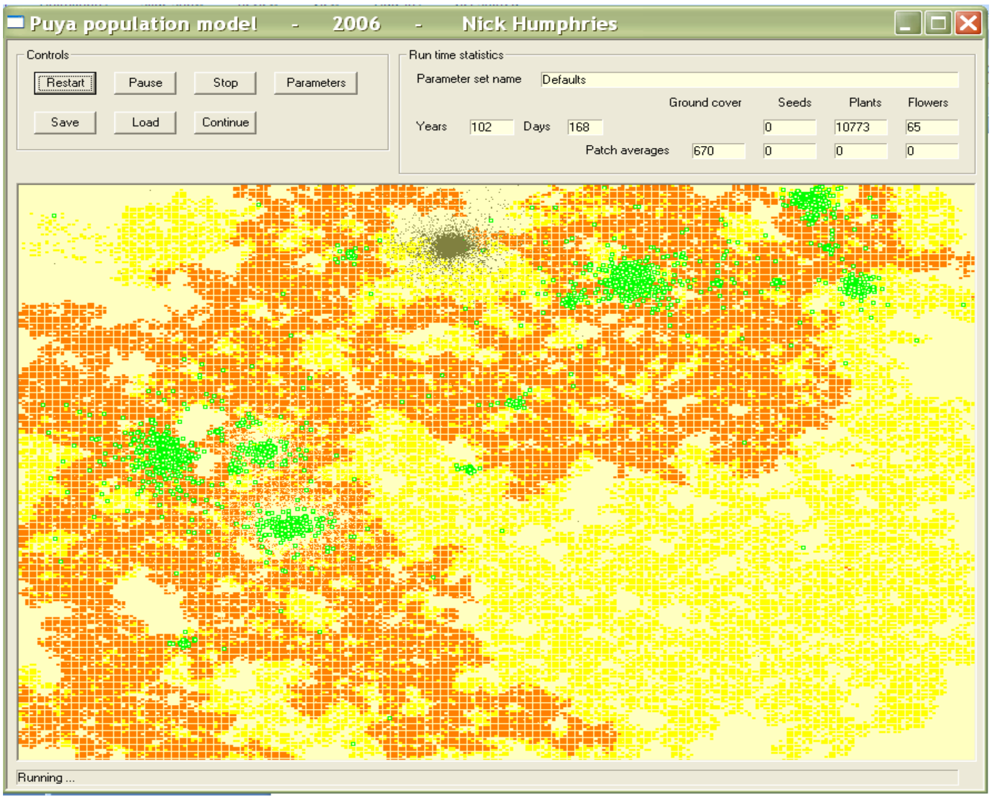


Parameter set name: Defaults

		Ground cover	Seeds	Plants	Flowers
Years 90	Days 168		0	23564	521
	Patch averages	445	0	0	0

Running ...

Figure 4.5. Example of the simulated pattern of *Puya hamata* plants in a burned landscape.

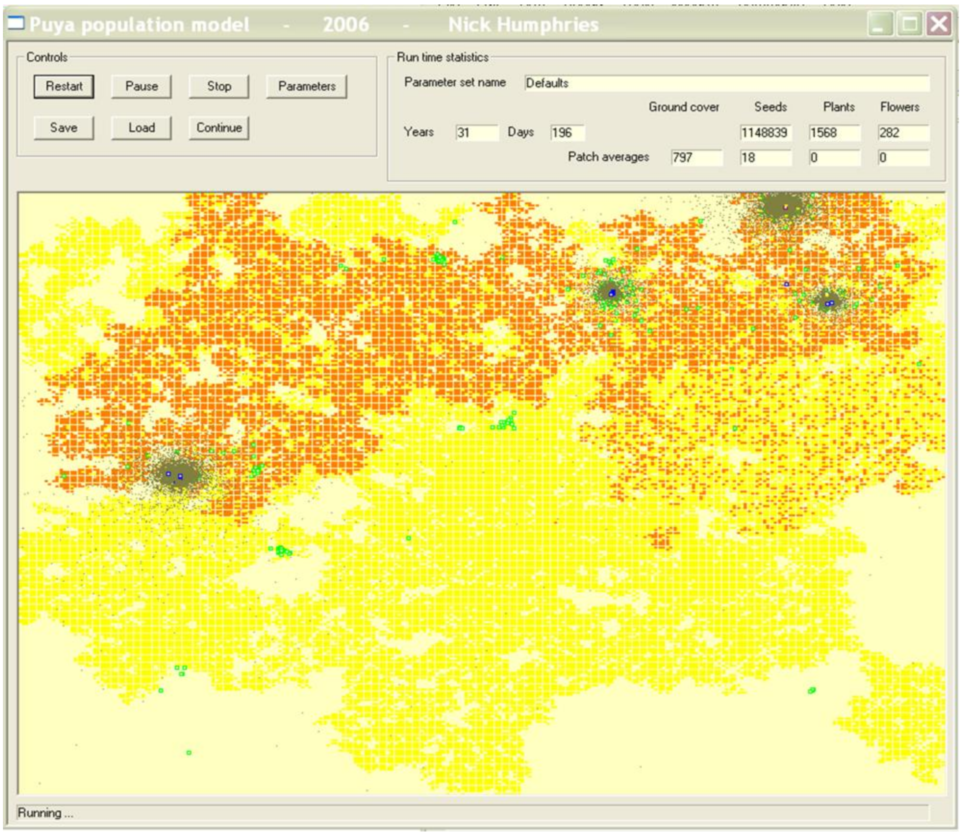


Parameter set name: Defaults

		Ground cover	Seeds	Plants	Flowers
Years 102	Days 168		0	10773	65
	Patch averages	670	0	0	0

Running ...

Figure 4.6. Two examples of simulated aggregation and patch distribution of *Puya hamata* populations in the presence of fires.

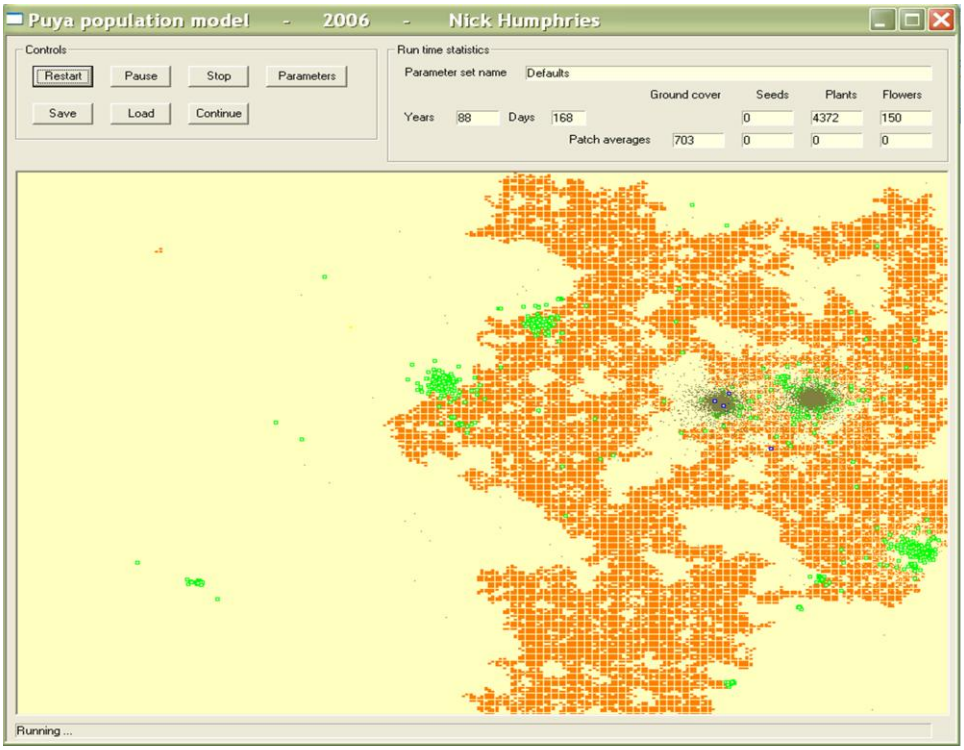


Parameter set name Defaults

Years 31 Days 196

	Ground cover	Seeds	Plants	Flowers
		1148839	1568	282
Patch averages	797	18	0	0

Running ...



Parameter set name Defaults

Years 88 Days 168

	Ground cover	Seeds	Plants	Flowers
		0	4372	150
Patch averages	703	0	0	0

Running ...

In terms of consistency, very few problems were identified. Some input field labels were not clear in the input screens, and these were changed.

Some runs took more than five hours to complete. Seed dispersal and germination, in particular, required significant computational resources—given hundreds of thousands of seeds produced by each plant. Similarly, a detailed reporting interval was used for seed production, but this level of detail was unnecessary. A more practical, longer reporting interval was used instead.

In all combinations of fire spread and start probabilities, an increase in population size was produced by the model (Figure 4.7). By contrast, the absence of fires decreased the number of individuals (Figure 4.8).

Figure 4.7. Simulated fluctuations in the number of *Puya hamata* plants over 100 hundred years in landscapes with fires.

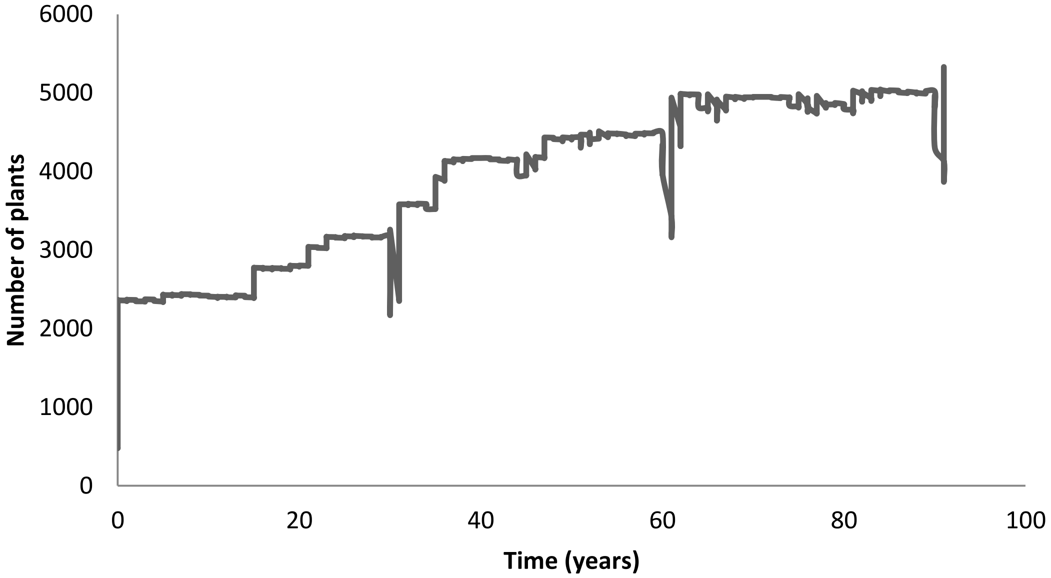
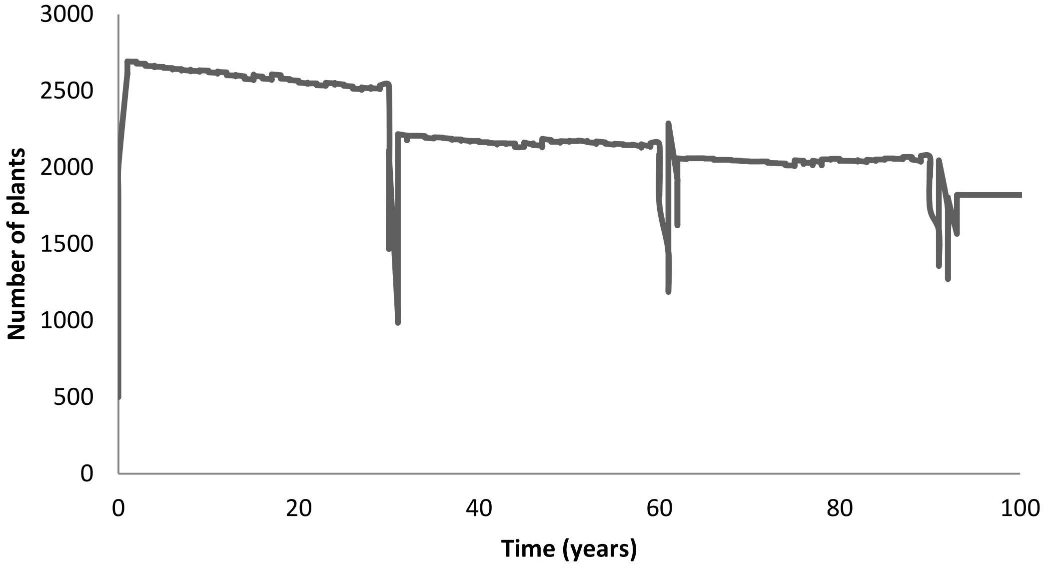
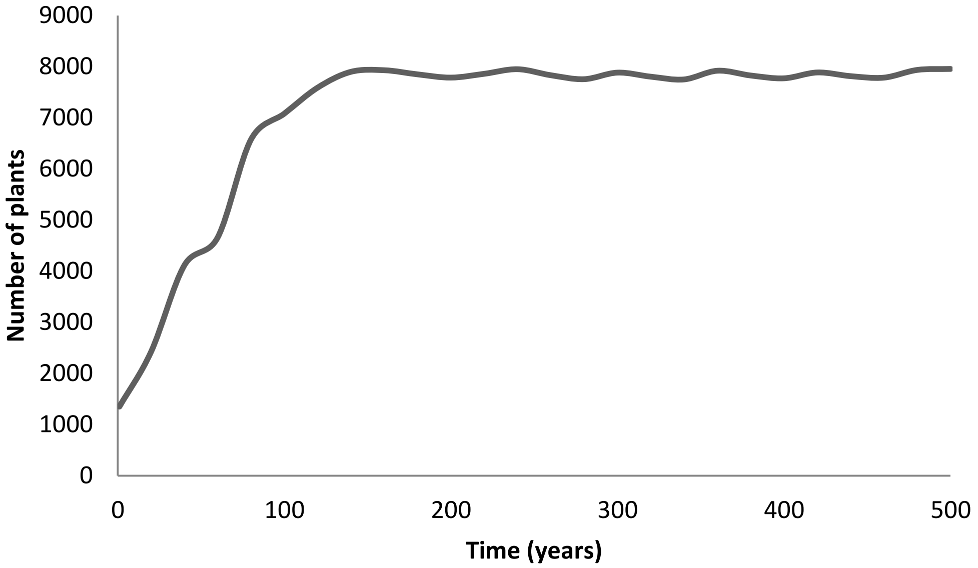


Figure 4.8. Simulated fluctuations in *Puya hamata* plant number over 100 years in landscapes without fires.



In some scenarios, stable *Puya hamata* populations resulted from the simulations, often reaching equilibrium after 100 y and maintaining population size until the simulation was halted after 500 y (Figure 4.9).

Figure 4.9. Simulated populations fluctuation in the number of *Puya hamata* plants over 500 years in landscapes with fires.



The data used in these early tests was rather unreliable. It gave a general impression of program's capabilities, running time and efficiency but, when real fieldwork data was used, several things changed and some readjustments were made as well.

The validation of the model with field data

To explore large spatio-temporal scales some readjustments were made because the number of plants found in the field was very high and the processes and values managed by the model increased when compared with our initial stable set.

Discussion

Early testing was very useful and led to significant improvements in LandBaSE-P, especially in terms of correctness, completeness and efficiency. Correctness is difficult to assess, being based mostly on subjective opinions, but nevertheless, picked up some important errors. However, some errors may still remain in the model. A few issues of completeness were corrected to ensure the model operated as intended.

Although a difficult issue to address, there are three ways to elucidate efficiency problems:

- Simplify the conceptual model: for example, some aspects of flowering phenology were greatly simplified, and the reporting intervals extended.
- Adapt the parameters entered to reduce computational load. For example, *Puya hamata* produces very large numbers of seeds but only a small proportion of these seeds germinate because the germination rate is

extremely low. The parameters can be changed to reflect this. If only 0.0001 % of 1,000,000 seeds germinated, the efficiency of the model could be increased by dispersing just 100 seeds, all of which germinate.

- Increase the computational support for the model, permitting the work to be completed more quickly. For example, the programming language could be changed to take advantage of the parallel processing abilities of most modern desktop computers. Alternatively, the hardware could be upgraded to address the problem by brute force. The use of networked computer grids might also offer some amelioration of the problems. At Plymouth University, such a network already exists: PlymGrid is the largest computational grid in UK higher education and provides a high performance computing platform from a leased fleet of over 2000 homogenous PCs. Many simultaneous runs of LandBaSE-P could be run on PlymGrid, significantly shortening the waiting time for simulation results.

By definition, early testing is based on estimates of parameter values and run at smaller scales. For this reason, it is unlikely to find problems that would appear if the parameters turned out to be very different from the original estimates, or if the simulations are carried out for finely-resolved landscape scales over long periods of time. Once all the field data had been collected and incorporated in the model, along with increased spatial and temporal scales, new problems appeared. Some of these will be discussed, in their proper context, in Chapter 9.

5

Basic phenology of *Puya hamata* and the consequences of fire-driven spatial pattern on reproductive output

Introduction

The LandBaSE-P model simulates *Puya hamata* populations at long-term, landscape-scales in a range of different land-management scenarios. In the real world, with very limited land-management scenarios present, it is not possible to assess a variety of situations by direct observation. This is the value of the modelling approach (He, 2008). However, for reliable conclusions from the model, good-quality information is needed to support the simulations (Bravo de la Parra & Poggiale, 2005).

Pollination and seed production are core components of the conceptual model for LandBaSE-P, presented in Figure 4.1. Various input parameter values are associated with these components of the model (Table 4.1), and should be based on good-quality estimates from field observations for reliable simulations. In particular, the model needs information about the timing of key reproductive phases (*i.e.,* seed production), estimates of reproductive outputs (*i.e.,* seed numbers), and estimates of variability from plant to plant.

The timings and durations of key reproductive phases are important because it may be important for different *Puya hamata* plants to synchronise their flowering to maximise cross-pollination by hummingbirds. These birds can visit several different species of food plant, but may specialise on certain plants during their flowering period. For example, there is evidence that the Shining Sunbeam (*Aglaeactis cupripennis*) migrates upwards from cloud forest to set up territories around dense patches of *Puya hamata* plants during synchronised flowering (Woods & Ramsay, 2001).

Only a proportion of *Puya hamata* plants in the landscape flower at any one time. An estimate of the density of these flowering individuals would be useful to set initial population size and to validate the outcomes from simulations (where simulated patterns match real-world observations). The numbers of flowers, fruits and seeds are also key parameters at the start of simulations, as are estimates of fruit- and seed-set. The numbers of inflorescences, flowers, fruits and seeds influence important ecological processes such as pollinator behaviour, pollination success and seed dispersal (Ghazoul & Shaanker, 2004).

There are several studies on phenology and reproductive output for other *Puya* species (Chaparro-Mendivelso & Mora-Ardila, 2003; Varadarajan, 1990). It is clear that these species are not identical in their phenologies and one cannot extrapolate from one species of *Puya* to another. Miller (1988) published some limited information on the phenology and numbers of flowers for *Puya hamata* from a single low-elevation 100 m^2 plot in El Ángel from 1984–86. Flowers were open from May–July and, on average, numbered 971 flowers per plant, with seeds developing from August–October. Miller (1988) noted that floral display was delayed in plants at higher altitudes. No other information has been published on the phenology or reproductive output of *Puya hamata*. Since phenological patterns vary regionally and altitudinally in the páramo, data from appropriate altitudes in the REEA is required for the model's study (Miller's study area is too small to be reliable for this work).

Another potential source of variability in reproductive output is the spatial patterns of plants that result from páramo fires. It appears that germination rates of *Puya hamata* are considerably higher after fires have removed dense vegetation (Lægaard, 1992). Since *Puya* plants tend to deposit their seeds close to the parent plant (Benzing, 2000; Miller, 1988), dense patches of young *Puya* plants sometimes appear within a few years of burning, if a reproductive adult was present at the time of the fire (pers. obs.). Subsequent low mortality rates mean that, years later, a dense patch of flowering *Puya* plants results. In fact, fire mosaics at the landscape scale can produce a range of *Puya* spatial contexts, from isolated individuals, through small patches with 4–10 plants, to large patches with more than 100 individuals in close proximity (pers. obs.).

The consequences of these fire-driven patterns for *Puya* reproductive output are uncertain. Several possibilities exist:

- High-density patches of mature plants could decrease reproductive output (Gunton & Kunin, 2009; Harper, 1977; Weiner, 1988). Resource availability for *Puya* plants in these patches could be low as a result of intraspecific competition. Thus isolated plants might be predicted to have more resources to invest in reproduction than plants in dense groups.
- High-density patches of mature plants could decrease seed viability. Dense floral displays of *Puya* are attractive to pollinating hummingbirds. Typical pollinated by trap-lining behaviours of páramo hummingbirds (*e.g.,* the Chimborazo Hillstar, *Oreotrochilus estella*) have been replaced by territorial behaviour of lower altitude species (*e.g.,* the Shining Sunbeam, *Aglaeactis cupripennis*) where dense inflorescences are found (Woods & Ramsay, 2001).

> Isolated plants might receive lower visitor rates, but have higher levels of cross-pollination (Mustajärvi *et al.*, 2001), seed set and seed viability, compared with plants in dense groups, especially those in the centre of large patches.

There are published studies that have investigated the consequences of spatial pattern on reproductive output (Dauber *et al.*, 2010; Tirado & Pugnaire, 2003; Vesk *et al.*, 2010; Weiner, 1988) but, particularly for *Puya,* these kinds of studies are scarce.

The aim of this chapter is to describe basic floral phenology for *Puya hamata*, both for a better understanding of *Puya* ecology, and more specifically to provide estimates of key parameters needed for the LandBaSE-P model. Additionally, the effect of spatial context on reproductive output of *Puya hamata* is assessed.

Methods

In 2008, the density of *Puya* inflorescences in the landscape was estimated using four belt transects within the REEA. The belt-transects were all the same width (40 m) but had different lengths (4500, 1280, 247 and 80 m), representing relatively consistent parts of the landscape mosaic. The dimensions of each transect were measured and delimited with the aid of maps and GPS coordinates (using a Garmin GPS Map 60Cx unit). Within each transect, immature, mature, and dead inflorescences of *Puya hamata* were counted separately.

The inflorescence and flower morphology of *Puya hamata* is shown in Figure 5.1. *Puya hamata* flower production and longevity were recorded in 2008 for three randomly-chosen inflorescences at 3785, 3786 and 3710 m located in the REEA

(UTM coordinates of 18 N 179910 75812, 18 N 179918 75817 and 18 N 180349 75242). Flower longevity was recorded from the date of opening of the first flower to the date of closing of the last flower on the entire inflorescence. The number of open flowers was estimated every 14 days throughout each inflorescence's lifetime using high-resolution photographs. Only one side of each inflorescence was photographed at each date (*e.g.,* Figure 5.1b) and the number of open flowers were counted, and doubled to give an overall estimate of total flower number. Only flowers in profile on the right-hand side of each inflorescence were included to avoid overestimation of the total number.

Ten flowers from each of the same three inflorescences were marked and their longevities recorded, as well as their corolla length (see Figure 5.1c). Nectar samples were taken from ten flowers from each of five other randomly-chosen inflorescences in the same area. First, the flowers were emptied at dusk using 0.5 mm diameter capillary tubes, and the entire inflorescence of each plant was covered with fine netting to prevent the removal of nectar by hummingbirds during the subsequent 24 h period. At the end of this period, all nectar was removed with capillary tubes. The sugar concentration (%) was measured with a Bellingham & Stanley Eclipse 0-50% hand-held sucrose refractometer. *Puya hamata* belongs to the sub-genus *Puyopsis,* a group in which the nectar is dominated by sucrose (Scogin & Freeman, 1984 cited in Baker *et al.*, 1998). Nectar volume was calculated from the height of nectar extracted in the capillary tube. Sugar mass was calculated from nectar volumes and concentrations, assuming a density of sucrose at 15°C of 1.0823 according to Dafni's (1992) formula:

$$\text{sugar mass (mg)} = \frac{\%\ \text{sugar}}{100} \times \text{volume } (\mu\text{l}) \times 1.0823$$

The reproductive output of *Puya hamata* was recorded over two periods from July to November in 2008 and 2009. Five different spatial contexts for reproductive *Puya* plants were chosen as treatments for this study:

- Isolated plants (I) were single plants with no other reproductive individuals within a 50 m radius surrounding them.
- Plants on the edge of a small group (SE) were plants located on the periphery of a group of approximately 20 reproductive individuals.
- Plants in the centre of a small group (SC) were plants located in the centre of a group of approximately 20 reproductive individuals.
- Plants on the edge of a large group (LE) were plants located on the periphery of a group of approximately 100 reproductive individuals.
- Plants in the centre of a large group (LC) were plants located in the centre of a group of approximately 100 reproductive individuals.

Eight reproductive plants in each treatment were selected at random from randomly-chosen groups of appropriate sizes in the south-eastern part of the REEA. For each plant, rosette diameter, total plant height and flowering inflorescence length were recorded.

The total numbers of flowers and fruits produced by each of these 40 plants were counted. Ten unopened, but ripe, fruits were selected at random from each plant and the seeds inside were counted. These fruits were assumed to be typical of all fruits on each plant, and the total seed production was estimated.

For the seed viability trials, seeds were randomly selected in 2009 from the five spatial context treatments as shown in Table 5.1. In total, 300 seeds were used. The viability of seeds was assessed using the tetrazolium test (Bedell, 1999). Seeds were soaked in water for 16 h to make them easy to dissect and to facilitate staining by tetrazolium chloride. Vadillo (2004) showed 16 h is the maximum imbibition time for seeds. Then, a small cut was made in each seed coat, near the radical, and the seeds were immersed in a 0.1% solution of 2,3,5-triphenyl-2H-tetrazolium chloride (TTC). Next, seeds were placed in individual plastic containers, which were then wrapped with two layers of aluminium foil and incubated at room temperatures for another 16 h. At the end of this incubation period, seeds were cut lengthwise to evaluate the staining of the embryos. If the embryo was viable it turned red or pink due to the production of hydrogen ions during respiration. Non-viable seeds did not turn red or pink (Figure 5.2).

In July–October 2009, 400 *Puya hamata* fruits were collected from the same plants used for the seed viability trials, representing the five different spatial aggregation contexts. Ten fruits from each of eight reproductive plants in each treatment were selected at random. The seeds were extracted, cleaned, stored in paper bags, and transported to the University of Plymouth, were they were kept at room temperature until germination trials were carried out in the laboratory from January to June 2010.

A random sample of 100 seeds was taken from each of the seed sources described in Table 5.1 and transported to the University of Plymouth and stored in the same way as the seeds for the viability trials. The seeds were sown onto 0.8% water agar in 9 cm diameter, sterilized Petri dishes. The agar was used because of its moisture retention capacity (Ellis *et al.*, 1985), and was autoclaved at 120 ºC for 15 minutes before use (Fuller & Fuller, 1995). Twenty seeds were distributed evenly across the surface of each dish with sterilized pincers. Five dishes (100 seeds) were used for each spatial treatment.

Light conditions for germination were selected based on conditions of tropical environments that are remarkably constant (Sarmiento, 1986). The annual range of daily solar radiation at latitude 0° slightly varies from 930-820 cal/cm^2/day (Sarmiento, 1986) or 10,000–25,000 lux. Day/night length is approximately 12/12 hours at the Equator. Humidity varies through the year, but to make this experiment simpler, only light and temperature were considered. Temperature was set based on previous Bromeliad optimal germination trials (Benzing, 2000). The germination trials were performed in a Sanyo MRL-350 temperature-controlled growth cabinet at 20 °C with cool white fluorescent lighting from 15 bulbs of 40-W each (20,000 lux) in a 12 h light/12 h dark photoperiod. All trials were run until no seeds germinated for a period of 72 h after germination had begun.

ANOVA and Tukey post hoc tests were carried out using STATISTICA 6 (StatSoft Inc, 2003). A manual *G*-test was calculated to compare the percentages of viable seeds from plants in different spatial contexts.

Figure 5.1. Morphological characteristics of *Puya hamata*: a) growth form, b) an inflorescence with open flowers, and c) a dissected flower.

Table 5.1. Summary of the numbers and sources of seeds used in the viability and germination trials for *Puya hamata*.

Spatial contexts	No of seed-donor plants	No of seeds (viability)	No of seeds (germination)
Isolated (I)	3	100	100
Plants on the edge of a small patch (SE)	2	40	100
Plants in the centre of a small patch (SC)	3	60	100
Plants on the edge of a large patch (LE)	3	60	100
Plants in the centre of a large patch (LC)	2	40	100

Figure 5.2. Evaluation of *Puya hamata* seed viability with the tetrazolium chloride method: a) seed with embryo not stained (not viable), b) seed with stained embryo (viable).

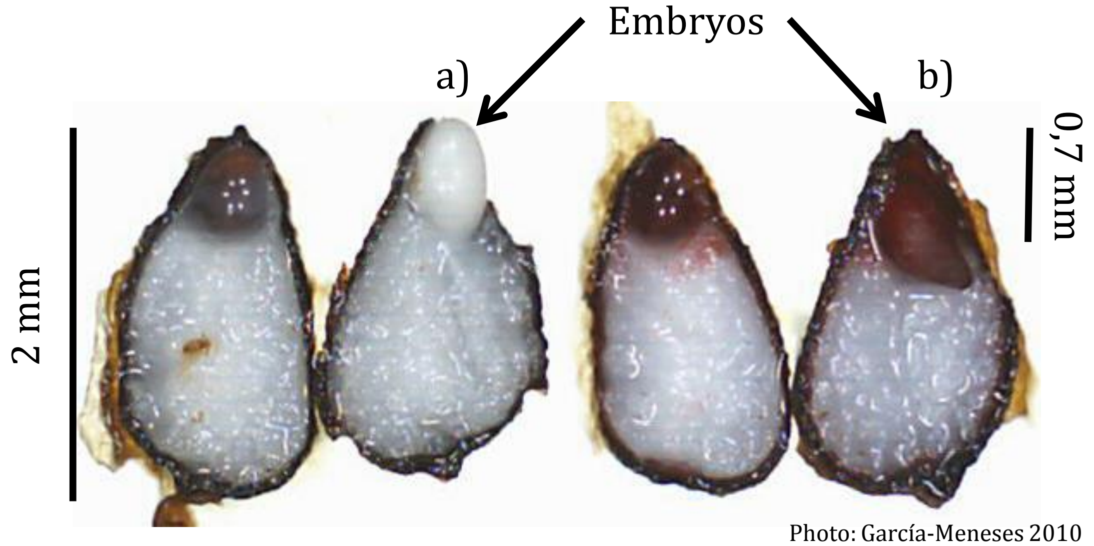


Photo: García-Meneses 2010

Results

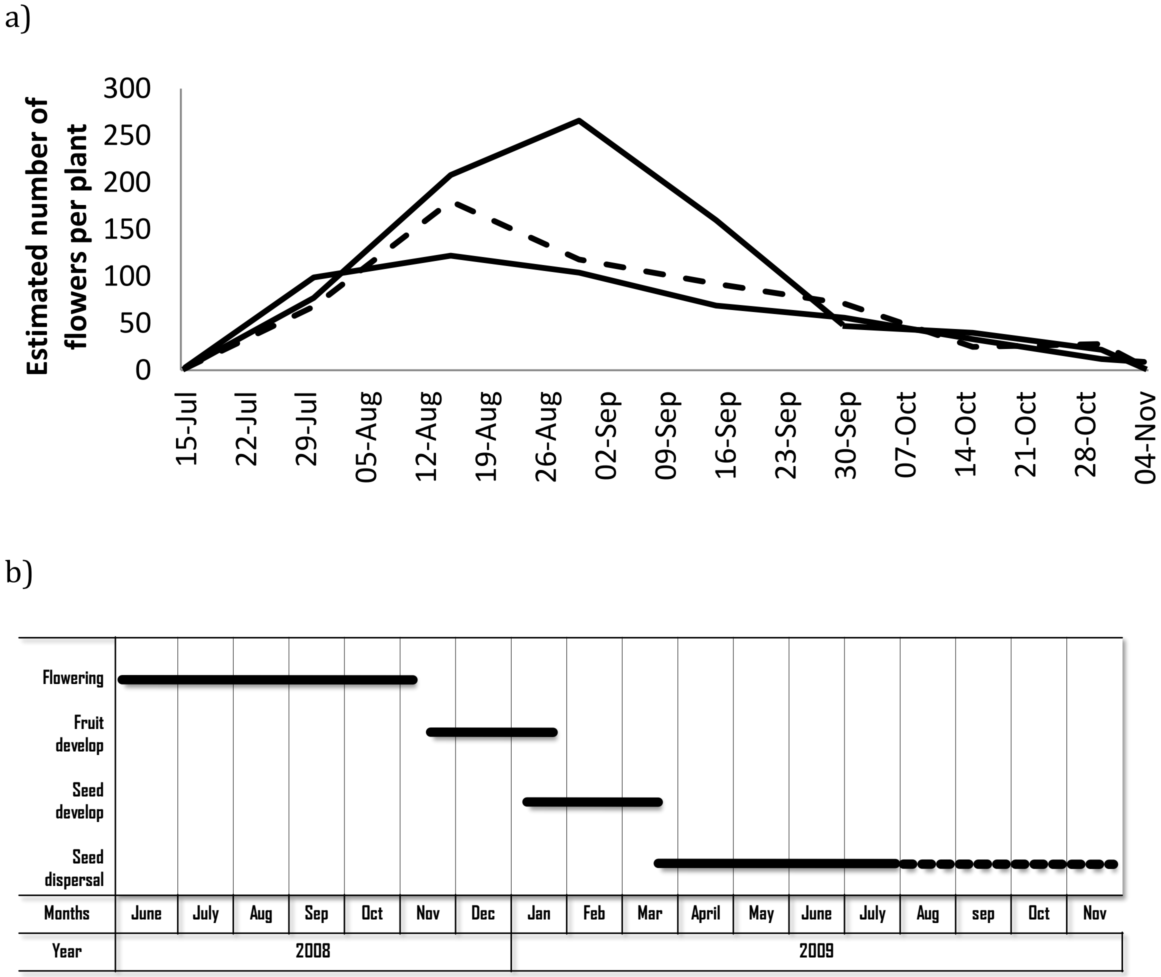
On average, about 20 *Puya hamata* plants ha^{-1} were found in the study areas, but varied considerably from place to place (Table 5.2). Locally, within part of one transect, plant density reached 480 plants ha^{-1}.

Puya hamata flowers are actinomorphic and with pubescent, pale-green sepals and blue petals. Mean corolla length was 69.6± 2.57 (*s*) mm (*n*=30). Mean flowering duration was 106.6 days per plant. Flowers were not produced evenly throughout this period and peak flowering, the highest number of open flowers on an inflorescence at one time, occurred from August to September (Figure 5.3a). The number of open flowers at peak flowering varied considerably from plant to plant ($\bar{X}$ =639.7, s=164.7, n=3). Flower longevity was relatively consistent ($\bar{X}$ =4.3 d, s=0.3 d, n=30). Fruiting duration was approximately two months and seed dispersal only occurred when all fruits on the inflorescence were mature. Seed dispersal occurred over six months, but some individuals continued to spread seeds for longer periods (Figure 5.3b).

Table 5.2. Density of *Puya hamata* plants with inflorescences from four large 40 m-wide belt transect surveys of different areas.

Survey area (ha)	**Altitude (m)**	**Number of immature inflorescences (ha^{-1})**	**Number of mature inflorescences (ha^{-1})**	**Number of dead inflorescences (ha^{-1})**	**Total of inflorescences (ha^{-1})**
18.00	3540–3700	8.44	22.39	21.22	52.06
5.12	3625	1.37	3.91	3.13	8.40
0.99	3620	6.06	8.08	1.01	15.15
0.36	3628	0	133.33	2.78	136.11
Overall					
24.47	3600	6.74	19.62	16.33	42.70

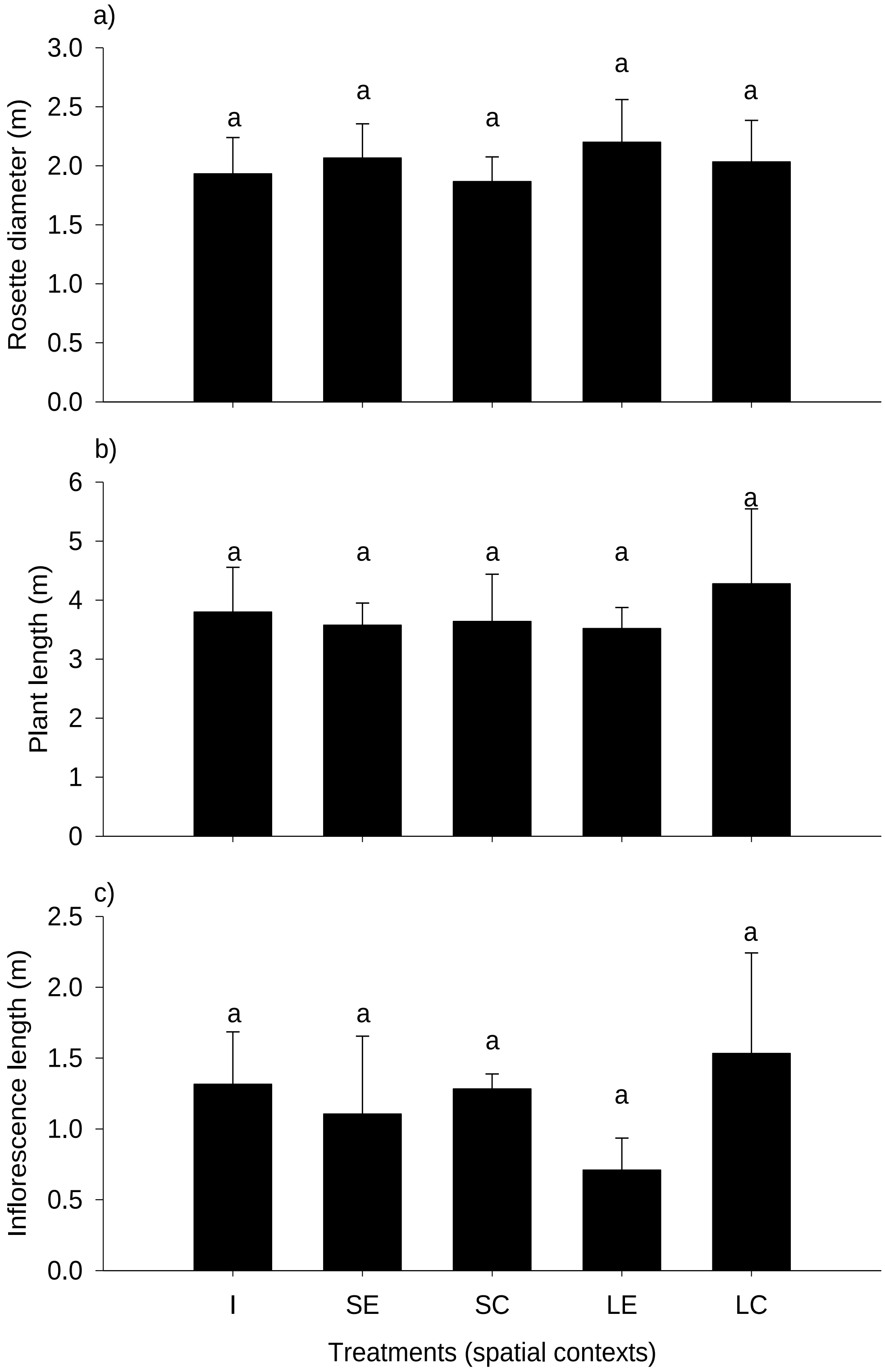
Figure 5.3. a) Number of flowers during flowering period at 14-day intervals for three different *Puya hamata* plants from July to November 2008. b) Summary of flowering, fruiting, seed development and seed dispersal of three *Puya hamata* inflorescences.



Nectar accumulated at the base of the corolla of each flower, and was accessed by hummingbirds through narrow passages between the filaments. Nectar volume, concentration, and sugar mass varied highly between flowers. Mean nectar volume was 5.01±6.34 (s) µl. Mean nectar concentration was 17.85 ± 9.38 (s) % and sugar mass was 1.74±1.66 (s) mg.

There were no significant differences in three components of plant size between the five spatial context treatments: rosette diameter (ANOVA: $F_{4,35}$ =0.883, p=0.484), total plant length (ANOVA: $F_{4,35}$=0.7352, p=0.5742) and flowering inflorescence length (ANOVA: $F_{4,395}$= 1.273, p=0.2291) (Figure 5.4a-c).

Figure 5.4. Rosette diameter, total plant length, and flowering inflorescence length in eight *Puya hamata* plants in each of five spatial context treatments. The five spatial context treatments were isolated (I), edge of a small group (SE), centre of a small group (SC), edge of a large group (LE), and centre of a large group (LC). Error bars represent standard deviation.



Basic measures of reproductive output were relatively variable and not statistically different between the five spatial contexts (Figure 5.5a–c): number of flowers (ANOVA: $F_{4,35}$=0.90102, p=0.47391), number of fruits (ANOVA: $F_{4,35}$=1.1816, p=0.33585), and number of seeds per fruit (ANOVA: $F_{4,35}$=0.680, p=0.610). In summary, then, *Puya hamata* plants produced a mean number of 1030 flowers and 840 fruits per inflorescence, each fruit containing a mean of 812 seeds. 81.5 % of flowers developed into fruits. Overall, mean seed production was 682,080 seeds per plant.

Plants at the edges and centres of small groups of *Puya* had a higher proportion of viable seeds than plants in other spatial contexts, and plants in the centre of large patches had the lowest proportion of viable seeds (G_4=28.88, p<0.0001, Figure 5.5d). The germination trials of *Puya hamata* seeds at 20 °C in full light showed that plants in the centre of small patches had the highest germination success, and plants in the centre of large patches had the lowest (G=48.1, p<0.00001), Figure 5.5e).

Using mean values for the number of fruits produced, number of seeds per fruit, seed viability and seed germination success, estimates were made for the number of seeds produced by a complete inflorescence, the number of viable seeds produced per plant, and the number of seeds produced that would germinate at 20 °C in full light (Figure 5.6). In terms of crude seed production, the output of isolated plants was higher than those in the other treatments. However, taking into account viability and germination, the number of effective seeds was highest in isolated plants and those at the edge of small groups. The lowest effective seed output was by plants in the centre of large groups.

Figure 5.5. Reproductive output of *Puya hamata* plants in five spatial contexts: a) number of flowers, b) number of fruits, c) number of seeds per fruit, d) percentage of viable seeds, and e) percentage of germinated seeds at 20 ºC in full light (from Chapter 7).The five spatial context treatments were isolated (I), edge of a small group (SE), centre of a small group (SC), edge of a large group (LE), and centre of a large group (LC).Error bars represent standard deviation. Means sharing a letter were not separated by a Tukey comparison of means test, or in the case of d) and e) by paired G-tests.

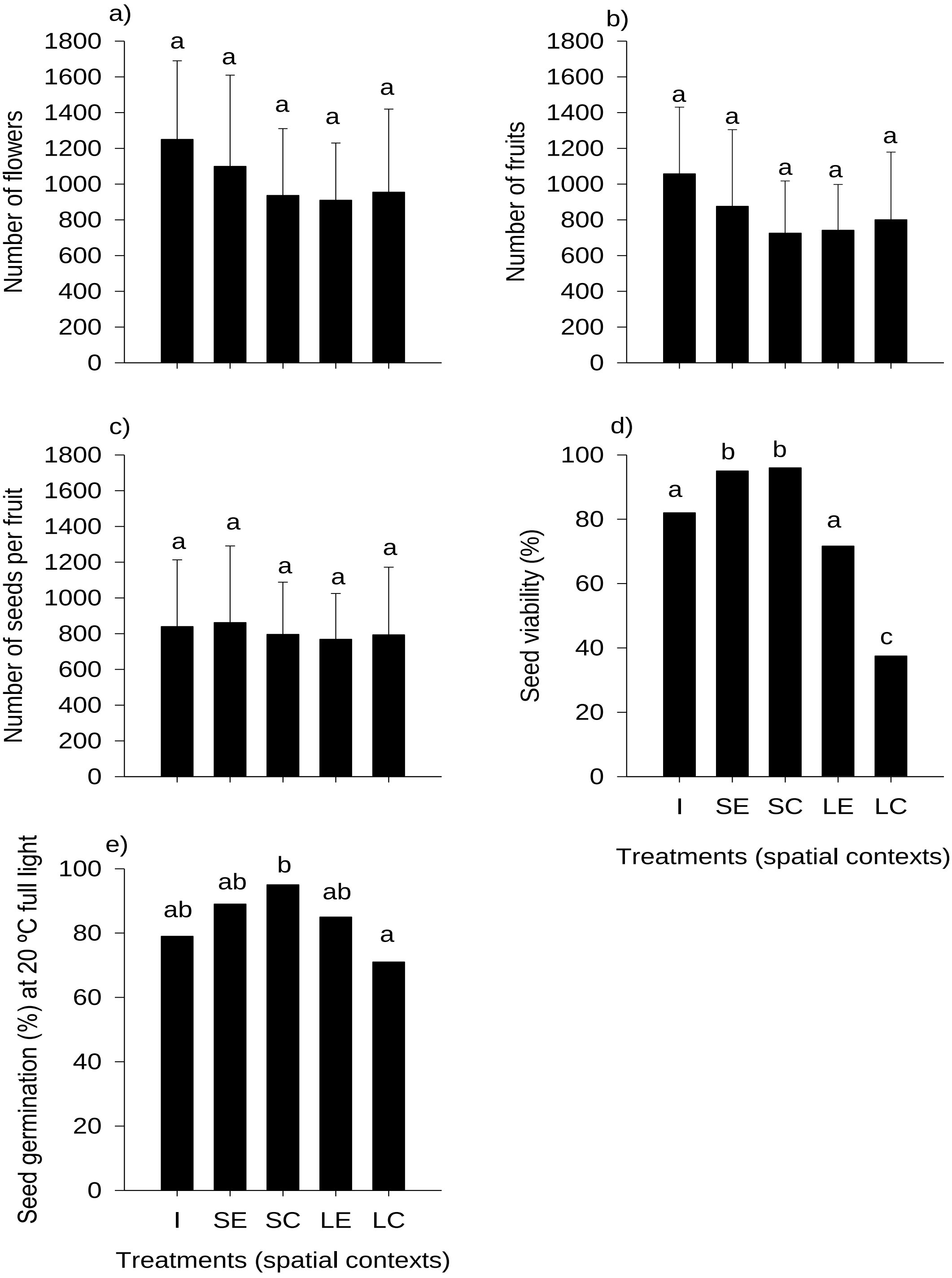
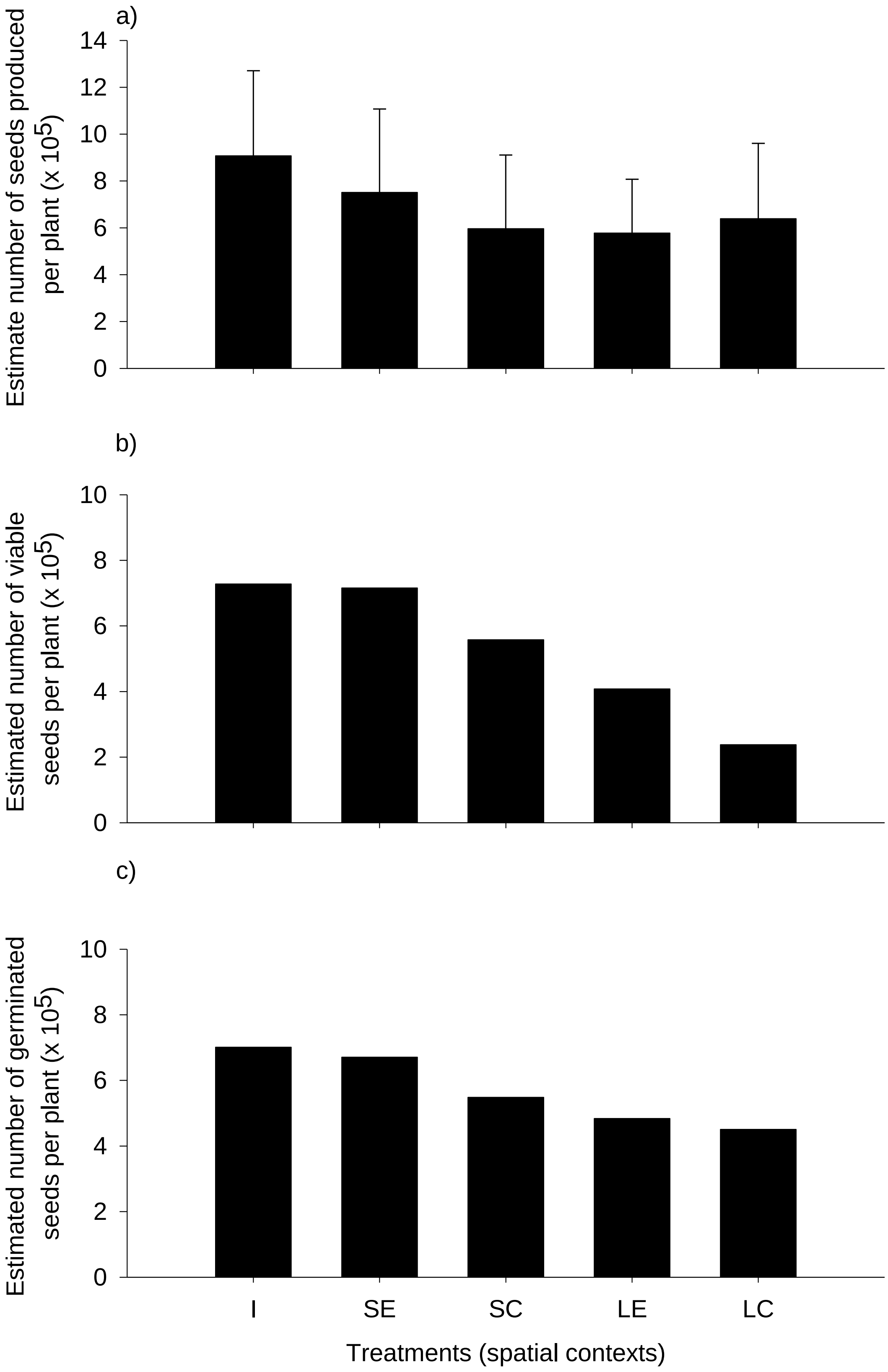


Figure 5.6. a) Estimated number of seeds produced per plant in five different spatial contexts. b) Estimated number of viable seeds per plant, using seed production and seed viability estimates. c) Estimated number of germinated seeds per plant at 20 °C in full light, using seed production and germination estimates.



Discussion

The density of reproductive *Puya* plants in the landscape varied by several orders of magnitude, from less than four inflorescences ha^{-1} to a localised peak of 480 inflorescences ha^{-1}. This difference in density is consistent with a fire-driven model of *Puya* population dynamics in a landscape mosaic subjected to regular burning (and is investigated further in Chapters 8 and 9). Furthermore, *Puya* plants were aggregated in groups of similar-sized plants, supposed to be mostly sibling plants that germinated synchronously as a cohort soon after a fire. These aggregations existed in a range of sizes from 2–5 plants to large groups of more than one hundred individuals in close proximity (pers. obs.).

Puya hamata flowers are bird-pollinated (Benzing, 2000), and their dense inflorescences of many flowers, blue-coloured petals, odourless flowers with long tubes, nectar volumes and sugar concentrations are all typical of the ornithophilous syndrome (Buzato *et al.*, 2000; Faegri & van der Pijl, 1971; Hanley *et al.*, 2009; Sazima *et al.*, 1996).

Nectar, as an attractant to bird pollinators, was rationed by a staggered turnover of flowers. Each *Puya hamata* flower lasted little more than 4 d, similar to that reported for *Puya clava-herculis* by Miller (1988). However, the turnover of hundreds of flowers extended the flowering period to from July to November, with a peak in numbers from August to September. These timings did not correspond with Miller's (1988) work in the same area, where *Puya hamata* displayed flowers from May to July and seeds developed during August-October. But, his plants were growing approximately 300–350 m lower at 3415 m and Miller (1988) recognized that flowering periods for both *P. hamata* and *P. clava-herculis* were delayed at higher altitudes. Comparing the two studies, flowering, seed development and seed dispersal for *Puya hamata* plants in our study at 3760 m is delayed almost three months compared with Miller's plants at 3415 m. Some caution is required here, though, since the studies were carried out in different years. Flowering and seeding periods of four *Puya* species (*Puya cryptantha*, *Puya trianae*, *Puya nitida* and *Puya goudotiana)* in the páramo of Palacio in Chingaza National Park, Colombia, occupy different altitudinal levels, and show similar inter-specific delays in phenology for higher-altitude species (Chaparro-Mendivelso & Mora-Ardila, 2003), potentially evolved for avoidance of competition for pollinators and reduction of hybridization (Fagua, 2002; Rathcke & Lacey, 1985).

Nectar for bird pollinators has low sugar concentration but high liquid volume (0.74–26.9 µl flower^{-1}d^{-1}), providing both energy and water at the same time (Arizmendi & Ornelas, 1990; Escobedo-Sarti, 2007; Pyke & Waser, 1981), both important to high-altitude hummingbirds (Salinas et al., 2007). Miller (1988) reported an increase in nectar volume and a decrease in sugar concentration for *Puya* species at higher altitudes. Preliminary experiments for *Puya raimondii* in Peru, 30.5–80.0 µl of nectar was measured in three plants at 6,000 m in Huascarán Park, but only 15.0–30.0 µl in a plant at 3,600–4,100 m in Canchayllo (Hornung-Leoni et al., 2007).

The results presented in the current study are consistent with nectar volumes and sugar mass for *Puya hamata* flowers in the páramo at 3,600 m on nearby Volcán Chiles; but 50% more nectar volume (mean 10.8 µl d^{-1}) was recorded for the Volcán Chiles plants (Woods & Ramsay, 2001), even though they were growing at lower altitudes. However, in our study, nectar was removed only once in 24 hours, compared with hourly removal for the Volcán Chiles flowers. Nectar removal by birds (or investigators) is well-known to promote higher volumes of more dilute nectar (Castellanos *et al.*, 2002).

Nectar provision for pollinators is relatively costly, especially considering potential inter- and intra-specific competition for pollinators (Reekie & Bazzaz, 2005). The semelparous strategy of *Puya hamata* enables individual plants to offer large rewards over relatively short periods of time—as a significant reward for pollinating birds. Interestingly, this strategy is common in similar tropical alpine environments, *e.g.,Lobelia* (Young, 1984) and other challenging environments like deserts, *e.g., Yucca, Agave* (Arizaga et al., 2000). This "big-bang" flowering strategy (Gentry, 1976) is confirmed by a mean of 1030 flowers per plant during the lifetime of the inflorescence, and similar to the numbers reported by Miller (1988) for the same species in the same area, but at lower altitudes ($\bar{X}$=971.4 ± s=286.8). The display of flowers on tall inflorescences is part of the cost associated with hummingbird pollination, and height enhances pollinator attraction (Ramirez & Berry, 1995; Sargent et al., 2007; Stiles, 1976) and seed production (Harper, 1977; Harper, 2010). In the study area, mean inflorescence height of *Puya hamata* was 3.86 m, making the floral displays conspicuous from distance.

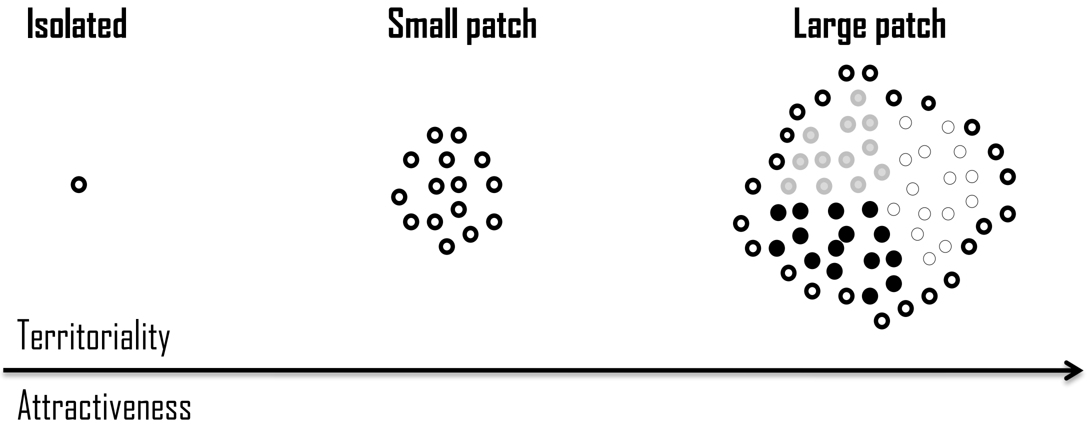
The attractiveness to pollinators of a display of numerous flowers on a single plant can be raised if several inflorescences are aggregated together. Pollinators spend longer and visit more flowers in large patches (Brody & Mitchell, 1997). Before the arrival of people, *Puya* inflorescences were probably scattered around the densely-vegetated landscape as isolated individuals or small groups. Typically, cross-pollination would have been carried out by co-evolved foraging of trap-lining hummingbirds. With the introduction of regular burning, larger aggregations of *Puya hamata* plants are likely to have formed, since the population of this species is promoted by burning (Lægaard, 1992; Miller & Silander, 1991). Therefore, in burned páramo landscapes, groups of *Puya* plants represent more valuable and attractive rewards for pollinators than single, isolated plants. If the resource is large enough, territoriality might be the favoured strategy of hummingbirds rather than trap-lining (Linhart, 1973).

Woods & Ramsay (2001) found eight species of hummingbird in Volcán Chiles (near to the site of the current study) feeding on *Puya hamata* plants. One of these species, *Agaleactis cupripennis*, defended territories enclosing *Puya* aggregations. The others showed trap-lining behaviour (*e.g., Oreotrochilus estella, Chalcostigma herrani*) and were mostly excluded from the *Agaleactis* territories. Similarly, *Lesbia victoriae* trap-lined on Volcán Chiles (Woods & Ramsay, 2001), but has been reported to defend territories around *Puya* inflorescences on Volcán Cotopaxi (Miller, 1988).

Isolated plants would be expected to be visited by trap-lining pollinators rather than territorial ones, leading to more cross-pollination and increased seed viability (Figure 5.7). Similarly, plants on the edge of territories are more likely to be visited by trap-lining hummingbirds than ones in the middle of other birds' territories. This increases cross-pollination and increased seed viability in plants at the edges of territories. Differences in visitation rates by trap-lining species might be enhanced by plant group size: plants in the centres of larger groups might be defended more vigorously than ones in the centre of small groups. In addition, resources for *Puya* to invest in reproduction might be limited in the centre of groups because of competition with neighbouring plants, further lowering their attractiveness to potential pollinators.

Thus, *Puya hamata* plants which are isolated or on the periphery of a group might be larger, produce more flowers, fruits and seeds (with higher viability and germination success) than plants in the centres of *Puya* patches.

Figure 5.7. Potential pollination of *Puya hamata* plants in different spatial contexts. The attractiveness of nectar resources, and therefore the likelihood of territoriality, increases with plant group size. Plants on the edge of a patch are more likely to be visited by trap-lining birds, even if defended by territorial birds. Bold open circles (○) represent plants accessible to trap-lining birds (with most opportunity for outcrossing), and the other circles represent the territories of different birds.



Puya hamata plant size did not vary by spatial context. Rosette diameters of flowering plants measured 2.01 m (very similar to the 2.03 m reported by Miller (1988) for the same species in the same study area). The relative consistency in reproductive rosette diameter for *Puya hamata* (1.9-2.6 m) contrasts with that reported for *Puya dasylirioides*, a mire plant in the páramo of Costa Rica, with diameters of 0.4–1.4 m (Augspurger, 1985). There is evidence of differential growth rates for *Puya*, depending on local environmental conditions (Augspurger, 1985; Miller, 1988), though no data exist for *Puya hamata*. It is possible that reproduction in *Puya hamata* plants is triggered by plant size, rather than age, which might explain the consistency in rosette size. Perhaps reproductive plants in the centres of large *Puya* aggregations are the same size but older than plants at the periphery. Further work on this would be useful.

There was no evidence to support the idea that the spatial context of a plant affected the production of flowers, fruits and seeds per fruit. Although, outputs were highly variable from plant to plant, they were similar in the five spatial contexts. Fruit and seed-per-fruit production in other semelparous rosettes like *Yucca* and *Lobelia* are also highly variable, and output has been related to resource availability (Young, 1990). Variability in fruit production in *Puya hamata* (203 to 1802) was as great as in *Puya dasylirioides*, where it ranged from 50 to 1224, rising exponentially with an increase in rosette diameter (Augspurger, 1985).

The estimated total number of seeds per plant did not vary according to the hypothesis. There were no significant differences between plants in different spatial contexts. However, this is not surprising, since all plants are visited by hummingbird pollinators—it is the level of outcrossing (performed mostly by trap-lining pollinators) that is expected to vary by spatial context, rather than the levels of pollination and fertilisation. For this reason, crude total seed output is not necessarily a good indicator of the consequences of spatial pattern on reproductive output.

Inbreeding depression, that might result if flowers are fertilised by pollen from the same or closely-related plants, is often reflected in seed viability and germination (Byers & Waller, 1999; Charlesworth & Charlesworth, 1987; Wallace, 2003). The pairing of deleterious recessive genes can lead to the early death of an embryo (Brink & Cooper, 1947). Lower seed viability results in lower seed germination

(Renison *et al.*, 2004). For these reasons, the best test of the hypothesis is using "effective" seeds, accounting for viability and/or germination.

The output of effective seeds closely matches the predictions of the hypothesis. The number of effective seeds was highest in isolated plants and those at the edge of small groups. The lowest effective seed output was by plants in the centre of large groups. This is the first study to demonstrate patterns in seed viability and germination rates according to spatial context in flowering aggregations.

Inbreeding in *Puya hamata* might operate at several levels (as discussed in general terms by Wilcock & Neiland, 2002):

- Self-pollination within the same flower, though this appears unlikely, since the anthers develop first and the styles become receptive only after the anthers have withered.
- Self-pollination with pollen from another flower on the same inflorescence, as hundreds of flowers are often open at the same time. It is possible that self-incompatibility might have evolved in *Puya* to prevent this. Conspecific pollen is often blocked at the stigma (Wilcock & Neiland, 2002).
- Fertilisation with pollen from neighbouring plants, which are almost certainly siblings which dispersed from the same parent plant and germinated together. Even if self-incompatibility has evolved in *Puya*, it might not be effective at filtering out close relatives.

In general, it is clear that studies of reproductive output should recognise the consequences of any spatial patterning of the plants which might result in differential pollination and/or inbreeding. In the case of *Puya hamata* in the páramo, further studies are required to explore the genetic consequences of the spatial patterning of *Puya* plants, reflected in the differences in effective reproductive output. One would expect higher inbreeding coefficients in *Puya* seeds produced by plants inside groups compared with isolated individuals, unless mechanisms have evolved to ensure outcrossing. Investigations of the consequences of spatial context for inbreeding coefficients would be useful and the existence of self-incompatibility mechanisms in *Puya*.

Another line of investigation should explore the effects of plant spatial pattern on the population sizes and diversity of hummingbirds in the páramo. It is likely that territorial birds will be favoured in fire-dominated landscapes and trap-lining species may be disadvantaged. The presence of some isolated plants, between aggregated patches, might provide some resources for trap-lining birds, and act as stepping stones for pollinators moving from one patch to another, in a similar manner to that described for *Agave* in the Mexican Sonoran Desert (Jeffrey et al., 2008).

In conclusion, regular fires in the páramo—associated with human land use—result in patchiness of *Puya hamata* plants. As well as higher densities overall, large aggregations of plants can form. Plant size and flower, fruit and seed outputs do not appear to be affected by aggregation. Several species of hummingbirds respond to patchiness in their food supply by establishing territories around aggregations of *Puya* that restrict opportunities for effective outcrossing of the plants. This study demonstrates that plants in the centres of groups, especially large groups, produce fewer viable seeds with lower germination rates. Burning in the páramo is, therefore, a disturbance that can influence the population dynamics (and perhaps genetic diversity) of a flagship giant-rosette species and the behaviour and community structure of their hummingbird pollinators.

6 Modelling seed dispersal of *Puya hamata*

Introduction

The LandBaSE-P model incorporates the most important processes of *Puya hamata's* life cycle to simulate its population dynamics. Seed dispersal is one of these modelled processes and a fundamental one because seeds are responsible for finding new sites for establishment and promote genetic interchange among populations (Cain *et al.*, 2000; Trakhtenbrot *et al.*, 2010).

Animal, water, self (ballistic), and wind dispersal are the most frequent vectors for seed dispersal (Fenner & Thompson, 2005; Howe & Smallwood, 1982; Matías *et al.*, 2010; Nathan, 2006). Tracking wind-dispersed seeds is a challenge because of the difficulties of following seeds over long distances (Bullock & Clarke, 2000; Bullock *et al.*, 2002; Cain *et al.*, 2000; Levey *et al.*, 2008; Nathan & Muller-Landau, 2000). It is feasible to track seeds at shorter distances from the parent plant. This approach can then be used to get a general idea of the numbers of seeds that are dispersed close to the parent plant. In addition, study of dispersal at short distances is also valuable because it can provide information that could explain aggregation patterns.

There is little work on seed dispersal on *Puya.* It is known that *Puya* seeds are dispersed by wind (Augspurger, 1985), and *Puya hamata* seeds fit the wind dispersal syndrome because of its morphology. Miller (1988) reported that seedling distributions around adult plants indicated that the majority of offspring appear to fall within a few metres from the parent plant (5–6 m). Gilmartin (1972) also worked on seed dispersal limitations of *Puya clava-herculis*.

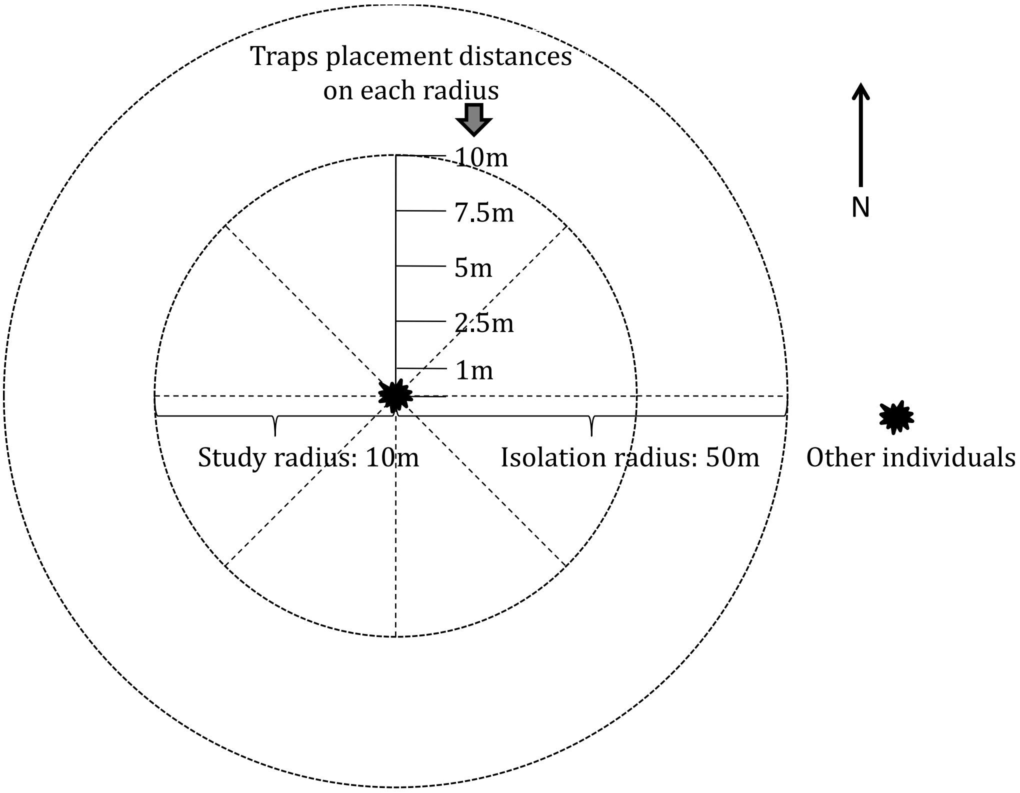
The study of seed dispersal at long distances is important because it might have an impact on the population dynamics at the landscape scale. To study seed dispersal at long distances, modellers have developed mathematical functions to describe how seeds are dispersed through space. In particular, ecologists have developed models using probability density functions (pdf) to fit dispersal data known as dispersal kernels (Bullock & Clarke, 2000). In other words, the dispersal distance kernel is the probability of seed deposition at a certain distance (Nathan *et al.*, 2008). These kernels have very specific performance due to the fact that they are developed for specific species (Bullock & Clarke, 2000).

LandBaSE-P works with large landscapes scales and the inclusion of an appropriate kernel to simulate short and long seed dispersal distances it is essential to provide realistic simulations of *Puya hamata* population dynamics. This chapter describes the physical characteristics of *Puya hamata* seeds, examines seed dispersal at short distances, and assesses a variety of seed dispersal kernels for inclusion in LandBaSE-P.

Methods

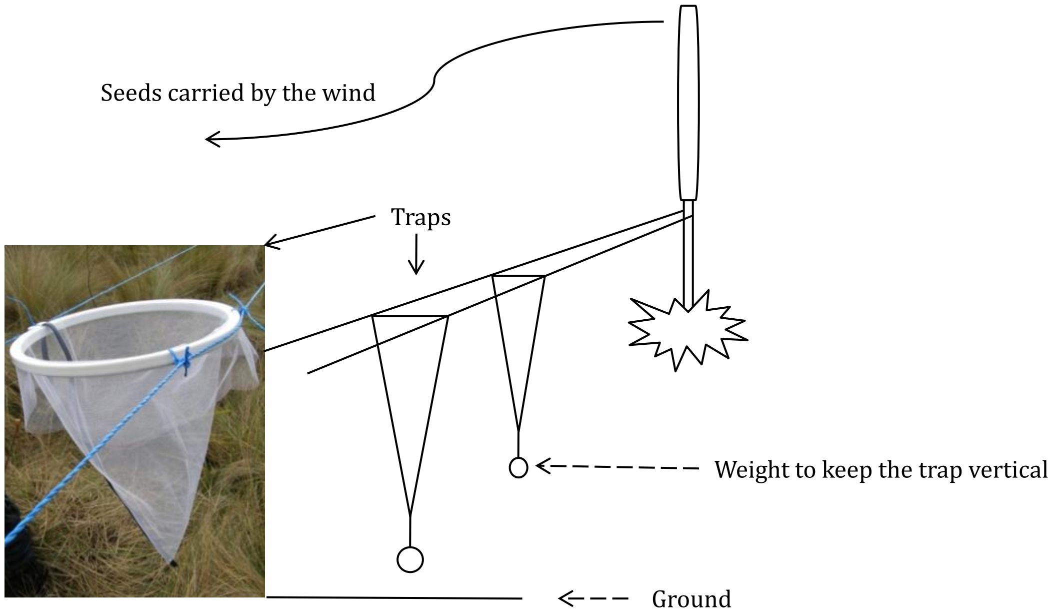
To observe seed characteristics, three hundred seeds from the seed viability trials presented in Chapter 5 were used (Table 5.1). They were weighed and the shape of every seed assigned to one of three shapes: triangular, round or irregular. To measure seed dispersal over short ranges from the infrutescence, a plant on flat ground more than 50 m from other infrutescences was selected for study. The study was carried out in October 2008 when *Puya* started releasing its seeds (Chapter 5). Eight radii were drawn up from the plant at 45° intervals and, on each radius, five seed traps were set at distances of 1, 2.5, 5, 7.5 and 10 m from the infrutescence (Figure 6.1). In total, 1% of the total area within 10 m radius of the parent plant was sampled with traps—though the proportion was relatively much higher closer to the plant. Each day, over a 14 d period, seeds in each trap were collected and counted. A wind vane and anemometer were set on top of the target plant to measure wind direction and velocity daily.

Figure 6.1. Seed trap layout around an isolated *Puya hamata* infrutescence.



The traps consisted of a light fabric cone supported by nylon lines and a weight in the apex of the cone helped to maintain its shape (Figure 6.2).

Figure 6.2. Seed trap design. Fixed traps helped to catch seed carried by the wind.



The following formula was used to calculate wind speed (W_s);

$$W_s = \frac{RPM \times \pi d}{60}$$

where *RPM* is the number of revolutions per minute and *d* represents the diameter of the vane (38 cm).

The number of seeds deposited within 10 m of a *Puya hamata* plant over a typical 300 d seed dispersal period was estimated with a concentric ring method. Each ring corresponded to each of the distances from the parent plant where traps were set. Thus, the first concentric ring started at 1 m and extended to 2.5 m from the *Puya* plant, and the last started at 7.5 m from it and extended to 10 m from it. The area of each concentric ring was calculated:

$$A_r = \pi(r_2^2 - r_1^2)$$

Where r_1 represents the innermost concentric circle, and r_2 the outermost. The area of each trap was 0.0707 m^2, and there were eight in each concentric ring (a total of 0.5655 m^2). The estimated number of seeds falling in each of the concentric rings was calculated as follows:

$$N_s = 300 \cdot N_t \cdot \frac{A_r}{0.5655} \text{ seeds } 300 \text{ d}^{-1}$$

Where N_t is the number of seeds caught in all eight traps and A_r the area of the concentric ring in question.

Results

The wind-dispersed seeds of *Puya hamata* are around 5 mm in length, consisting of a wing surrounding an approximately 2 mm "proper" seed (Figure 6.3).

Mean seed weigh was 0. 6 ± 0. 1 (*s*) mg (*n*= 300). The majority of seeds were triangular but some round and irregular seeds were found (Figure 6.4).

Figure 6.3. *Puya hamata* seed features.

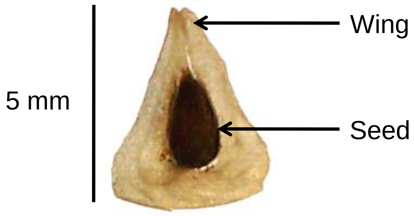
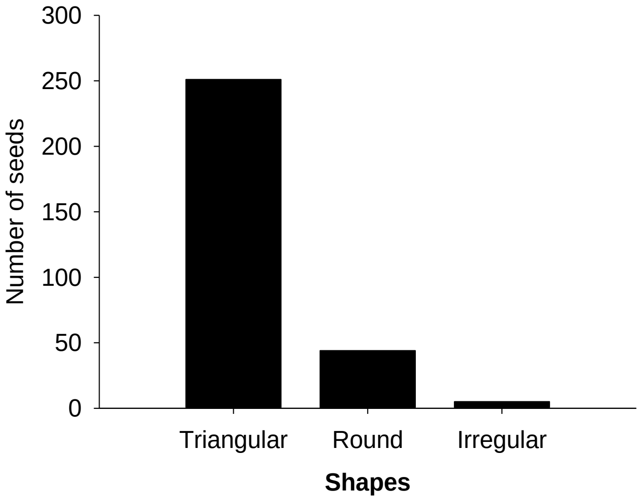
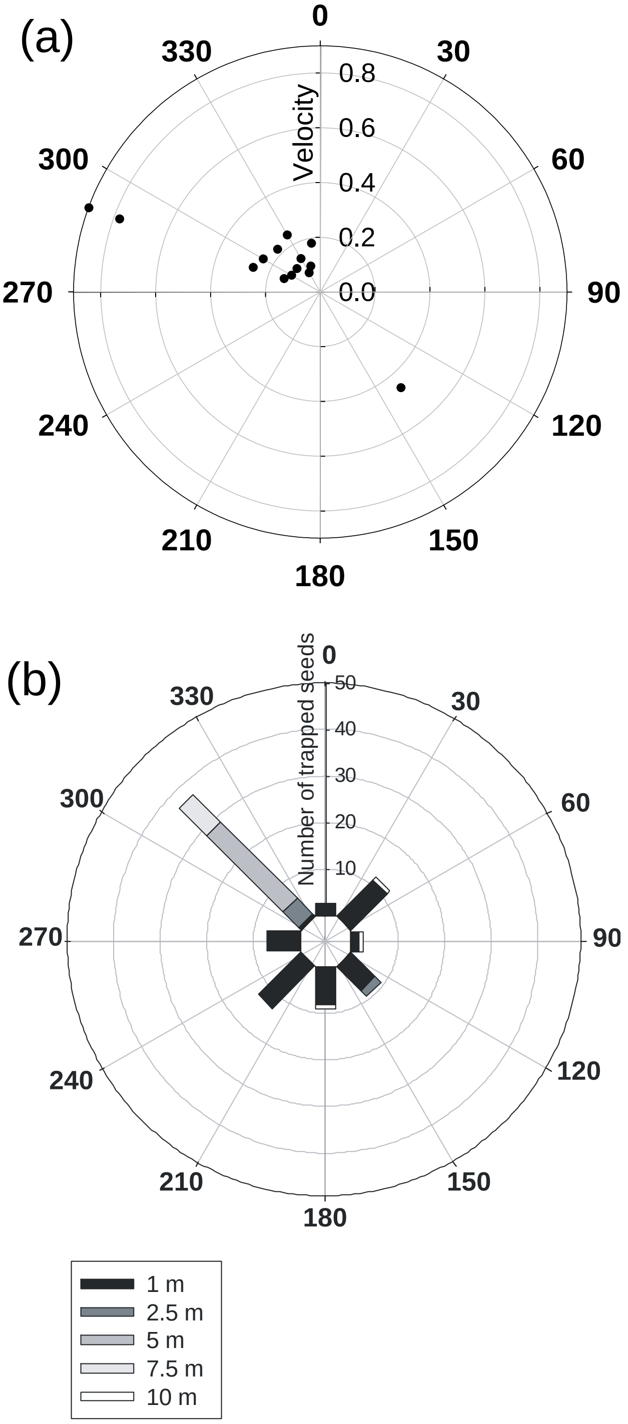


Figure 6.4. Distribution of seed shapes found in 300 *Puya hamata* seeds.



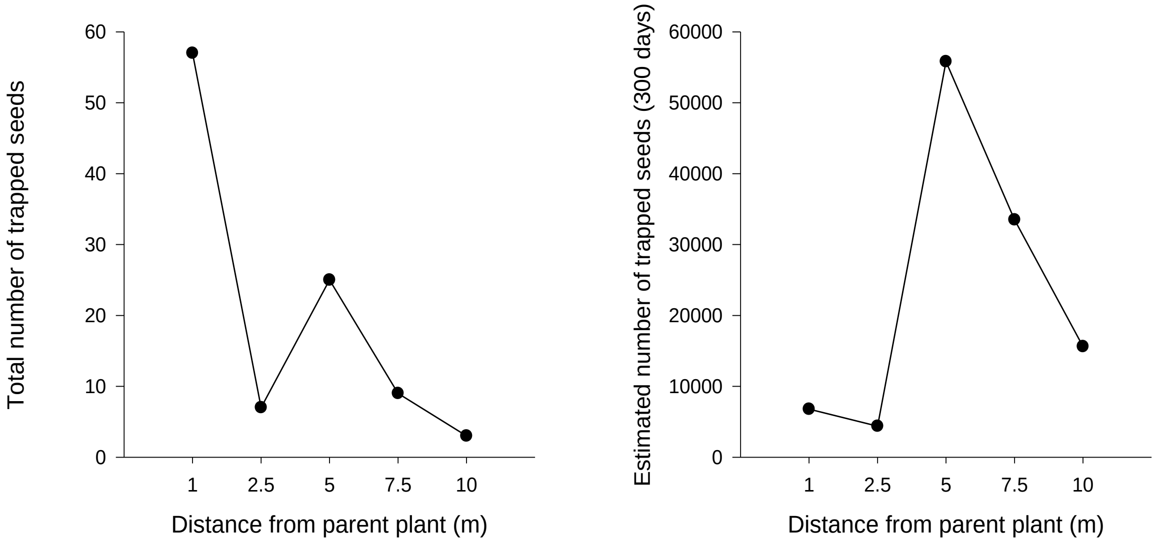
During the 14 d study period mean wind speed was 0.283 ± 0.254 (*s*) m s^{-1}, and wind direction was mostly from the east to south directions, blowing the seeds west to north. Average wind velocity is shown in Figure 6.4a; most measurements of wind speed were less than 0.25 m s^{-1}, reaching a maximum of 0.9 m s^{-1}. In the same period, a total of 101 seeds were collected from the 40 traps altogether. The highest number of seeds was found at 1 m and 5 m distant from the parent plant (Figure 6.4b)

Figure 6.5. a) Daily wind velocity (m s^{-1}) at midday during 14 d period. Each daily measurement is represented by a dot symbol. b) Distribution of trapped *Puya hamata* seeds around the parent plant over the same period. The shading in b) shows the number of seeds at each of the five distances where traps were set, and the radial 0° axis represents magnetic north in both figures.



Over the 14 d trapping period, 56 % of the seeds were caught 1 m from the parent plant (Figure 6.4b).

Figure 6.6. a) Total number of seeds caught in eight seed traps at the five different distances from the parent plant. b) Estimated number of deposited seeds around the parent plant over a typical 300 d seed dispersal period.



Discussion

The description of *Puya hamata*'s seeds corresponds with a typical wind dispersal syndrome (Cousens *et al.*, 2008; Miller, 1988): seeds have wings, weigh just a few milligrammes and are released in high numbers. It is clear the role wind plays in dispersion of *Puya hamata* seeds. Even at short dispersal distances, seed rain and wind velocity are related.

The mean seed production for a single *Puya hamata* plant was 682,060, dispersed over 6 months or more (Chapter 5). Considering constant wind velocity and seed dispersal for the 14-d period monitored, and extrapolating for a 300-d dispersal period, an estimated 17% of seeds would fall within 10 m from the parent plant. For a plant with a reported heavy bias for short-distance seed dispersal, this proportion seems low. There are five potential explanations for a shortfall in seeds near the parent plant in this study:

1. *pre-dispersal predation*

   One of the most common types of pre-dispersal seed predators are insects. They lay their eggs on the buds and whose offspring spend their larval phase as feeders entirely within a single capsule or pod (Fenner & Thompson, 2005). Crawley (1992) lists 60 studies of pre-dispersal seed predation by insects in a wide range of plant families. Miller (1988) found predation on fruits of *Puya clava-herculis* from a Nitidule beetle but he did not report predation on fruits of *Puya hamata.* I observed beetle predation on *Puya hamata* fruits in the REEA.

2. *Seed dispersal lasts longer than 300 days*

   In a previous chapter, it was reported that seeds dispersed throughout one year (Figure 5.2a). If seeds were dispersed for a longer period, the estimated proportion of seeds near the parent plant would be increased—though the extra time needed to make a significant difference would be quite large.

3. *Seeds are dispersed in pulses*

   Seeds are potentially dispersed in pulses, after extended periods of dry weather, rather than continuously (Soons & Bullock, 2008). Weather conditions in the 14 d study, while not unusual in the páramo, were not dry. Perhaps the results presented here represent seed dispersal in wet conditions but it is very likely that during dry conditions dispersal rates increase considerably.

4. *Many seeds may never disperse*

   Seeds can get trapped in the fruits and never be dispersed, and some could fall very close to the inflorescence, amongst the rosette leaves of the parental plant (Wenny, 2000).

5. *Seeds are mostly dispersed further than 10 m from the parent plant*

   Previous reports have been based on indirect evidence of seedlings around parent plants (Miller 1988), and this may be misleading. However, the overwhelming circumstantial evidence in favour of short-distance dispersal would suggest other interpretations might be more likely.

The fate of seeds dispersed more than 10 m from the parent plant is not known. Longer distance dispersal could play a role in determining regional survival of the plant species (Soons & Ozinga, 2005), but it is virtually impossible to quantify. Instead, careful selection of an appropriate seed dispersal kernel permits the modelling of long-distance seed dispersal and an investigation into its contribution to population dynamics.

A kernel for *Puya hamata* should take into account:

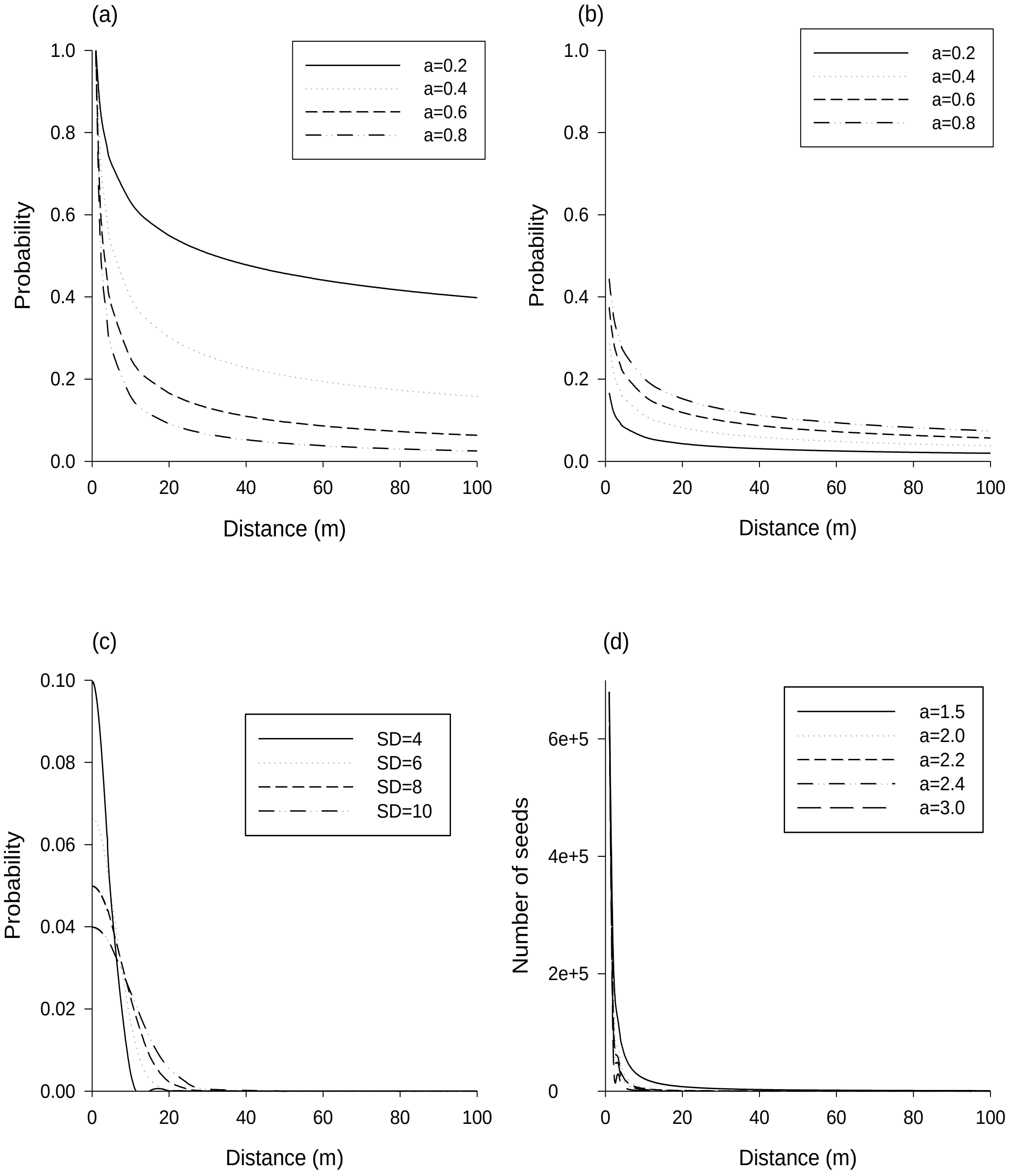
- that the majority of seeds should be dispersed close to the parent plant.
- that the modal dispersal distance should be 5–6 m from the parent plant.
- that a small number of seeds achieve long distance dispersal.

Table 6.1 presents an outline of the kernels considered for modelling of *Puya hamata* seed dispersal.

Table 6.1. Common kernels used in long distance seed dispersal by wind.

Formula	Description	Advantages	Disadvantages
The negative exponential $\frac{1}{x^{a}}$	Group of continuous probability distributions. The exponential distribution describes the distance for a continuous process (Figure 6.7a)	The approach is simple and explains the decline in dispersal distance. Exponential variables can also be used to model situations where certain events occur with a constant probability per unit length.	This approach is unrealistic because it assumes such a constant rate of change. Most seeds fall next to the parent plant, and the number reaches zero over short distances (the distribution has a short tail).
Exponential fat-tailed family $\frac{a}{a+x^{\frac{1}{2}}}$	Distribution taken from the exponential distribution. This distribution is called fat-tailed because it elongates the distribution to the right but the decay takes longer than the normal exponential (Nathan *et al.*, 2008). (Figure 6.7b)	It stretches and elongates the exponential distribution and it makes it more realistic (Laherrere & Sornette, 1998).	Functions like fat-tailed are leptokurtic, but overestimate dispersal near the source (Nathan & Muller-Landau, 2000)
The Gaussian $ae^{-\frac{(x-\mu)^{2}}{2\sigma^{2}}}$	The normal distribution is often used to describe any variable that tends to group around the mean. It is a continuous probability distribution where e = 2.71828, μ= mean and, σ^2 = variance. (Figure 6.7c)	Simple model for complex phenomena. Fast run times, easy set-up, and simple calculation (Arya, 1999).	The normal distribution starts at negative infinity. This can result in negative values for some of the results.
Pareto distribution $\frac{\alpha x_{m}^{\alpha}}{x^{\alpha+1}}$	The Pareto distribution is a simple model for non-negative data with a power law probability tail (Aban *et al.*, 2006) (Figure 6.7d).	Pareto distribution has a better fit to most seed dispersal data (Burroughs & Tebbens, 2001a; Burroughs & Tebbens, 2001b)	The ordinary Pareto distribution needs to be truncated. It is important to select a correct alpha value because this parameter significantly changes the shape of the distribution (White *et al.*, 2008).

Figure 6.7. Probability distributions used as kernels for wind seed dispersal with hypothetical data. a) The negative exponential, b) Exponential family fat-tailed distribution, c) Gaussian distribution and, d) Pareto distribution.



The negative exponential, exponential fat-tailed family, Gaussian and Pareto distribution have long probability tails. Bullock and Clarke (2000) recognized size and shape of the tail of the seed dispersal curve is important in determining the spatial dynamics of plants, but it is difficult to quantify. Tests with these four kernels for seed dispersal showed that the negative exponential and fat tailed exponential are useful to predict a constant rate or probability for changes in distance units but these patterns are unsuitable for *Puya hamata*'s dispersal characteristics.

Gaussian distributions place seeds within a wide range of distances (Nathan & Muller-Landau, 2000), but the desired kernel should distribute most seeds close to the parent plant. The Pareto distribution achieves short and long placement of seed with a narrow distribution at the beginning of the curve and a very long tail of long-distance dispersal. An illustration of the patterns produced by the Pareto distribution for an "average" *Puya hamata* plant is shown in Table 6.2. It satisfies two of the desired criteria (1 and 3) but not the second.

Table 6.2. Number of seeds expected to be dispersed further than the following distances using a Pareto distribution function with α=2.0, and an $x_{\min}$ of 1 m. The initial number of dispersed seeds is the average number of seeds produced by a single *Puya hamata* plant.

Distance (m)	Number of dispersed seeds	Cumulative percentage of all seeds
1	680000.00	0.0000
2	170000.00	75.0000
3	75555.56	75.0000
4	42500.00	88.8889
5	27200.00	93.7500
6	18888.89	96.0000
7	13877.55	97.2222
8	10625.00	97.9592
9	8395.06	98.4375
10	6800.00	98.7654
20	1700.00	99.7230
30	755.56	99.8400
40	425.00	99.9184
50	272.00	99.9506
60	188.89	99.9669
70	138.78	99.9763
80	106.25	99.9822
90	83.95	99.9862
100	68.00	99.9889
200	17.00	99.9956
300	7.56	99.9984
400	4.25	99.9992
500	2.72	99.9995
600	1.89	99.9997
700	1.39	99.9998
800	1.06	99.9998
900	0.84	99.9999
1000	0.68	99.9999

The Pareto distribution can be adjusted to make it finite (Aban *et al.*, 2006). By truncating it, a maximum distance for dispersed ($x_{\max}$) can be set. Truncation used for real applications of the Pareto distributions is based on Aban *et al.*'s (2006) studies, where they found a natural upper bound useful for general purposes.

Of the kernels considered here, the Pareto distribution kernel was best-suited for *Puya hamata* (though not perfect) and therefore was included in the LandBaSE-P model.

In general, models of wind seed dispersal can offer well-defined descriptions of seed dispersal patterns, facilitating insights into the evolution of dispersal ability and its role in population dynamics (Andersen, 1991). Nowadays, spatial models have become extremely sophisticated, although they regularly have to make do with poor dispersal data, or rely on hypothetical formulations of dispersal.

Other tools that help to quantify long distance seed dispersal is genetics. Genetic estimates of dispersal generally are based on seedlings or later stages of development. This kind of genetic estimates of dispersal reflect both the dispersal movement *per se* and establishment of seeds (effective seed dispersal) (Cain *et al.*, 2000). A variety of genetic markers can be used to quantify seed dispersal curves: markers like allozymes, DNA sequences, microsatellites, restriction fragment length polymorphisms (RFLPs)(Hoelzel, 1998; Ouborg *et al.*, 1999), and DNA randomly amplified from the genome such as RAPDs and AFLPs (Krauss *et al.*, 2009).

It is not possible to know the destiny of all seeds. But the short-distance seed dispersal experiment was useful to understand the initial patterns at the beginning of the seed distribution curve, making it easier to select an appropriate kernel to simulate populations dynamics of *Puya hamata* in LandBaSE-P. However, even the most complex kernels are unable to track seed dispersal closely (Silvertown, 1991; Turchin, 1998). Several parameters cannot be modelled, or recorded in the field, and that makes seed dispersal a challenging topic. Later in the thesis, LandBaSE-P will be used to evaluate the potential impacts that short and long seed dispersal might have on burned páramos.

7 Field and laboratory germination of *Puya hamata* seeds

Introduction

Some *Puya* species, such as *Puya cryptantha*, *Puya trianae* (Mora *et al.*, 2007), and *Puya dasylirioides* (Augspurger, 1985), can propagate vegetatively. However, like other monocarpic members of the genus, for example *Puya raimondii* (Hornung-Leoni & Sosa, 2008) *Puya hamata* reproduces exclusively by seed (Miller, 1988).

Puya hamata produces a high numbers of seeds (about 700,000 per plant in this study), and *Puya raimondii* can produce as many as 12 million seeds per plant (Cano *et al.*, 2000) not apomictic (Sgorbati *et al.*, 2004). This large number of genetically different seeds provides variability for some individuals to pass through the challenging filters of high mountain environments, via germination of seeds and establishment of seedlings (Grubb, 1977; Körner, 2003). There are only a few studies on germination in *Puya* (Mora *et al.*, 2007; Vadillo *et al.*, 2004). Understanding the germination of seeds is a vital part of understanding *Puya hamata* population dynamics.

It is clear that not all of the seeds produced by a single plant of *Puya* germinate, or seedlings survive otherwise there would be an exponential explosion of *Puya hamata* plants. It is not clear what limits *Puya* seeds germination. In general, common requirements on germination are certain conditions of temperature, light, ventilation, water, and nutrient availability (Evenari, 1980; Fenner & Thompson, 2005). Bromeliad species can differ greatly in their requirements like light and temperature for germination (Benzing, 2000).

In the case of *Puya hamata*, germination appears to be higher in burned areas than in densely vegetated areas (Lægaard, 1992), but there is no quantitative evidence for this. Light is generally high in the equatorial zone and high-altitude páramo (Sarmiento, 1986), but dense vegetation cover prevents this light from reaching the ground. Light provides warmth and, potentially, this enhances seed germination in open areas. Therefore, light and temperature could be limiting factors in the germination success of *Puya hamata*. In general, vegetation removal often improves germination by raising light and temperature levels (Baeza & Roy, 2008; Grubb, 1977). Smith and Downs (1974 cited by Vadillo *et al.*, 2004) recognized the important role that temperature has on germination of *Puya berteroniana*, and Suni *et al*. (2001) reported that *Puya* species require direct light to germinate.

The aims of this study were to estimate germination rates of *Puya hamata* in vegetated and unvegetated páramo in the field, and to assess the effects of temperature and light on germination, in controlled conditions that simulated a range of vegetation densities. In addition, these studies provided estimates of germination parameters for inclusion in the LandBaSE-P model.

Methods

In order to assess germination rates of *Puya hamata* in the field, unvegetated and vegetated field germination experiments were carried out in 3 m × 3 m plots, lacking large *Puya* plants, and at least 50 m away from reproducing *Puya* plants. In July 2008, all vegetation in two plots was cut back to ground level, while two vegetated plots were left in their natural state, except that existing *Puya hamata* seedlings (three) were removed. For one vegetated-unvegetated pair of plots, enhancement sowing of 1000 *Puya hamata* seeds per plot was carried out with seeds from mature fruits harvested directly from local plants and used immediately. The other pair received no additional seeds. One year later (July 2009), the total number of *Puya* seedlings present in each plot was counted.

In July–October 2009, ten *Puya hamata* fruits were collected from 40 randomly-selected reproductive plants in the south-west of the REEA and its neighbouring buffer zone. The seeds were extracted, cleaned, stored in paper bags, and transported to the University of Plymouth, where they were kept at room temperature until germination trials were carried out in the laboratory from January to June 2010.

The effect of a wide range of temperatures on *Puya hamata* germination was carried out using a Grant thermostatic bath (one cold and one hot water bath, linked by a 40 cm × 20 cm aluminium plate), set to produce a temperature gradient from 10 °C to 32 °C. At regular intervals, seven rows of five Petri dishes (5.5 cm diameter) were placed on the aluminium plate. Each dish contained 20 seeds, sown onto 0.8% set water agar. The agar was used because of its moisture retention capacity (Ellis *et al.*, 1985) and was autoclaved at 120 °C for 15 minutes before use (Fuller & Fuller, 1995). Inside the dishes, seeds were arranged in four lines of five seeds, each line experiencing a different temperature from neighbouring lines. Since the dishes were five deep across the plate, there were 35 replicate seeds at each temperature. The temperatures experienced by the seeds were measured using regularly-spaced DS-1920 temperature *i*-button data-loggers. Cool white fluorescent lighting was provided by 15 bulbs of 40-W each in a 12 h light/12 h dark photoperiod. All trials were run until no seeds germinated for a period of 72 h after germination had begun.

A second experiment was performed to investigate the combined effects of light (100%, 60%, 30% and 0%) and temperature (10 °C, 15 °C and 20 °C), the latter representing temperatures that might commonly be found on the ground surface in the field study area. Four DS-1920 temperature *i*-buttons were used to confirm the temperature throughout the experimental period. Petri dishes containing the seeds in the 100% light treatment were left uncovered, those in the 60% and 30% light treatments were wrapped in one layer of 40% and 70% greenhouse shade netting, respectively, and those in 0% light (complete darkness) were wrapped in three layers of aluminium foil. Seeds at 0% light were only observed on the final day of the experiment (Figure 7.1).

Figure 7.1. Petri dishes containing the *Puya hamata* seeds in the 100% 60% 30% and 0% light.

The seeds were sown onto 0.8% water agar in 9 cm diameter, sterilized Petri dishes. Twenty seeds were distributed evenly across the surface of each dish with sterilized pincers. Five replicates (100 seeds) were used for each treatment combination. The germination trials were performed in a Sanyo MRL-350 temperature-controlled growth cabinet with cool white fluorescent lighting from 15 bulbs of 40-W each in a 12 h light/12 h dark photoperiod. All trials were run until no seeds germinated for a period of 72 h after germination had begun or for a maximum of 30 days if no germination occurred at all.

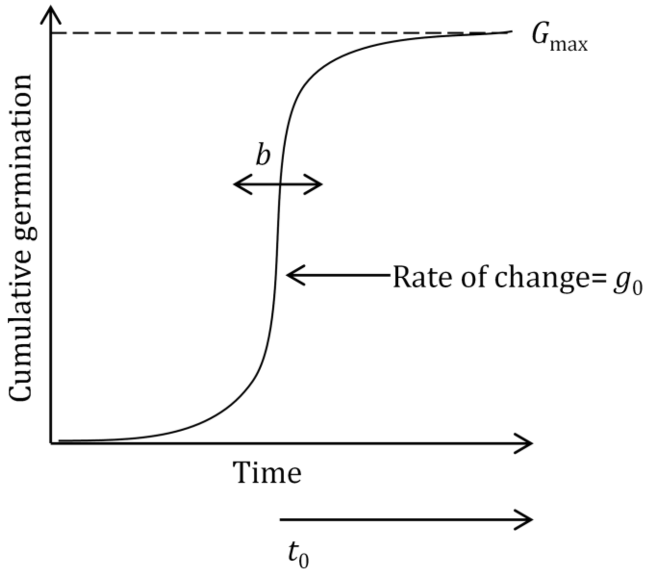
Germination was assessed using Franco & Franco (In prep) model, because it partitions different components of germination for comparison. A simplified account of the model parameters is given in Box 7.1. Curve fitting of cumulative germination curves (the proportion of germinated seeds through time) was applied to compare treatment responses.

Box 7.1. A simplified account of the model parameters in Franco & Franco's (In prep) model.

The model has the form:

$$G = G_{max}\left(1-\left(1-\frac{g_0}{1+e^{-b(t-t_0)}}\right)^t\right)$$

Where G is the empirically recorded proportion of germination over time (t), $G_{\max}$ represents the observed final percentage of germinated seeds, g_0 is the intrinsic rate of germination, b the change in germination rate over time, and $t_0$the time-lag of the response. Changing one parameter while keeping the others constant, g is proportional to the slope of the curve near its inflexion point, b is inversely related to the time that it takes for the bulk of germination to occur, and t_0 measures the shift of the curve to the right:



$G_{\max}$ was obtained directly from the data, while g_0, b and t_0 were estimated by non-linear regression using SPSS Statistics 18.0 for Windows (SPSS 18.0, 2009). The Levenberg-Marquardt algorithm with sum of square residuals loss function was employed. Starting values for the SPSS fit, which allowed raping convergence in all cases, were: $g_0 = 0.1$, $b = 0.5$ and $t_0 = 10$.

The estimated values of g_0, b and t_0 were fed back into the model equation to plot the expected cumulative germination curve. The following derivative from Franco and Franco's (In prep) model quantifies the changing rate of germination with time:

$$\frac{dG}{dt} = G_{max}\left(1 - \frac{g_0}{1 + e^{-b(t-t_0)}}\right)^t \left(\frac{g_0\, be^{-b(t-t_0)}t}{\left(1 - \frac{g_0}{1+e^{-b(t-t_0)}}\right).(1 + e^{-b(t-t_0)})^2} - ln\left(1 - \frac{g_0}{1 + e^{-b(t-t_0)}}\right)\right)$$

This probability density function, scaled by G_{max}, provides useful parameters such as the mean, median, skew, kurtosis and time taken for specific percentiles to germinate ($t_{\%}$). These parameters were calculated in Maple 13.0 (Maplesoft, 2009). one way and two-way ANOVAs and Student-Newman-Keuls post-hoc tests were used to compare model parameters between treatments temperature and light in SPSS 18 (SPSS 18.0, 2009).

Results

Germination in the field was extremely low. No seedlings were observed in the control plots, without enhanced sowing of *Puya hamata* seeds (Table 7.1). In the plots with 1000 additional seeds sown, only one seedling was found after one year in the unvegetated plot. A detailed search for ungerminated seeds on the soil surface revealed far more seeds in the unvegetated treatments compared with the vegetated ones.

Table 7.1. Number of seeds (on the soil surface and inside tussocks) and seedlings found in treatment plots in the field. Only one plot per treatment combination was used.

Treatment	**Unvegetated**		**Vegetated**	
	Seeds	**Seedlings**	**Seeds**	**Seedlings**
Sown	18	1	1	0
Control	93	0	1	0

No germination was observed below a temperature of approximately 14 °C in the experimental temperature gradient (Figure 7.1). The final percentage of germinated seeds ($G_{\max}$) peaked between 17 and 27 °C, falling away sharply such that no germination was observed above 28 °C. For most of the temperature range in which seeds germinated, the proportion of germinated seeds was higher than 80%.

Confirming the results from the temperature gradient, not one seed germinated at 10 °C, in any of the four light treatments (Figure 7.2). Combining all the light treatments, 30% more seeds germinated at 15 °C than at 20 °C. In full light, there was no difference in the final percentage of germinated seeds ($G_{\max}$) at 15 °C and 20 °C, but partial shade reduced $G_{\max}$ significantly at 20 °C, whereas at 15 °C it was only reduced in complete darkness (ANOVA interaction: $F_{2,24}$=23.828, df=3, p<0.0001; Figure 7.3).

The intrinsic rate of germination (g_0) did not differ between temperature treatments, but was lowest in full light (ANOVA temperature: $F_{2,24}$=7.658, df=2, p=0.003).

The change in germination rate over the time (b) was unaffected by temperature or light (ANOVA temperature: $F_{2,24}$=0.044, *df*=2, p=0.835; ANOVA light: $F_{2,24}$=3.022, *df*=2, p=0.068).

The time-lag of the germination response (t_0) was unaffected by light conditions at 15 °C, and the same at 20 °C in full light, but was longer and more variable in the shade at 20 °C (ANOVA interaction: $F_{2,24}$=6.365, *df*=2,p=0.006; Figure 7.5).

The cumulative germination curves for the three light conditions at both temperatures are shown in Figure 7.6. The relative consistency of the shape of these curves at 15°C for all light intensities and in full light at 20 °C is evident. However, at 20 °C in shaded conditions, the curves are more variable and of different shapes to the rest.

The probability density functions (Figure 7.7) reiterate the consistency in germination at 15 °C and in full light at 20 °C—most of the germination happens over a ten day period after day 10. In the shade at 20 °C, germination tends to happen later, is much more variable than the other treatments, and the overall proportion of germinated seeds (G_{max}, the area under each curve) is smaller.

Figure 7.2. Percentage of germinated *Puya hamata* seeds in an experimental thermal gradient from 10.8 to 31.5 °C.

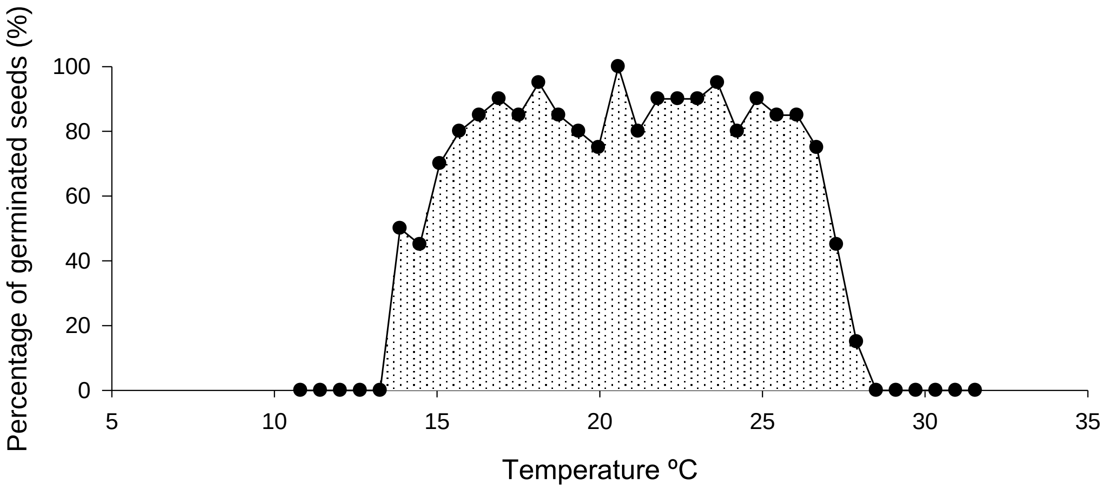


Figure 7.3. Mean proportion of germinated *Puya hamata* seeds: a) at the three different temperatures, and b) at four different light regimes.

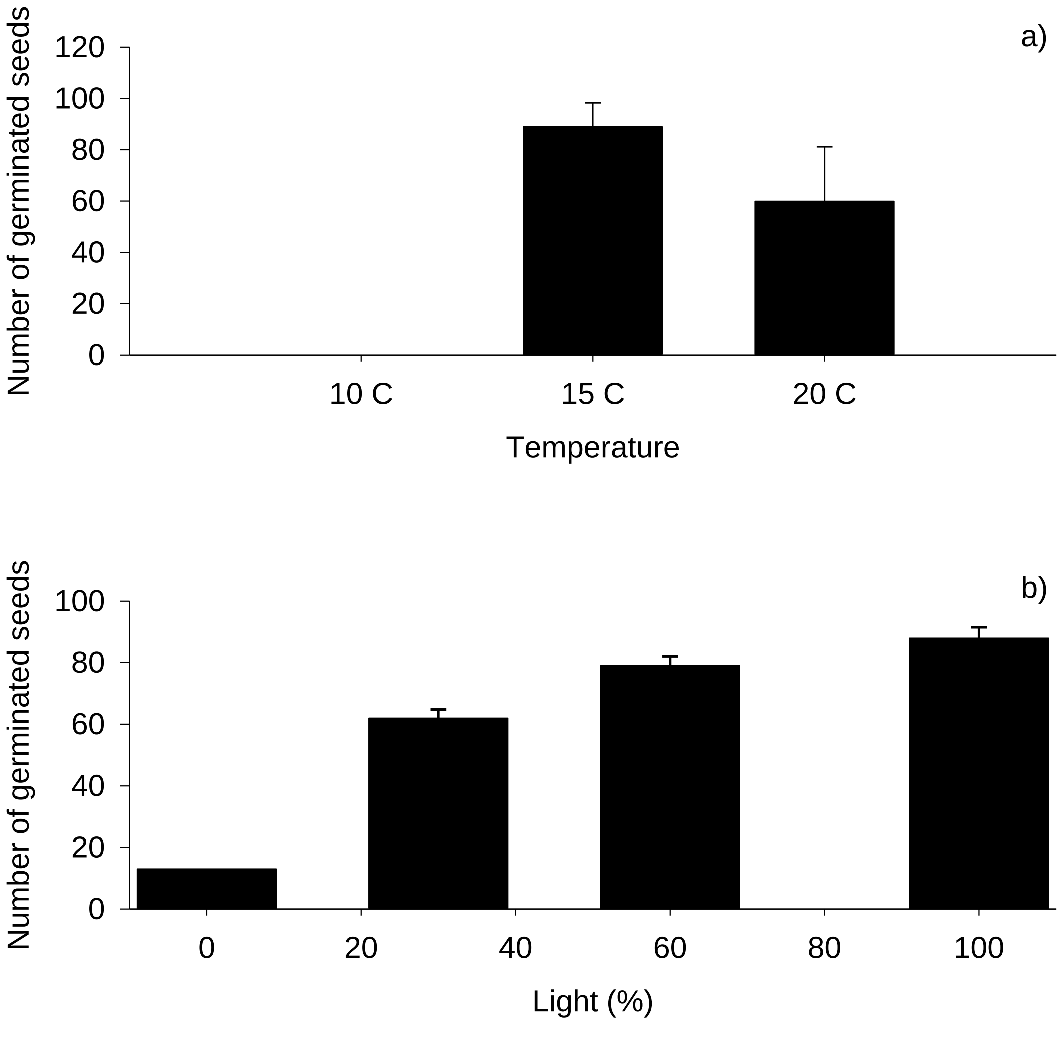


Figure 7.4. Mean final percentage of germinated seeds (G_{max}) at two temperatures and four light conditions. Temperature at 15 °C (solid line) and 20 °C (dashed line). Means sharing a letter were not statistically different according to a Student-Newman-Keuls multiple comparison of means test.

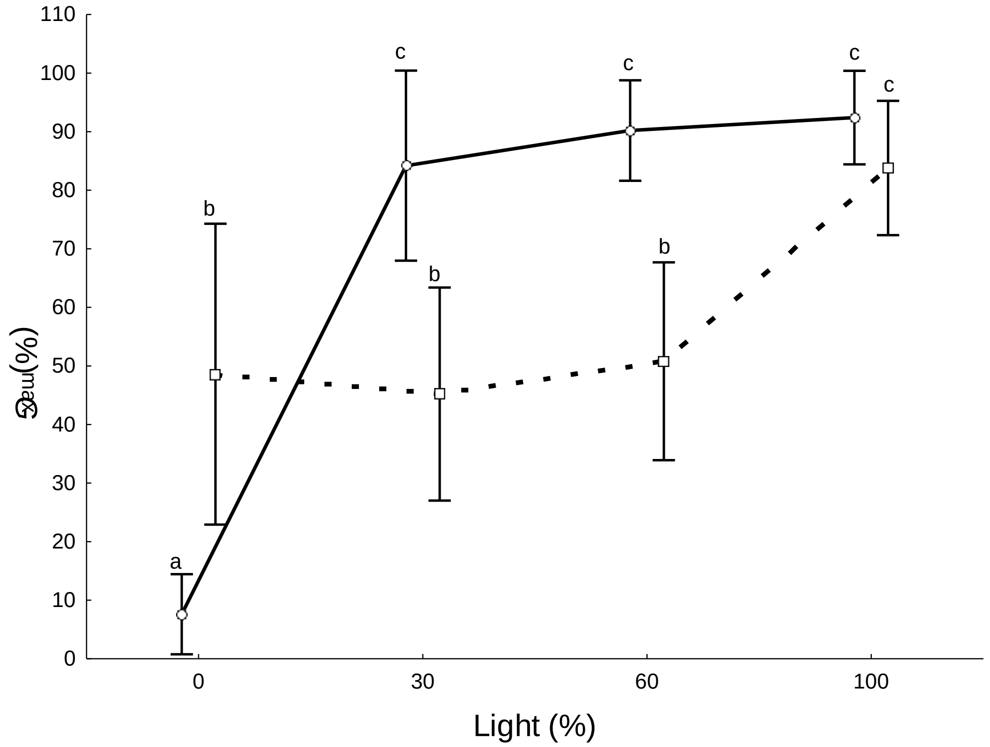


Figure 7.5. Mean intrinsic rate of increase (g_0) at two temperatures and three light conditions.

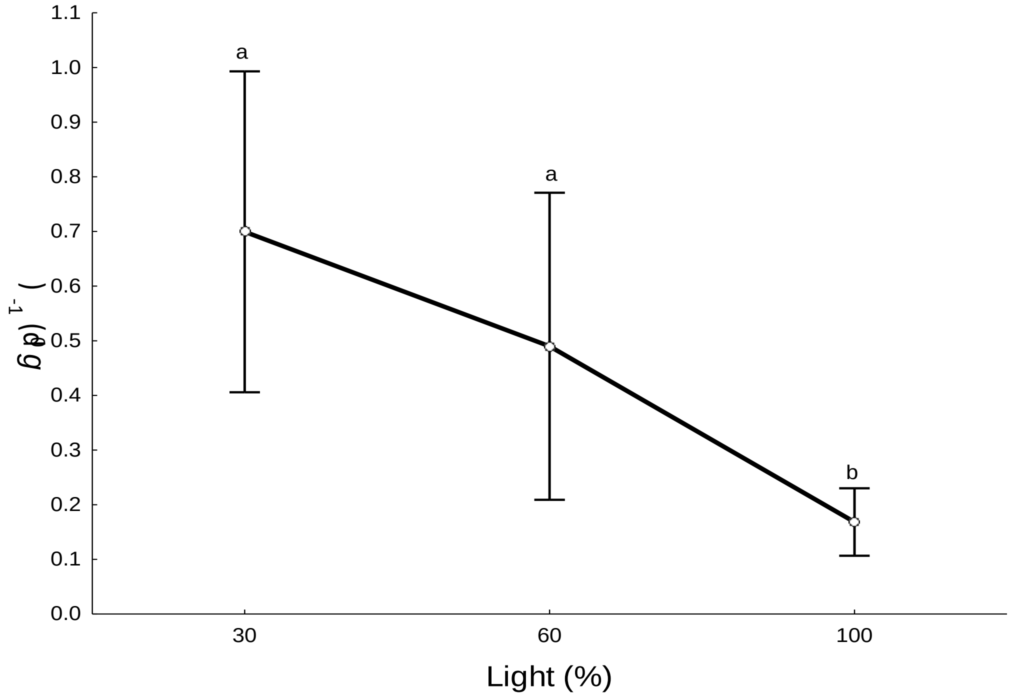


Figure 7.6. Mean time-lag of the germination response (t_0) at two temperatures and three light conditions. Temperature at 15 °C (solid line) and 20 °C (dashed line). Means sharing a letter were not statistically different according to a Student-Newman-Keuls multiple comparison of means test.

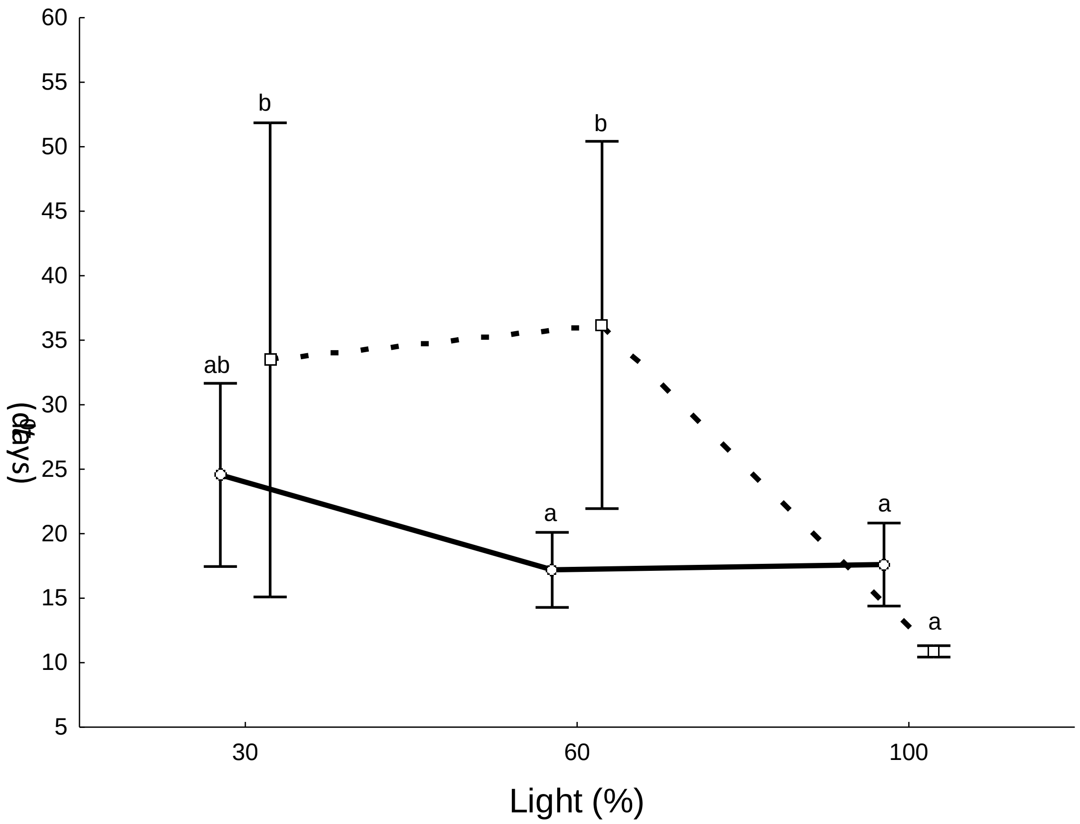


Figure 7.7. Curve-fitting of cumulative germination for all treatments. Curves in each graph are copies derived from 100 seeds.

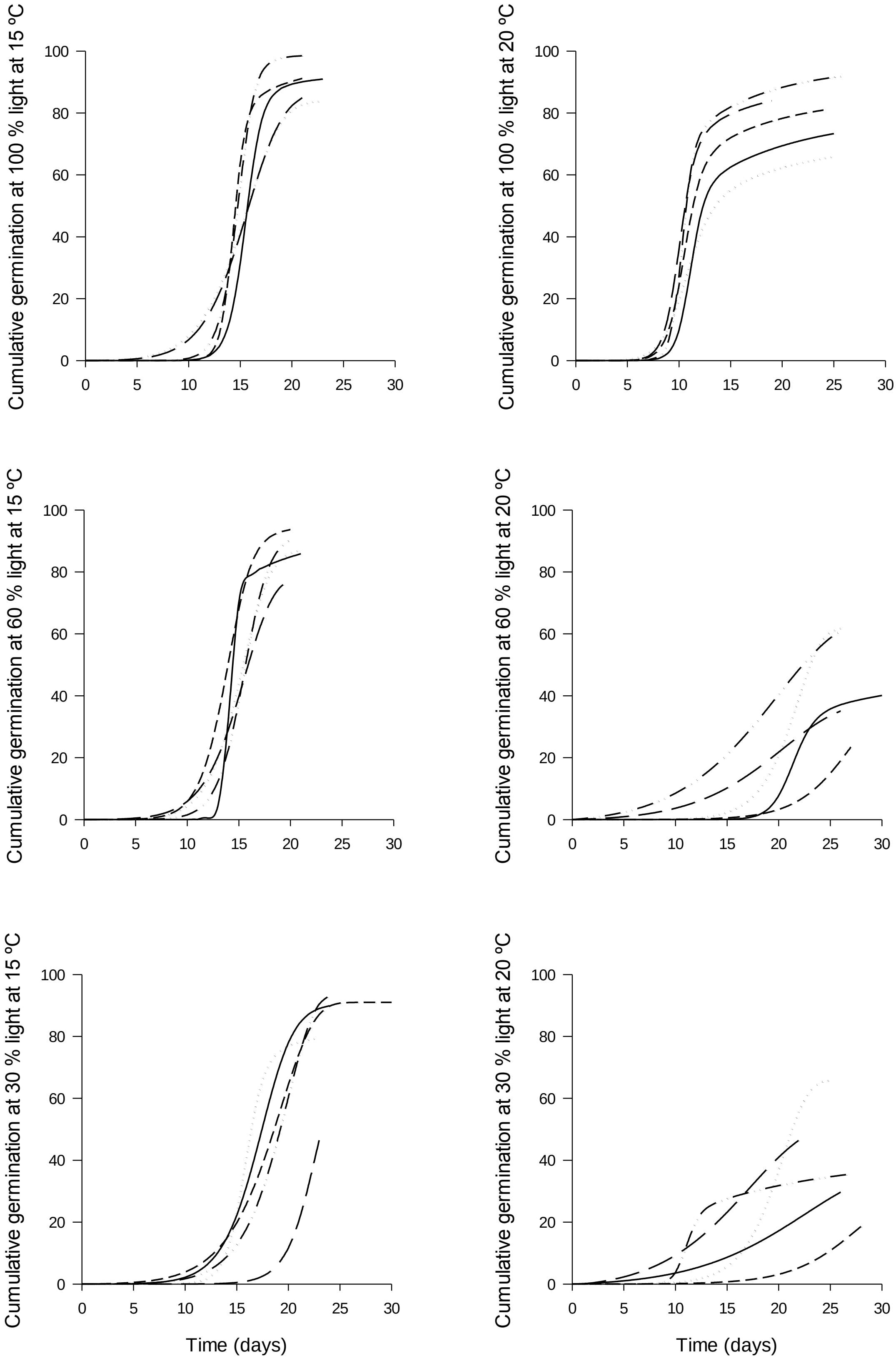
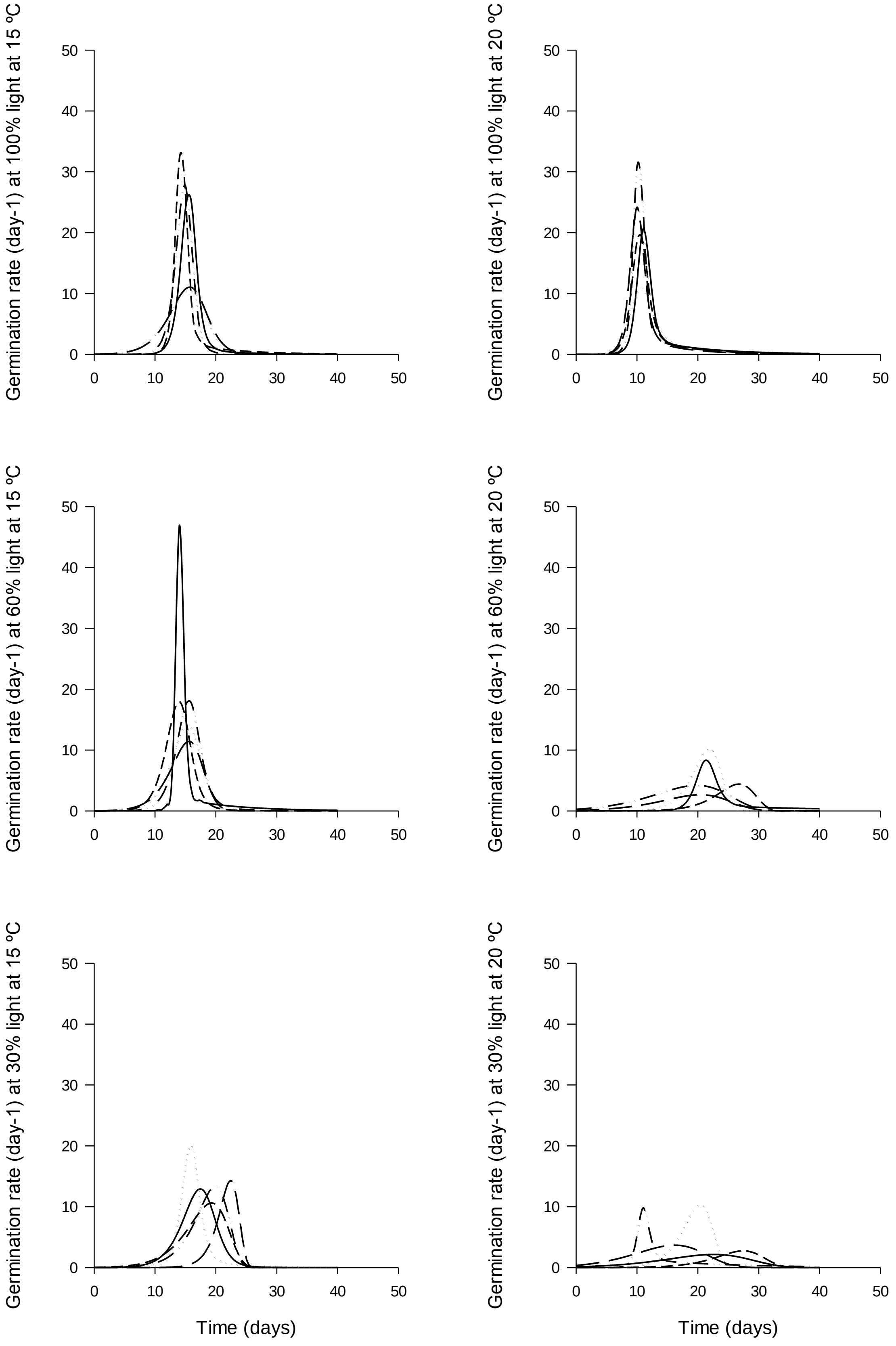


Figure 7.8. Germination rates for all treatments. Probability density functions PDFs Kurtosis and skewness did not showed statistical differences among treatments F(5,24)=1.8071, *p*=0.1495 and F(5,24)=2.5001, *p*=0.058 respectively. Curves in each graph are replicates derived from 100 seeds.



Discussion

The number of seeds that germinated in the field experiment was very low. Only one seedling was found across all the plots, and this was present in the cleared plot with a 1000 additional seeds sown. However, it is expected that *Puya hamata* has very low seedling recruitment rates. To maintain the population size only one seed in 700,000 needs to germinate, and seedling survives to maturity. Furthermore, since many of the seeds tend to be dispersed within 10 m of the parent plant (estimated at 17% in Chapter 6), seed rain is expected to concentrate around *Puya* inflorescences. Assuming an even spread of seeds throughout a radius of 10 m from the plant, and only 17% of the approximate 700,000 seeds produced, a density of 379 seeds m^{-2} would be expected. For a 3 m x 3 m plot, this equates to a total of nearly 3,500 seeds. In this context, the additional 1000 seeds sown in some plots was a rather small contribution.

More seeds were found on the surface of the unvegetated plots. Vegetated plots would be expected to trap more seeds, but to have, perhaps, higher predation rates (the vegetation offering better cover for seed predators) and faster decomposition rates (higher humidity and more stable temperatures within the vegetation). This would potentially lead to the observed seedling density. *Puya hamata* seeds are not released from their capsules until all seeds are mature (Chapter 5). Synchronous seed dispersal might therefore minimise seed predation (by satiating predators Fenner & Thompson, 2005; Peres, 1991), but a smaller number of seeds—such as the number sown in this experiment—might be more vulnerable to attack.

Another possibility, of course, is that the seeds were easier to find in the more open plots, though very thorough searches were carried out. Interestingly, although these plots were located more than 50 m away from flowering *Puya* plants, seeds did arrive—93 seeds were observed in one of the control plots.

There is the possibility that *Puya hamata* forms a seed bank. Vasak (1969) germinated an unidentified *Puya* seed after 30 months, confirming the potential for *Puya* seed banks, although there are no other reports to support the idea. However, there was little variability in seed germination behaviour in my trials, which suggest *Puya hamata* does not form a seed bank. In any case, seeds may be destroyed by fires if they are not buried. Temperatures in páramo fires can reach 120 °C on the ground surface between tussocks, but remain below 65 °C just 1 cm below ground (Ramsay & Oxley, 1997).

Nevertheless, conditions for germination should have been acceptable, in the cleared plots at least. As demonstrated elsewhere in this study, seed viability should not have been a problem. Germination rates in the wild are often very low (Körner, 2003). Low rates have been reported for *Puya cryptantha* and *Puya trianae* in Colombian páramos, especially when compared with potential rates in laboratory conditions (Chaparro-Mendivelso & Mora-Ardila, 2003; Mora *et al.*, 2007). Similar patterns have been reported for other high-altitude species, *e.g., Espeletia timotensis* (Guariguata & Azocar, 1988), *Allium tricoccum* (Nault & Gagnon, 1993), and *Lobelia* species in Mount Kenya (Young, 1994).

Proportions of *Puya hamata* germination in the laboratory were much higher than in the field. However, *Puya hamata* did not germinate below 14 °C, but rapidly reached more or less optimum levels by 17 °C—only three degrees separated very good germination and none at all. There was an upper temperature limit to germination at around 27 °C.

Interestingly, *Puya hamata* does not appear to be able to germinate at the ambient daytime temperature typical of its habitat. The media temperature reported for the REEA is 10 °C (Coello & Planificador, 1994; Ministerio del Ambiente, 2008). Measurements of soil temperature by Ramsay (2001), at 4000 m on nearby Volcán Chiles, were around 7 °C; compensating for altitude, assuming a lapse rate of 0.6 °C per 100 m (Sarmiento, 1986), the ambient soil temperature in my study area is estimated at about 9 °C.

One explanation for situation is that *Puya hamata* may be at its upper elevational limit for germination. *Puya* is a tropical taxon which radiated both altitudinally (especially in the central Andes) and latitudinally (in the northern Andes) during the Pliocene and Pleistocene (Varadarajan, 1990). As the Andes uplifted during this period, *Puya* adapted to the cooler conditions that appeared in the mountains (Van der Hammen & Cleef, 1986). This tropical genus is likely to be constrained by temperature at the upper limit of its altitudinal distribution.

Several species of *Puya* are associated with páramo bog and running water (*e.g., P. dasylirioides, P. hamata*). In these places, ground temperatures may be elevated compared with free-draining soils nearby. Ramsay (2001) described a 2 °C difference at 4000 m on Volcán Chiles between soil temperatures of neighbouring páramo and mire habitats. As the temperature gradient trial showed, a few degrees difference can significantly affect *Puya hamata* germination, and this species may be able to colonise wetter areas at higher altitudes as a result. It is well known that species of waterlogged habitats have high temperature requirements for germination (Dinsdale *et al.*, 2000).

Some characteristics of *Puya* germination at the upper end of the temperature range could be more relevant to ancestral conditions than those of the present day. Germination at high temperatures in *Puya hamata,* up to 28 °C, is probably a vestigial characteristic because these higher temperatures are probably not relevant in the páramo where it lives. However, soil temperatures of 56 °C have been reported in strong sunlight in the páramo (Diels, 1934). Some *Puya* species appear to have lost some ability to germinate at higher temperatures: *Puya berteroniana* (Chile) germination declined at temperatures above 15 °C, with low germination at 25 °C (Smith & Downs 1973 cited by Vadillo *et al.*, 2004). A much lower proportion of seeds of *Puya raimondii* (Peru) germinated at 21–26.5 °C than at 18.5–23 °C (Vadillo *et al.*, 2004).

In my germination trials, there was a clear interaction between light and temperature in *Puya hamata* germination. At lower light levels, the proportion of seeds that germinated was reduced. $G_{\max}$ fell between 60% and 100% light at 20 °C, but the fall at 15 °C did not occur until lower light levels: between 30% and 0% light. This suggests there may have been some selection for *Puya* plants able to germinate in shaded conditions at temperatures of around 15 °C. Some germination did occur in complete darkness, also reported for *Puya raimondii* in Peru (Vadillo *et al.*, 2004).

Germination response was slowed by shading at 20 °C and was more variable compared with other treatments. In the majority of treatments, germination was first noted nine days after the start of the trials. This corresponds to similar observations for *Puya raimondii* (Vadillo *et al.*, 2004).

The spread of germination was relatively consistent for all temperatures and light regimes, mostly occurring over 10 days after the trial began. This supports my field observations of synchronous *Puya* germination and establishment, and the development of clear defined cohorts of plants.

The location of the páramo, at high altitudes on the equator, means that solar radiation is extremely powerful and raises surface temperatures significantly above those of the air (Fischer, 1985). In open areas, the sun can warm the ground to temperatures that permit *Puya hamata* seeds to germinate. However, in places with taller, dense vegetation cover, ground temperatures are likely to remain close to ambient air temperature with little input from solar radiation, and *Puya hamata* seeds may not be able to germinate.

Therefore, the patterns in germination may explain the altitudinal limits of *Puya hamata*, as well as its higher abundance in short vegetation, either after fires or near water. To confirm this link, more detailed and comprehensive temperature profiles for a range of páramo vegetation types are required, in relation to canopy cover and light levels.

8 Demography of a semelparous rosette and its fire-driven size distribution

Introduction

The Reserva Ecológica El Angel is a burned landscape mosaic. Fire regimes affect plant populations dynamics (Cochrane, 2009), especially dynamics of *Puya hamata* which seems to be favoured by fire. *Puya hamata* appears to form patches in time and space, and its size distribution patterns might reflect fire regimes. If this is the case, *Puya hamata* could be potentially useful as an indicator of fire regime.

Much has been written about the effect of fire regime on population structure in grassland plants (Bragg, 2007; Dyer, 2003; Gibson, 2009) but there is little literature about the effect of fires on giant rosette plants in mountain grasslands (*e.g.*, *Lobelia* or *Puya*). Kovář (2001) found that burning decreased *Espeletia pycnophylla* densities of in páramos of Volcán Chiles, Ecuador. There is also little information about size distribution in *Puya* species: Augspurger (1985) investigated the demography of *Puya dasilyriodes* in bogs of Costa Rica, and Miller and Silander (1991) studied the distribution of giant rosette species of *Puya* in the Ecuadorian páramos.

Fire regime might modify recruitment, growth and mortality of plants (Guinto *et al.*, 1999). These three processes are reflected by size structure through time (Begon *et al.*, 2006). Fires burn at different intensities depending of factors like wind, fuel load, time of the year, time since last fire, vegetation and slope (Bond & Van Wilgen, 1996; Gill *et al.*, 1981), and spread more rapidly through drier fuels, up slopes, and with the wind (Cochrane, 2009; Gill *et al.*, 1981). All these factors vary in combination across the landscape, changing the physical combustion process of energy release from organic matter—the fire intensity (Keeley, 2009).

The aims of this chapter are to describe the rosette size-class structure of *Puya hamata* populations within the burned landscape mosaic of the REEA and its buffer zone, to estimate recruitment, growth and mortality rates for *Puya hamata,* and to assess the impact of different intensities of burning on *Puya hamata* mortality.

Methods

To determine the population size structure, mortality, recruitment and growth rates of *Puya hamata* rosettes, 20 permanent plots, 20 × 20 m in area, were established in randomly chosen locations (Table 8.1). In July–August 2008, the coordinates (to the nearest 10 cm) and diameter of all *Puya hamata* plants in these 20 plots were recorded. The same plots were recorded again in July–August 2009. Unfortunately, the permanent marker posts for four plots had been removed and these plots could not be re-surveyed.

Table 8.1. Locations of 400 m^2 plots used for demographic survey of *Puya hamata* plants. Black dots represent the surveyed years. Meters above sea level (m.a.s.l.) was the standard metric measurement to record altitude in REEA.

Plot number	UTM Coordinates	Altitude (m.a.s.l.)	Year 2008	Year 2009
1	18 N 180258 74921	3702	•	•
2	18 N 180022 75560	3761	•	•
3	18 N 180089 75799	3768	•	•
4	18 N 178775 73543	3623	•	•
5	18 N 179754 74880	3732	•	•
6	18 N 179462 74314	3667	•	•
7	18 N 179559 74181	3654	•	•
8	18 N 180685 75446	3687	•	•
9	18 N 180812 75286	3656	•	•
10	18 N 179470 74121	3665	•	
11	18 N 179802 74152	3619	•	
12	18 N 179582 73851	3636	•	
13	18 N 180151 76113	3777	•	•
14	18 N 179862 75175	3771	•	•
15	18 N 179168 74281	3723	•	
16	18 N 179665 75081	3770	•	•
17	18 N 178110 71383	3430	•	•
18	18 N 178144 71536	3446	•	•
19	18 N 178335 71597	3449	•	•
20	18 N 177990 71391	3434	•	•

On 3rd August 2009, a fire burned the páramo in the SW part of the REEA and, owing to the topography and wind conditions on the day, a mosaic of unburned and burned patches of different fire intensities was created in one area. Normally, a fire burns until it meets barriers that prevent further spread (streams, cliffs, *etc.*) or it rains. In this case, the local fire brigade, reserve rangers, and investigators attempted to control the spread of the fire, and this resulted in fire boundaries that were not associated with the usual barriers. Fire was prevented from spreading to some areas that would otherwise have burned.

This known fire provided an opportunity to investigate *Puya hamata* mortality rates according to fire intensity. Four “treatments” were determined by observing the fire during its course and preventing its spread in some places (Photos by Paul M. Ramsay):

- unburned controls (estimated burned area = 0%)
  which would have burned without intervention to prevent the spread of fire
  UTM coordinates 18 N 181134 75111

- low intensity burn (estimated burned area = 25%)
  where the fire spread upslope with the wind behind it
  UTM coordinates 18 N 180691 75166

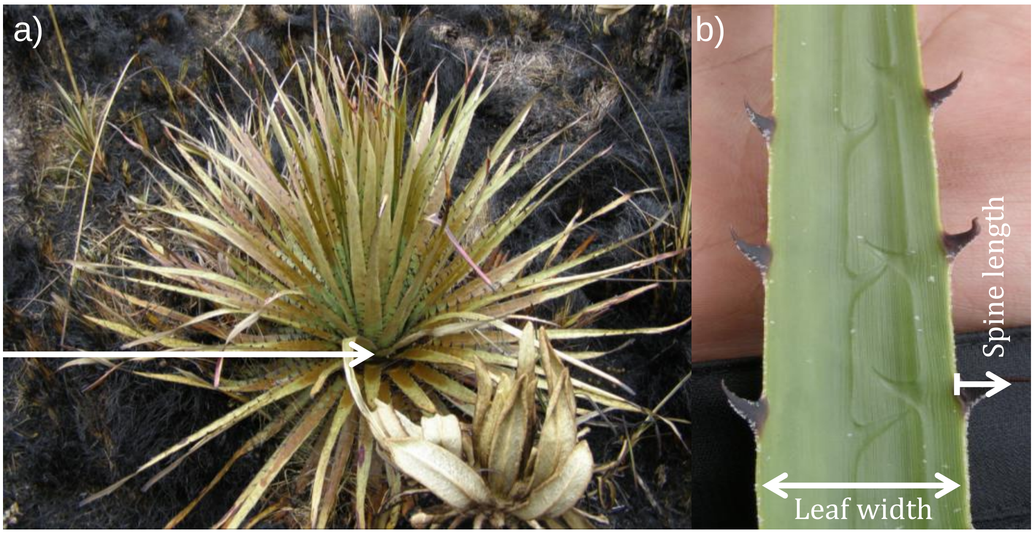
- medium intensity burn (estimated burned area = 60%)
  where the fire spread across relatively flat ground with the wind behind it
  UTM coordinates 18 N 180577 75013

- High intensity burn (estimated burned area = 100%)
  where the fire spread downslope against the wind
  UTM coordinates 18 N 181159 75149

One month after the fire, these areas were revisited and a single plot of 20 m x 20 m was established in each. The coordinates inside each plot of all *Puya hamata* plants were recorded, live or dead.

In the case of the control plot, or plants that escaped the fire in the burned plots, the diameters of *Puya* plants was measured. However, most of the plants in the high-intensity burned plots were badly damaged by the fire and the diameters of the plants before burning could not be measured. To reconstruct the original sizes of damaged *Puya* plants, a pilot study was established, using 50 *Puya hamata* rosettes across a wide range of diameters, to examine two correlates of plant size: leaf width and leaf spine length (Figure 8.1). For each plant, two horizontally-orientated leaves were sampled at random. For each leaf, leaf width near the base was recorded, and the lengths of two leaf spines were measured, from the point where the spines change direction from backward- to forward-pointing. Leaf width and spine length was calibrated against rosette diameter. Following this pilot study, the original diameters of damaged *Puya* rosettes was estimated from leaf width measurements on the burned plants.

Figure 8.1. Morphological correlates of *Puya hamata* rosette diameter used to reconstruct rosette sizes of burned plants. a) Diameter of the *Puya* rosette, b) leaf width, and spines length of *Puya hamata* were measured at the nearest point of emergence.



Results

Population size structure, mortality, recruitment and growth rates of *Puya hamata* rosettes was assessed using data from 400 m^2 permanent plots. In total, 1310 *Puya* rosettes, from 20 plots, were measured in 2008—representing a density of 0.14 m^{-2}. Only 16 plots were recorded in both years, and they contained exactly 1000 plants. Of these 1000 plants, 0.6% had died by the following year. One large rosette (1.6 m diameter) had been eaten, most likely by a spectacled bear (*Tremarctos ornatus*). The remaining five mortalities were for rosettes 0.1–0.5 m diameter. In these same 16 plots, only 27 new plants were recruited over the year. Mean rosette diameter of reproducing *Puya hamata* plants was 2.01 m (min=1.3 m, s=0.33 m, n=63).

The size distribution of *Puya hamata* rosettes varied from plot to plot (Figure 8.2). Broadly, three different size distribution patterns were observed:

- low plant number across all size ranges

- a single dominant peak at a particular size
- Two dominant peaks at distinct sizes

After one year, the size distributions had shifted a little, reflecting the growth of *Puya* rosettes and their movement into larger categories (Figure 8.3).

The mean annual diameter growth rate of *Puya hamata* rosettes was 0.081 m y^{-1} (s=0.032, n=1000). The growth rates measured from the diameter were different from one category to another (Table 8.2). Life span of *Puya hamata* was 27.5 years based on growth rates. Clonal growth or vegetative propagation was not recorded in *Puya hamata* plants.

Annual growth rate declined with rosette diameter (Figure 8.4a), but this does not mean larger plants grew less. The increase in overall plant biomass associated with a change in diameter of 1 cm is much greater for large plants than small ones. If annual growth rate is plotted against rosette area (in plan view) or volume (assuming the rosette is a perfect hemisphere) the true pattern of biomass accumulation becomes clearer (Figures 8.4b and c).

Both *Puya hamata* leaf width and spine length were closely related to rosette diameter, with the best predictor being leaf width (Figure 8.5). Therefore, the original rosette diameters of *Puya* plants damaged by fire were estimated using measurements of leaf width.

Plots recorded after burning were different from each other, number or individuals varied. Distribution of plants is presented in the figure 8.6. Dead plants were found in plots with high and medium intensity. Mortality rates was not affected between intensities of burning (G_{adj}= 9.893, df= 3, p=0.019).

Medium and high intensity of burning affected mortality in small plants (G_{adj}= 93.44, *df*=3, *p*<0.0001 and G_{adj}= 7.63, *df*=3, *p*=0.054 respectively; Table 8.3). Small plants were more likely to die. The high intensity of burning killed 4.5% of the total recorded plants (*n*= 286). Dead plants belonged to small categories (<50 cm diameter). Medium intensity burning killed 2.3% of the small plants. Low intensity and control had not mortality after one month of the recorded date of burning (Figure 8.7).

Table 8.2. Mean growth rates for 1000 *Puya hamata* rosettes according to size class.

Size-class (cm)	**Mean growth rate (m y^{-1})**	**Standard Deviation**
>0-0.3	0.10	0.03
0.6	0.08	0.03
0.9	0.07	0.03
1.2	0.06	0.03
1.5	0.06	0.03
1.8	0.05	0.03
2.1	0.07	0.03
2.4	0.04	0.03
2.7	0.05	0.03
3	0.01	0.01
Overall Mean	**0.06**	**0.03**

Figure 8.2. Size distributions of 1338 plants of *Puya hamata* from twenty 400 m^2 plots, surveyed in 2008. High density of small-diameter rosettes: P1, P7, P10 and P9. Plots with both juveniles and adults, representing several recruitment pulses: P4, P19, P12, P13. Plots with all categories of plants: P11, P17. Plots low density of large "adult" plants: P14, P20, P6, P5. The remaining ones had a wide range of rosette sizes and a positively skewed distribution.

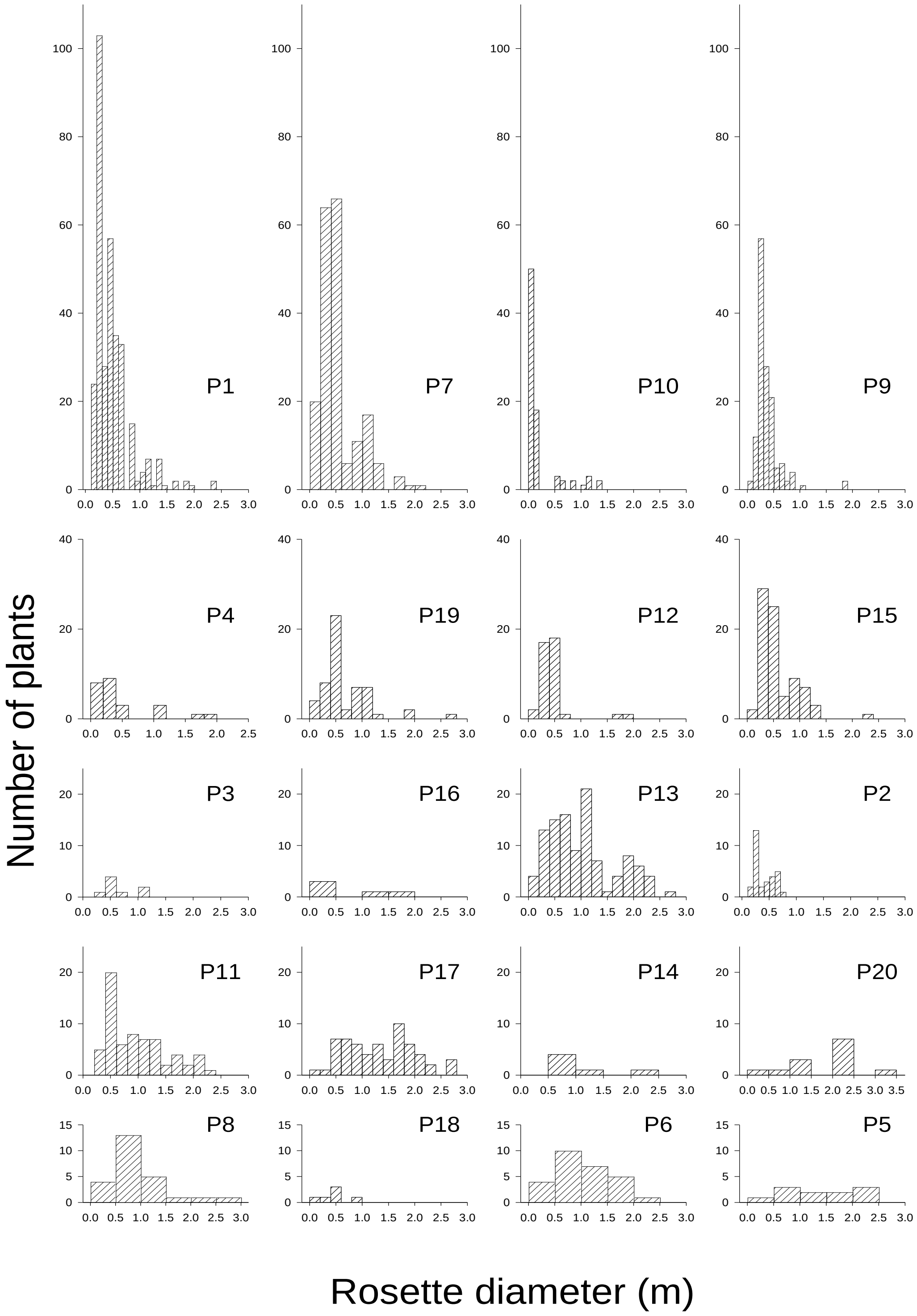


Figure 8.3. Changes in *Puya hamata* rosette size distributions from 2008 to 2009 in two example plots (P1 and P7). These two plots were selected because illustrate very clearly the redistribution of rosettes through time.

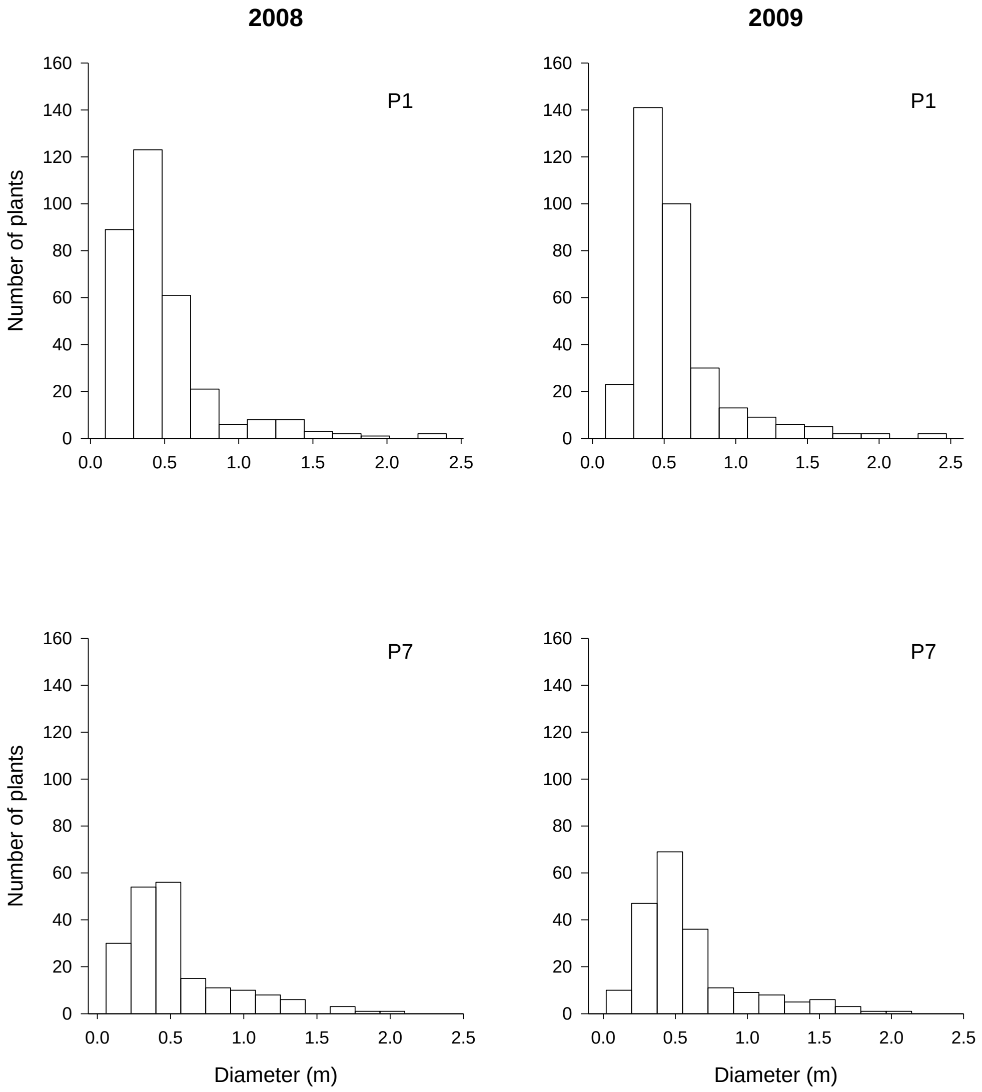


Figure 8.4. Annual growth rate of *Puya hamata* rosettes according to size categories: a) diameter (r^2=0.921, p<0.05), b) area (r^2=0.970, p<0.05) and, c) volume (r^2=0.976, p<0.05).

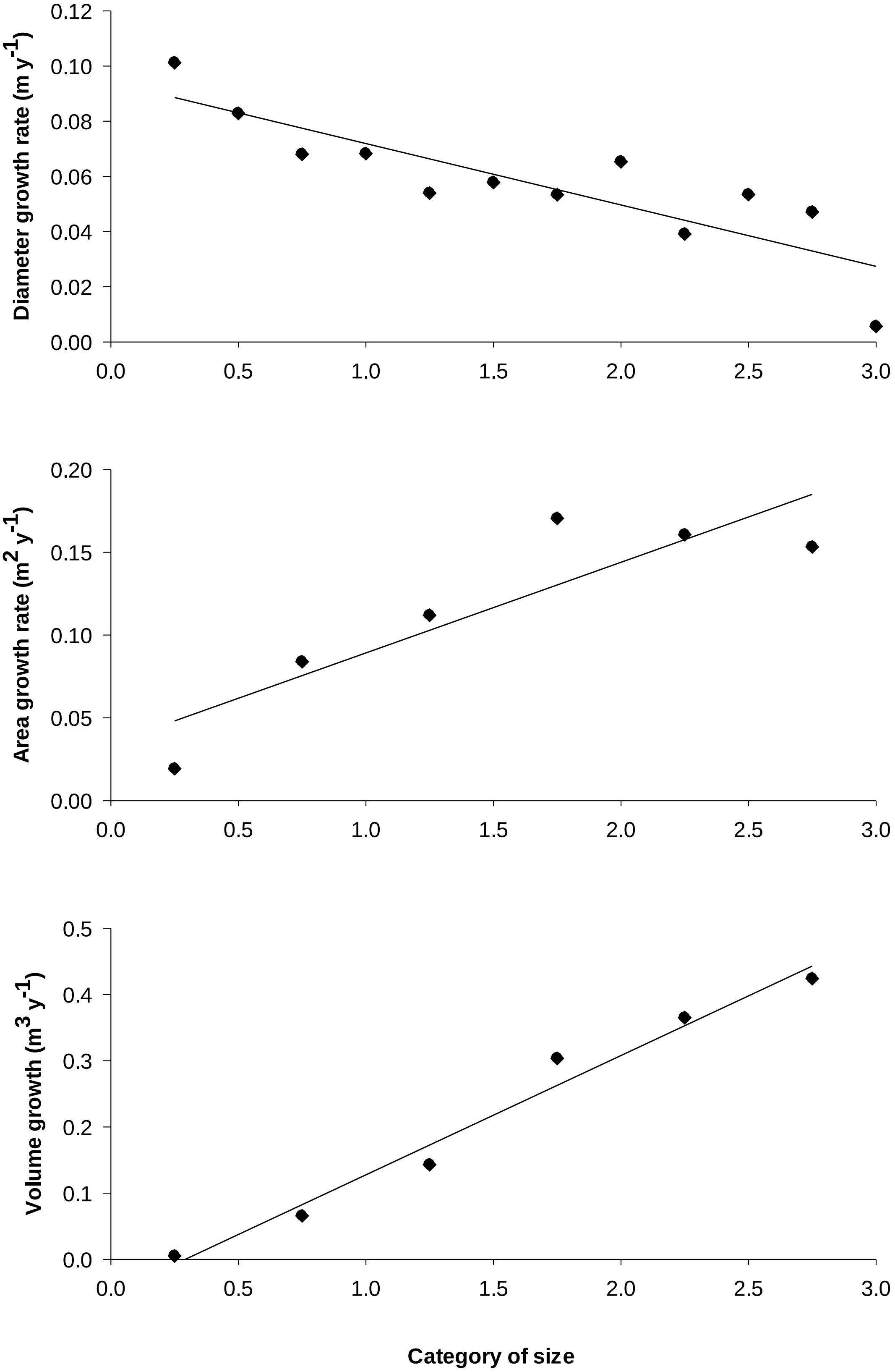
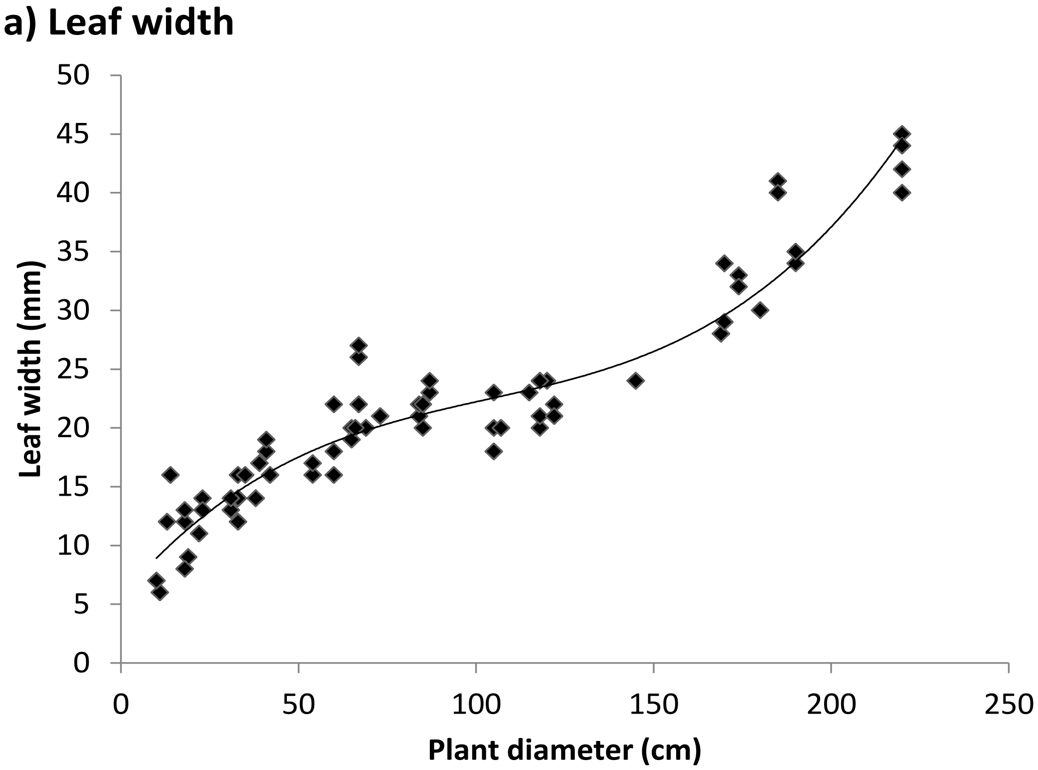


Figure 8.5. The relationship between rosette diameter and a) leaf width, and b) spine length, from a sample of 50 *Puya* plants. Both are positively correlated $r^2=0.907$, $p<0.05$ and $r^2=0.863$, $p<0.05$ respectively.



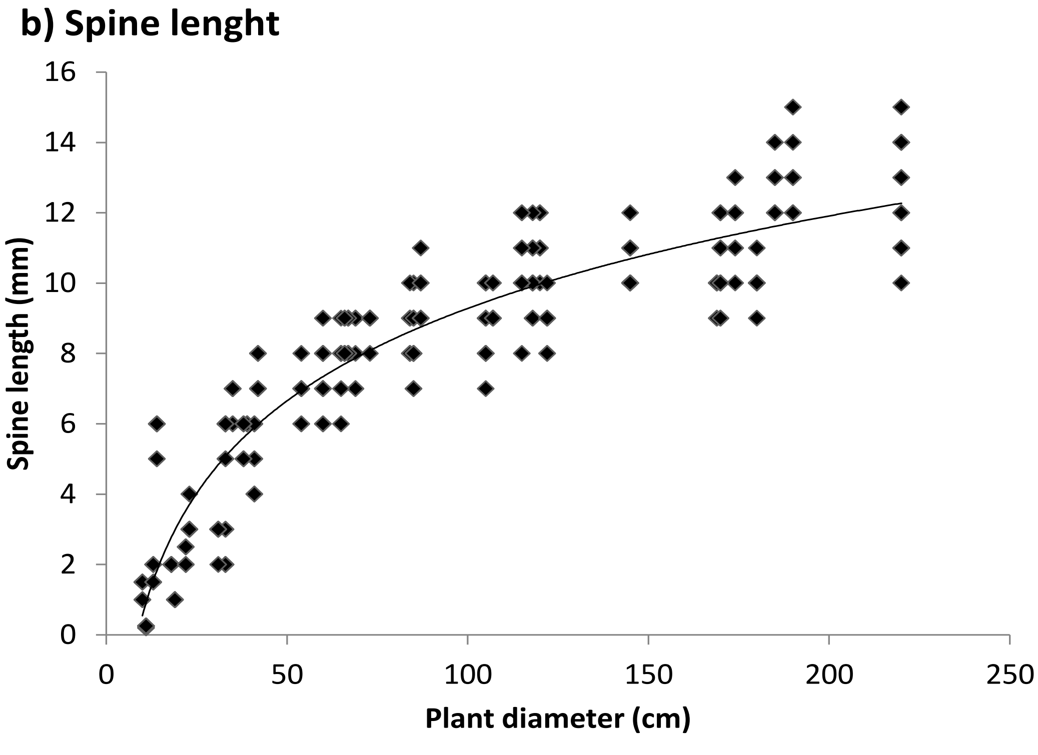


Figure 8.6. Sizes distribution of sizes of a) the control plot (without record of burning), b) plot with low, c) medium and d) high intensity of burning.

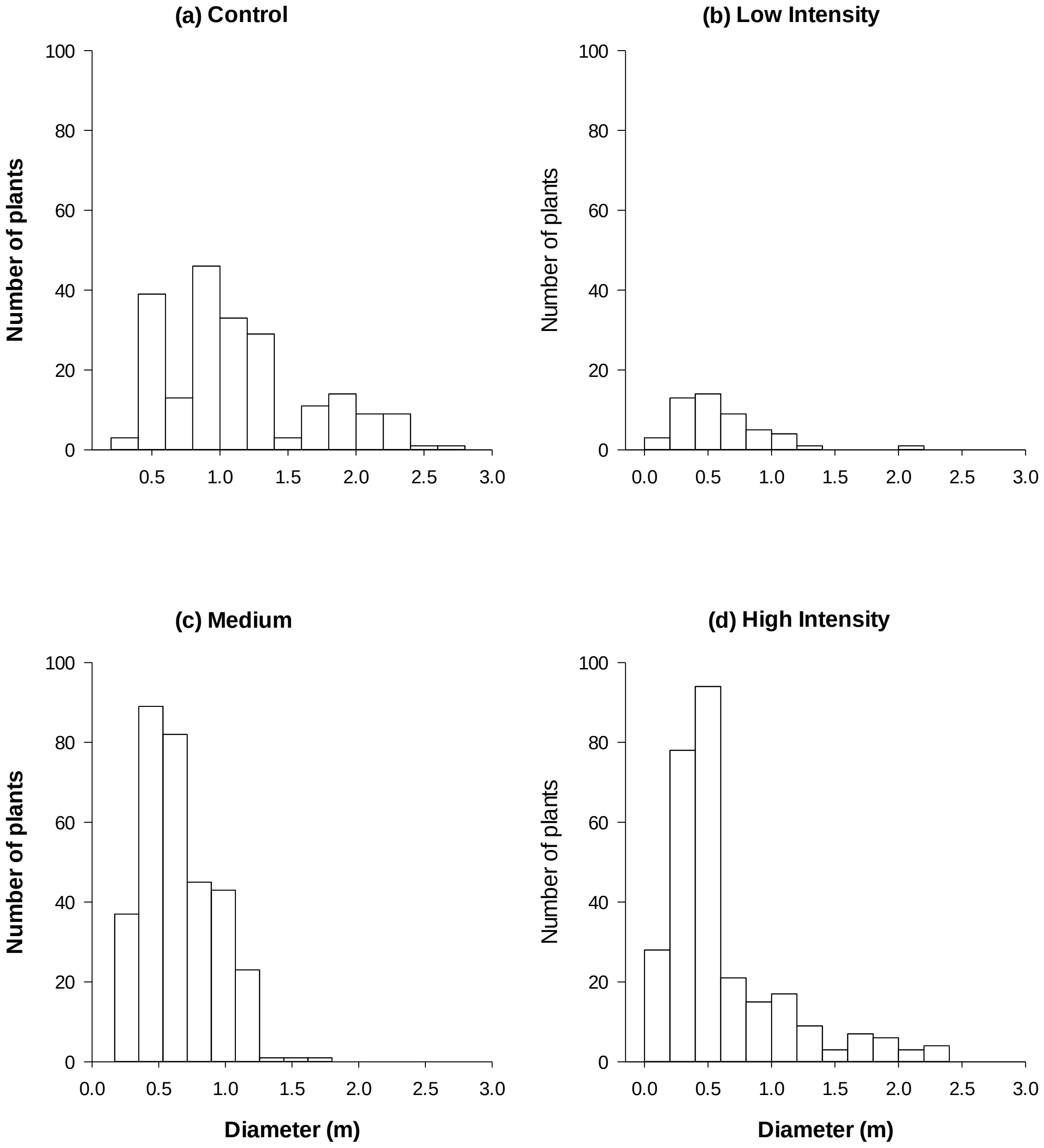


Figure 8.7. Percentage of *Puya hamata* dead plants recorded after one month at three different intensities of burning and control plot at REEA.

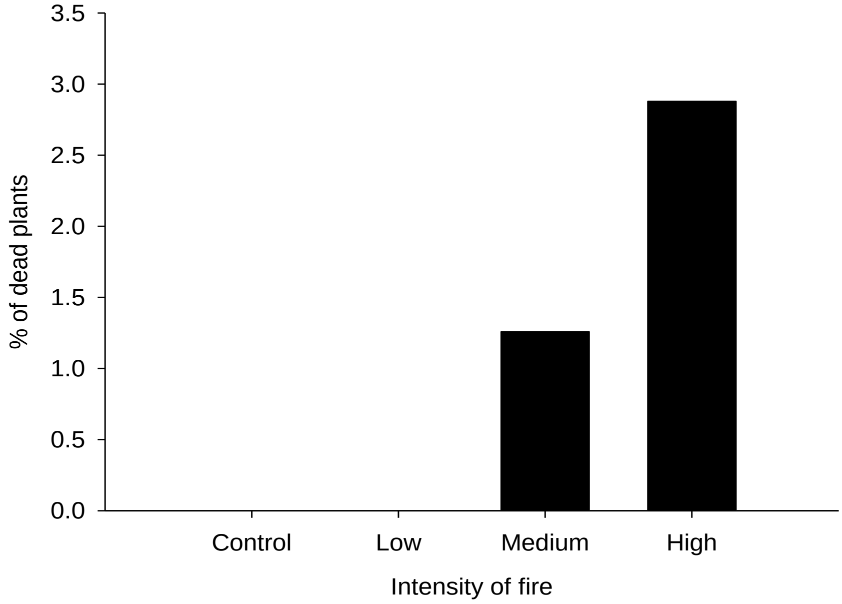


Table 8.3. Number of *Puya hamata* dead plants found in plots exposed to medium and high intensity burning per size category at REEA.

	High intensity			Medium intensity		
Size diameter (m)	Alive	Dead	%	Alive	Dead	%
0 – 0.50	176	8	4.3	126	3	2.3
0.51–1.00	64	0	0	170	1	0.6
1.01–1.50	26	0	0	25	0	0
1.51>1.5	20	0	0	1	0	0

Discussion

Puya hamata growth rate was not the same for all size categories. Miller (1988) found that *Puya clava-herculis* also showed considerable variation in growth rates between categories. He reported that rosettes found in well drained, low elevation sites grew faster and flowered at larger sizes than rosettes from a higher elevation site. Even though *Puya hamata* showed considerable variation in the growth rates between categories there was no variation in the size of reproductive rosettes. It is difficult to say whether all reproductive plants had the same age because great variation in growth rates makes adult diameter an unreliable estimate (Smith & Young, 1987), but it is notable that the majority had similar diameter at the time of reproduction (2.01 m).

Based on growth rates calculated in this study, the mean time that *Puya hamata* takes to become a potential reproductive plant of 2.01 m diameter is 27.5 years. Other species of *Puya* like *Puya dasylirioides* have a minimum critical size (40 cm diameter) before sexual maturity (Augspurger, 1985). *Puya raimondii* is estimated to grow for at least 120 years before reproduction (Ruiz, 1978).

Low recruitment rates were found in the field. Plots with high density of small individuals (1, 7, 8, 9 and 13) were the only ones which presented recruitment. In 2008, these plots already had a high density of small plants. These plots were characterised by short sparse tussock grass vegetation. Miller and Silander (1991) found that conditions such as bare ground, low temperatures, solifluction, and moisture stress reduce the probability of *Puya* establishment. *Puya* seedlings establish in areas dominated by cushion and mat plants (Miller & Silander, 1991).

Probably recruitment fluctuates as a consequence of spatio-temporal conditions (Hanley & Sykes, 2009) that fires can produce.

Puya hamata needs temperatures over 14 °C to germinate and most of the seeds of the experiments germinated in full light (Chapter 7). Open areas—most common after fires—provide conditions for germination and cushion and mat plants promote recruitment in places with low density vegetation. Miller and Silander (1991) recognized that the amount and type of ground cover as well as the distance and growth form of nearest neighbours are important factors that determine the local distribution of some *Puyas.*

Size structure of *Puya hamata* varied from plot to plot and these differences might be related to fire history. Myers (2006) recognised that virtually all terrestrial ecosystems have a fire regime, and that the history of fire has shaped or affected structure of the species.

Three size structure patterns were found:

- *Plots with low plant number across all size ranges (with some stochasticity)*
  This pattern results from the absence of fires during life time of the *Puya* plants, and resulting low but constant recruitment rates (illustrated in Figure 8.8, t_0).
- *Plots with a single dominant peak at a particular size*
  This pattern is caused by a single fire during the last 30 years that produced open vegetation. Recruitment was low before the fire, then, for a short period after the fire, there was higher recruitment. Thereafter, low recruitment returned (see Figure 8.8 *t*5, *t*15).

- *Plots with two dominant peaks at distinct sizes*

  The pattern is occasioned by two fires during 30 years. There are two periods of recruitment but otherwise low recruitment levels are present (Figure 8.8, *t*28).

These results agree with Enright & Lamont (1989) and Bond & Keeley (2005): in grassy/shrubby ecosystems, fires are frequently provide safe sites for seedlings and fire-stimulated seedling recruitment. Perturbations at large scales can lead to a population structure with distinct cohorts and also to very uneven size and age distributions (Ramsay, 1998; Smith & Young, 1982; Smith & Young, 1987). It seems that *Puya hamata* size structure inside the REEA reflects fire regimes in more than just the density of individuals.

Mortality was low at all sizes in the revisited plots from 2008 to 2009. However, the smallest plants were the most vulnerable. It is well known that small plants have higher probabilities of death (Doak & Morris, 2010; Fenner & Thompson, 2005; Gatsuk *et al.*, 1980; Rogers, 1985). Only one large plant died in this period of time, mostly lately due to damage caused by a large animal. Spectacle bears (*Tremarctos ornatus*) inhabit the páramos of REEA and are probably are the only predators of *Puya* capable of dealing with the spiny leaves. As they seek the developing inflorescences of *Puya* (Cuesta *et al.*, 2003; Gallo *et al.*, 2011; Kattan *et al.*, 2004; Peyton, 1980).

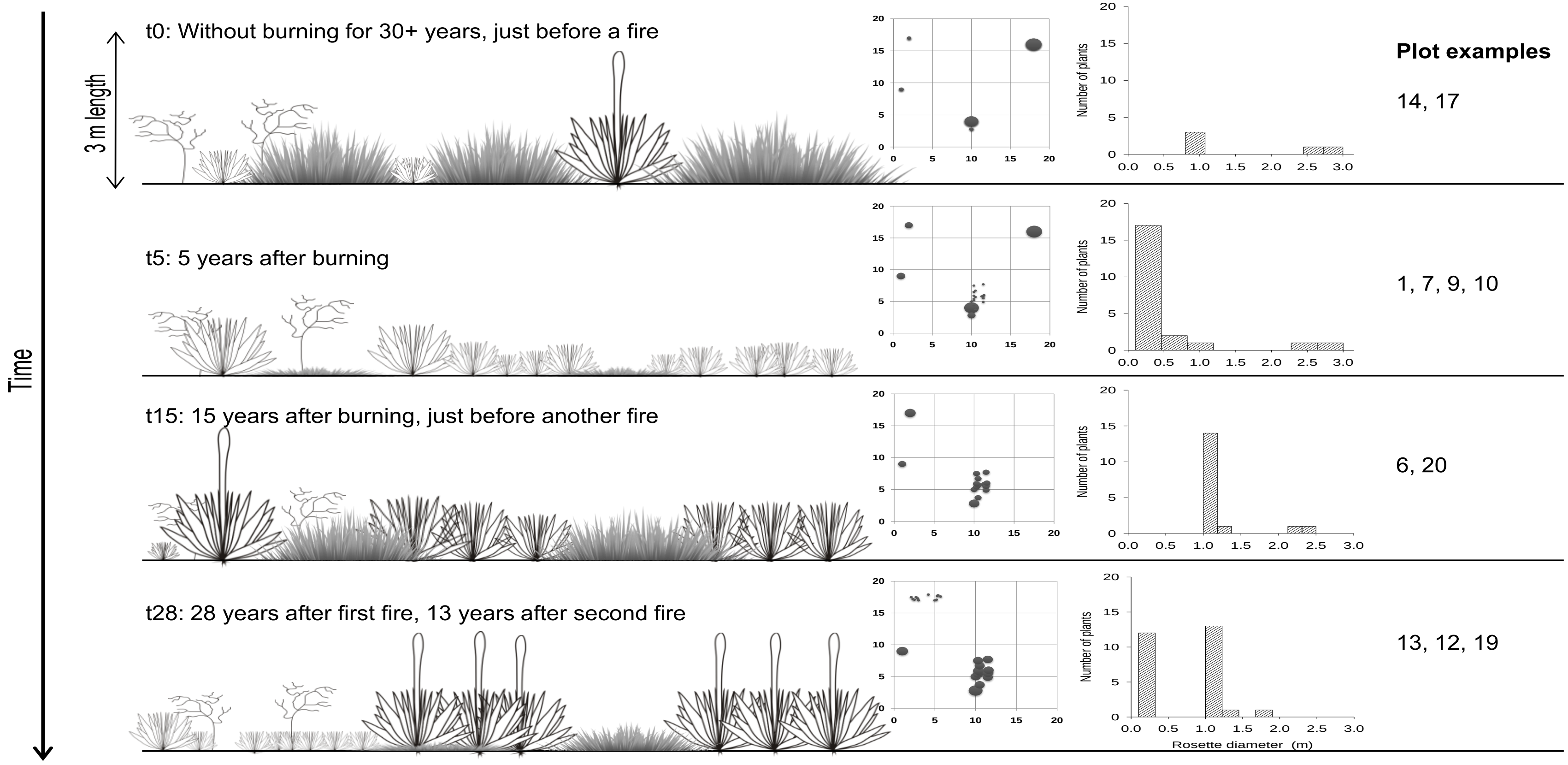
Plots marked after the fire in 2009 presented dead *Puya* plants only at medium and high intensities in REEA. The low intensity fire plot had no observed plant mortality, but in the medium intensity fire plot, 2.3 % of small plants (<0.5 m) died, and 4.3% of plants <0.5 m diameter died in the high fire intensity plot. It is possible that more plants from small categories died later, but this will need to be confirmed in additional studies in the future. Such work on mortality rates in burned and unburned areas are essential to understanding the impact of different intensities of fires on *Puya hamata* populations. Low mortality juveniles and adults is assumed to be a prerequisite for the semelparous life history strategy (Young & Augspurger, 1991) and it would be expected that typical fires in the páramo have little impact on most existing *Puya* plants—but this needs to be demonstrated.

In general, *Puyas* do have low mortality rates. *Puya hamata* is well adapted to survive burning after they reach certain size. Basal rosettes—as defined by Ramsay and Oxley (1997)—are life forms in páramo that protect their central meristem. Rosetophilic life forms keep the central meristem protected from drought conditions, cold, snow (Smith & Young, 1987) and fires (Simon *et al.*, 2009) in tropical alpine habitats (*e.g., Lobelia, Agave, Draba, Senecio* and *Puya*). Fires can burn away almost all *Puya* leaves but if the meristem is undamaged the plant will recover afterwards. In general terms, plant rosettes tend to be rather tolerant to disturbances (McIntyre *et al.*, 1995). This can be seen in members of the family Bromeliaceae like *Cryptanthus, Dyckia* and *Encholirium* native of the south of Brazil, *Ayensua* and *Brocchinia melanacra* of highlands habitats from Guyana, *Hechtia* in México and some Andean *Puyas*, which resist fire by having mantles of persistent insulating basal leaves (Benzing, 2000).

Demographic patterns like low recruitment, long lifespan and low mortality rates, make *Puya hamata* a potential indicator of recent fire history during an approximate 30 y window, with potential to identify several different fires during this period. The marcescent leaves of *Espeletia pycnophylla*, another páramo giant rosette plant, could also be used as a record of fire frequency/history (Ramsay *et al.*, in preparation). Burning signs on *Espeletia* only provide information about the last fire to occur in a particular place. The use of both these plants together could give a good indication of fire history, but more development of this method is necessary.

The evolution of semelparity in *Puya hamata* is closely related to low mortality rates (Young, 1984; Young, 2010). There are studies of the evolution of life histories that identify the survival and reproduction factors that favour a delay in reproduction (Stearns, 1977; Young, 1990; Young, 1984). However, specifically for *Puya* more studies of mortality and reproductive episodes are necessary to understand the evolution to semelparity. Simulations with LandBaSE-P could test various different scenarios in this context.

Figure 8.8. Succession of population dynamics in *Puya* plants after burning. *t0*) Profile of an unburned site with large individuals, *t5*) Profile of an burned site with new individuals *t15*) Profile after 15 years burning and *t28*) Profile after 28 years of burning. All profiles have their spatial distribution of plants and histogram of this hypothetical population.



9

Simulation modelling of *Puya hamata* populations in response to fire regimes, dispersal patterns and germination responses

Introduction

The long-term study of population dynamics at the landscape scale is a valuable approach, because it is at these scales that some important ecological processes occur (Turner *et al.*, 1995). For example, pollination by hummingbirds is a process that occurs at large scales but one which is disrupted if there are changes in the availability of food (Steffan-Dewenter *et al.*, 2001). Long distance seed dispersal is another landscape scale process, facilitating the genetic connectivity between landscapes (Bacles *et al.*, 2006). These two processes are key in the population dynamics of *Puya hamata*. Fires are an important landscape-scale disturbance which interacts in a complex way with population dynamics (Bond & Van Wilgen, 1996; Eva & Lambin, 2000).

However, studies at landscape scales over long periods of time are complicated (Turner, 2005) and computer simulation is often the only practical approach to address population dynamics. The LandBaSE-P programme was developed for studying the population dynamics of *Puya hamata* at large spatio-temporal scales. It simulates population dynamics using parameters of the plant's life cycle. Some of these parameters were estimated from experimentation in the field and laboratory. On the other hand, others are uncertain or completely unknown. For these, the researcher can infer them based on educated guesses (Grant *et al.*, 1997), but the impact of these assumptions can be tested to some extent using simulations. Thus, models provide an opportunity to explore the impact of uncertain parameters, as well as population processes at large scales.

The generation of simulated environments that closely match the real world is not as easy task. One single simulation at a large spatio-temporal scale could take days to run in a programme that considers large number of parameters. Nevertheless, the potential of simulations to offer replication and across a variety of scenarios make this approach a powerful tool for the study population dynamics.

The aims of this chapter are to illustrate simulations of *Puya hamata* populations in páramos subject to different fire regimes at the landscape scale and over long periods of time, to explore the impact of uncertain parameters in the model, to evaluate the suitability of LandBaSE-P for research and to propose future research using LandBaSE-P.

Methods

LandBaSE-P simulations were carried out on an Intel Xeon Processor X550 computer with 16 cores at 2.67 Hz and 16 GB RAM memory.

Fire regimes

As a first step, LandBaSE-P was used to explore the range of potential fire regimes within the model environment. These fire regimes form the backdrop for *Puya hamata* population simulations in later simulations.

The regimes were based on the concepts of fire frequency and fire extent. Fire frequency was defined as the amount of time it takes to burn the equivalent of a specified area—with the understanding that some areas may not burn while others burn more than once during a cycle—and the fire extent was defined as the area of a given fire (Cochrane, 2009).

Target fire regimes for use in the simulations were:

- No fires
- Rare extensive fires. Fires every 100 years or more on average.
- Occasional medium-sized fires. Fires every 25-30 years on average.
- Frequent relatively small fires. Fires every 10-12 years on average.
- Very frequent small fires. Fires every 4-5 years on average.

Initial values were fixed to start the sets of simulations (landscape dimension, time of the run, cell size) and were selected as follows (Figure 9.1):

- The landscape dimension was fixed at 9 km^2. This scale was selected because it reduces the effect of stochasticity and reflects an appropriate scale at which ecological processes like pollination and seed dispersal take place (Contreras *et al.*, 2011).
- All runs were limited to 100 years.
- Two cell sizes were selected. Cell of 16 m^2 were tested because at this size cell the spatial arrangement of plants was more realistic. But cells of 400 m^2 were used because this matched the survey plot size used in Chapter 8.
- The fuel ignition threshold was set at 1000 arbitrary units. Once a cell accumulates this many units, it can burn, and the fuel units are reset at zero. Every year, 200 arbitrary units of fuel accumulate, meaning that it takes five years for the fuel levels in a cell to recover after a fire to the point where another fire could take place.

Fire regime is mostly controlled by fire start probability and fire spread probability (from cell to cell). Initial scoping simulations were established to find where the key transitions in fire regime took place, simulating fires in 49 combinations of seven fire spread and seven start probabilities. Each combination had 10 replicates. Table 9.1 shows the detail of the rest of the simulation set-up.

Fire regime was assessed using the total number of fires during the 100 y period, the percentage (%) of landscape burned (which may be more than 100% if fires burn several times during simulation period), fire frequency and fire extent (mean fire area).

Table 9.1. Parameters of LandBaSE-P its allocations and the values used for the runs in the exploration of fire regime, seed dispersal and seed germination probabilities of *Puya hamata* population dynamics. User and fieldwork designations are the allocation of the information. The field with the designation of "treated with different values" were values that changed to be tested.

Parameters	Allocation	Values used for the runs
Landscape		
Landscape dimensions	User	25 km2
Cell size (side)	User	16 m2 and 400 m2
Fuel accumulation per year	User	200
Ignition threshold	User	1000
Germination threshold	User	800
Fire start probability	User	Treated with different values
Fire spread probability	User	Treated with different values
Time step	User	2
Seeds		
Initial no of seeds	User	
Seed longevity	Fieldwork	5
Longevity SD	Fieldwork	1
Dispersal distance	Fieldwork	Treated with different values
Germination probability (Normal)	Fieldwork	Treated with different values
Germination probability (Burnt)	Fieldwork	Treated with different values
Fire death probability	Fieldwork	
Time step	User	1
Plants		
Initial No of plants	User	4, 062, 500
Max no of plants	Fieldwork	Treated with different values
Mean maturation age	Fieldwork	28
Maturation age SD	Fieldwork	2
Fire death probability	Fieldwork	2
Time step	User	2
Flowers		
Start of flowering season	Fieldwork	Week 26
End of flowering season	Fieldwork	Week 43
Number of flower on each inflorescence	Fieldwork	1
Flower life time	Fieldwork	18 weeks
Number or seeds/from each flower	Fieldwork	Treated with different values
Max pollination distance	User	1000
Pollination probability	User	100
Fire death probability	User	0
Time step	User	2 months
Statistics		
Statistics interval	User	2 months
No of age classes	Fieldwork	30
Spatial statistics	User	N/A

The impact of rare, long-distance seed dispersal

Chapter 6 discussed suitable kernels for seed dispersal. The selected kernel was the Truncated Pareto distribution. This Pareto distribution locates the majority of the seeds close to the parent plant but also has a very long tail which represents the rare events of long seed dispersal. The truncation of the distribution is the maximum value of seed dispersal distance ($X_{\max}$).

Six distance values (truncation) of $X_{\max}$ were used to explore the impact of rare, long-distance seed dispersal on *Puya hamata* population dynamics: 10, 50, 100, 500, 1000 and 5000 m. The minimum dispersal distance ($X_{\min}$) was set at 1 m. A value of $\alpha=2.0$ was used in all simulations.

One simulation for each scenario was run over 500 years at 9 km^2 and a cell size of 400 m^2. The comparisons were assessed with *Puya hamata* population size. ‘No fire’, ‘rare’, ‘occasional’ and ‘frequent’ fire regimes were run.

Relative germination rates for burned and unburned páramo

Germination rates of *Puya hamata* in the field are low but the actual rates are uncertain. Three relative germination responses were defined, to represent extremes of potential *Puya hamata* germination in response to fire in the simulated environments. Germination probabilities in burned and unburned areas can generate two extreme scenarios and all the variation in between:

1. *Stable in burned páramo*

   Populations maintain themselves only if there are continual fires. Without fires, populations disappear because the unburned germination rate is low.

2. *Stable in unburned páramo*

   Populations maintain themselves without fires; populations grow quickly because the burned germination rate is much higher.

3. An intermediate scenario is any variation in between the first two defined scenarios 1 and 2.

Although each plant on average produces 68,000 seeds, only one of these needs to germinate (assuming low mortality) to maintain population size. With potentially thousands of *Puya* inflorescences producing billions of seeds in the simulated landscape each year, the number of calculations required to run the model would be very high—and unnecessary because almost every seed would fail to germinate. To enable the model to run more effectively, the number of seeds dispersed was cut down to the minimum necessary, and the germination rates adjusted to achieve the levels required.

Three relative germination weights were used to explore the balance of germination response between burned and unburned páramo:

- Germination 5 times more likely in burned than in unburned areas
- Germination 25 times more likely in burned than in unburned areas
- Germination 100 times more likely in burned than in unburned areas

‘No fire’, ‘rare’, ‘occasional’ and ‘frequent’ fire regimes were run.

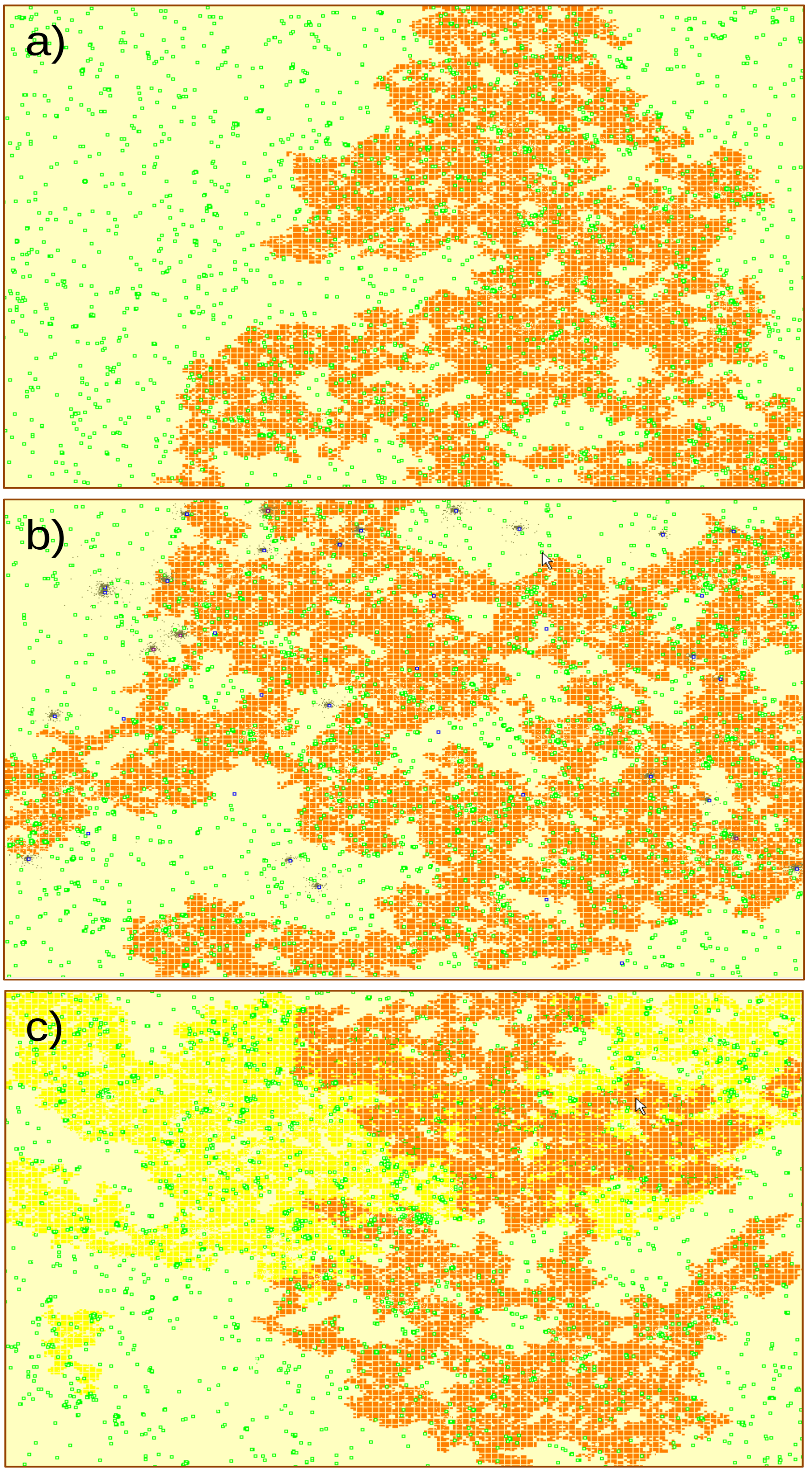
Results

Fire regimes

The simulation of páramo fires produced a burned landscape mosaic, with patches of unburned and burned páramo in various stages of recovery (Figure 9.1). The patchiness occurs across a wide range of spatial scales. Maps generated by

LandBaSE-P simulate the expected patterns. They had a variety of burned and unburned areas.

Figure 9.1. Display shots of LandBaSE-p which showed a mosaic burning at large scales. Green squares represent Puya plants, orange shading represent fires, pale yellow are not burned areas and yellow shading are recovering zones after a fire.

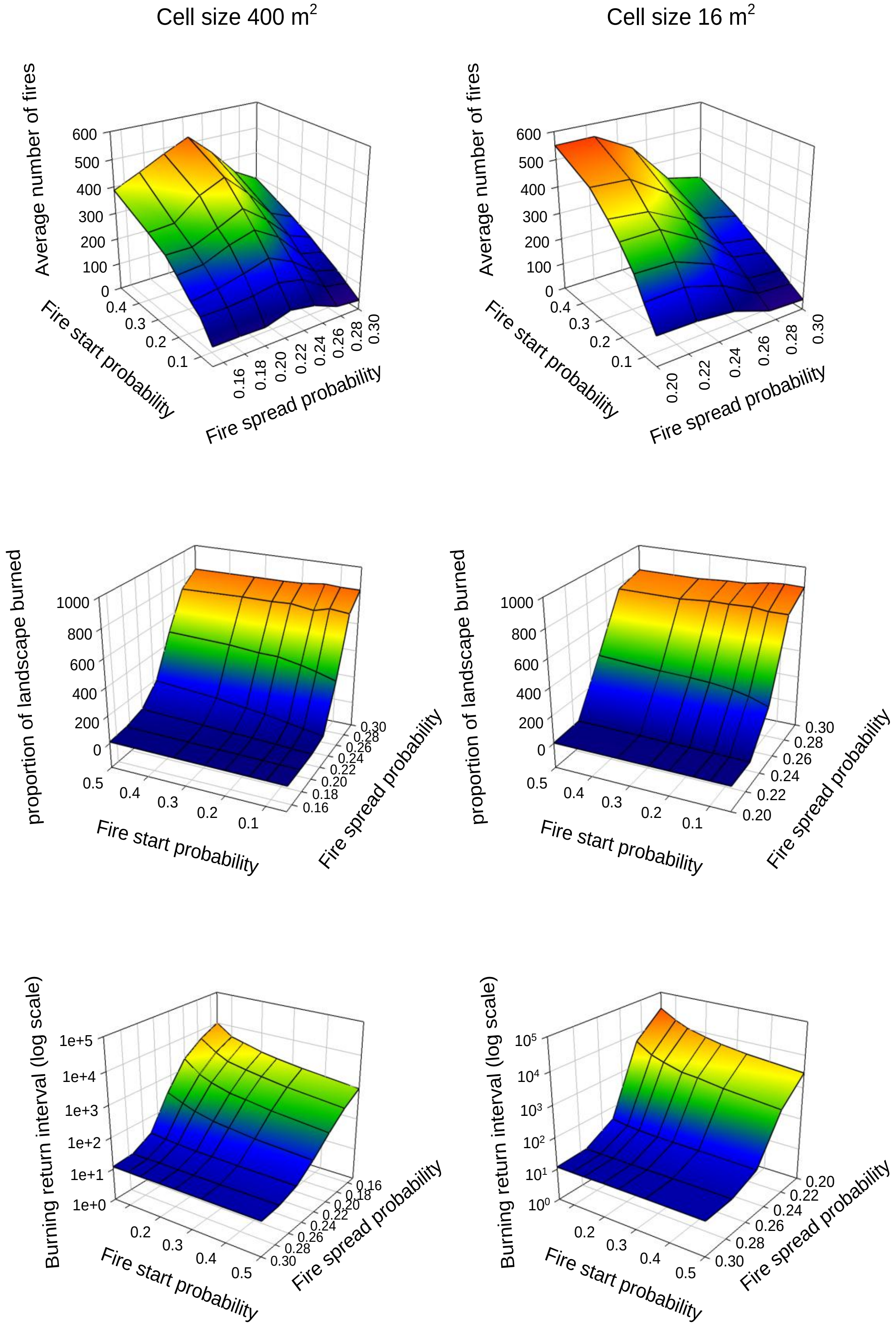


Cell size does not affect the basic pattern of fire regime, which is controlled by a combination of fire start probability and fire spread probability (Figure 9.2). It was found that fire spread probability is the most important parameter controlling fire regime in the simulation model. From these simulations, four fire regimes (at 400 m^2 cell size) were chosen to represent scenarios of interest for conservation and land use management: 'no fire', 'rare', 'occasional' and 'frequent' fires (Table 9.2).

Table 9.2. Fire regime statistics used to select four fire regimes in simulated environments with LandBaSE-P. Fire regimes were defined based on the return interval, number, proportion and size of fire.

Regime	**Fires start *p***	**Fire spread *p***	**Return interval (years)**	**Number of fires**	**Burned proportion**	**Fire patch size (km^2)**	**Fires patch size (*s*) (km^2)**
No fires	0	0	0	0	0	0	0
Rare	0.20	0.24	112	110	90	0.16	0.28
Occasional	0.20	0.26	50	90	203	0.57	1.23
Frequent	0.50	0.80	22	97	335	0.87	1.59

Figure 9.2. Comparison of the 49 combinations of fire start and spread probabilities simulated with two different cell size 400 m^2 and 16 m^2 in LandBaSE-P to find the four fire regimes used in this Chapter.



The impact of rare, long-distance seed dispersal

‘No fires’, ‘rare’, ‘occasional’, ‘frequent’ fires regime scenarios were used and it was found that $X_{\max}$ did not affect population size in these fire regimes (Figure 9.3). The population of *Puya hamata* declined more or less constantly over the simulation period—and would eventually become extinct—in the ‘no fires’ scenario. In the ‘rare fires’ scenario, the *Puya hamata* population remained stable but replicates were variable between them (Figure 9.3b). Increases in the number of fires decreased fluctuations in the number of individuals in ‘rare’, ‘occasional’ and ‘frequent’ fire scenarios but long-distance seed dispersal was not different. After results of seed dispersal were obtained an $X_{\max}$ of 1000 m was used for the subsequent simulations.

Relative germination rates for burned and unburned páramo

In the simulations of relative germination rates the four fire regime scenarios were used (‘no fires’, ‘rare’, ‘occasional’, and ‘frequent’ fires). ‘No fires’ and ‘rare’ fire regime scenarios showed similar patterns in population dynamics according to relative germination response and weights. *Puya hamata* declined to extinction in both ‘stable in burned’ and ‘intermediate treatments’, but this happened faster in the ‘stable in burned’ vegetation response and as the relative advantage of burned páramo for germination increases. ‘Stable in unburned’ response, by definition, maintained a very stable population in the ‘no fires’ scenario. *Puya hamata* population increased almost twice in ‘stable in unburned vegetation’ as a response of ‘rare fires’. The population increased slowly and was maintained stable though time.

In ‘occasional’ and ‘frequent' fires also *Puya hamata* declined to extinction in ‘stable in burned’ but it is maintained in ‘intermediate’ treatments. ‘Stable in unburned’ response, maintained a very stable population in ‘occasional’ and ‘frequent’ fires scenarios too (Figure 9.4).

Relative germination weights (5, 25 and 100 times) did not show effects on *Puya* populations simulations in ‘stable in burned’ and ‘unburned’ treatments. But in ‘intermediate’ treatments relative germination weights has an effect. Relationship between germination in unburned and burned areas was the most realistic of all simulations.

Figure 9.3. *Puya hamata* population size with different seed dispersal distance in four fire regimes ('no fires', 'rare', 'occasional', 'frequent' fires). Each line represents a different X_{max} value.

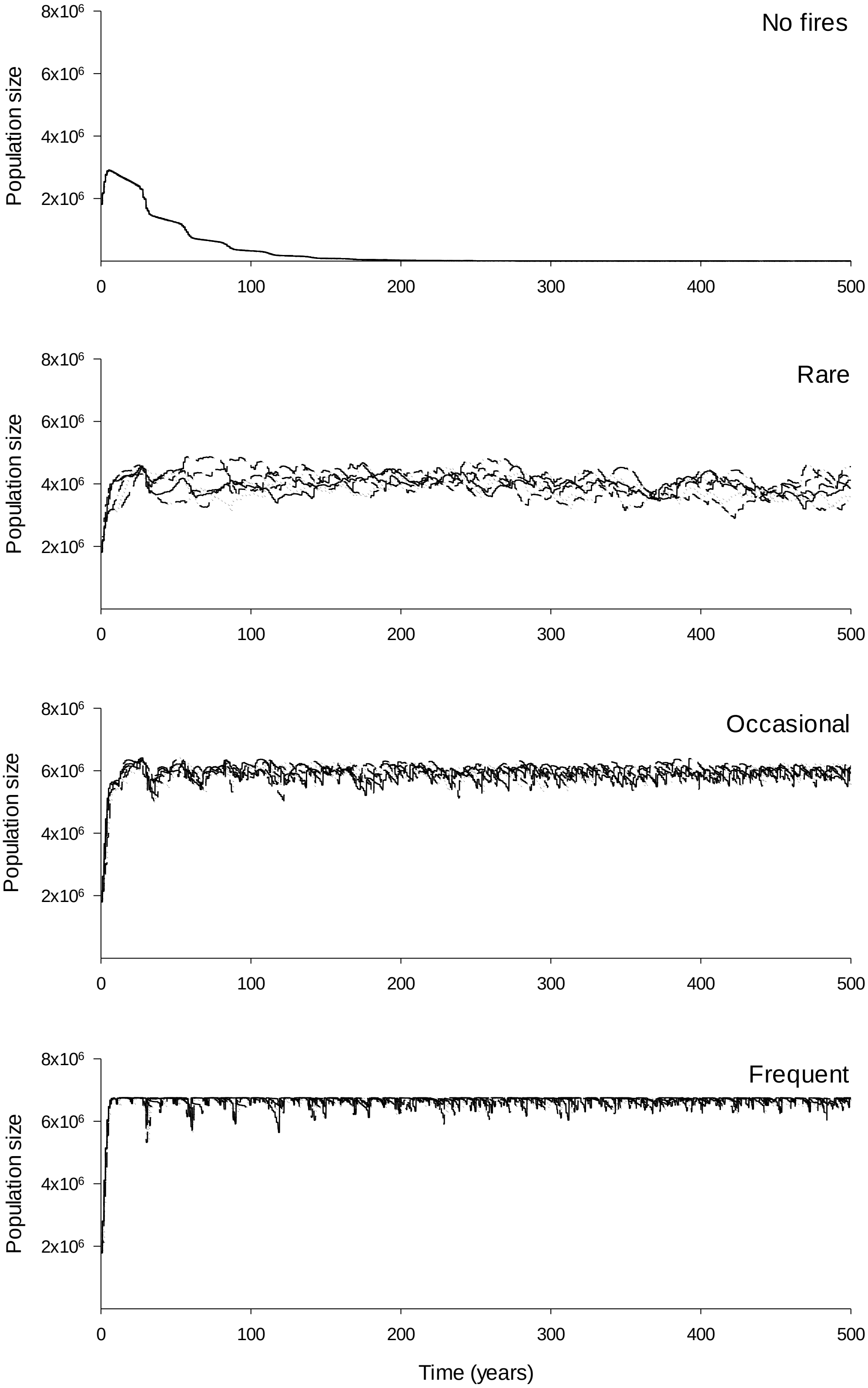


Figure 9.4. *Puya hamata* population size with three relative germination weights. Solid lines represent the germination 5 times (more likely in burned than in unburned). Dotted lines represent germination 25 times (more likely in burned than in unburned), and dashed lines represents germination 100 times (more likely in burned than in unburned) in 'no fire' regimes.

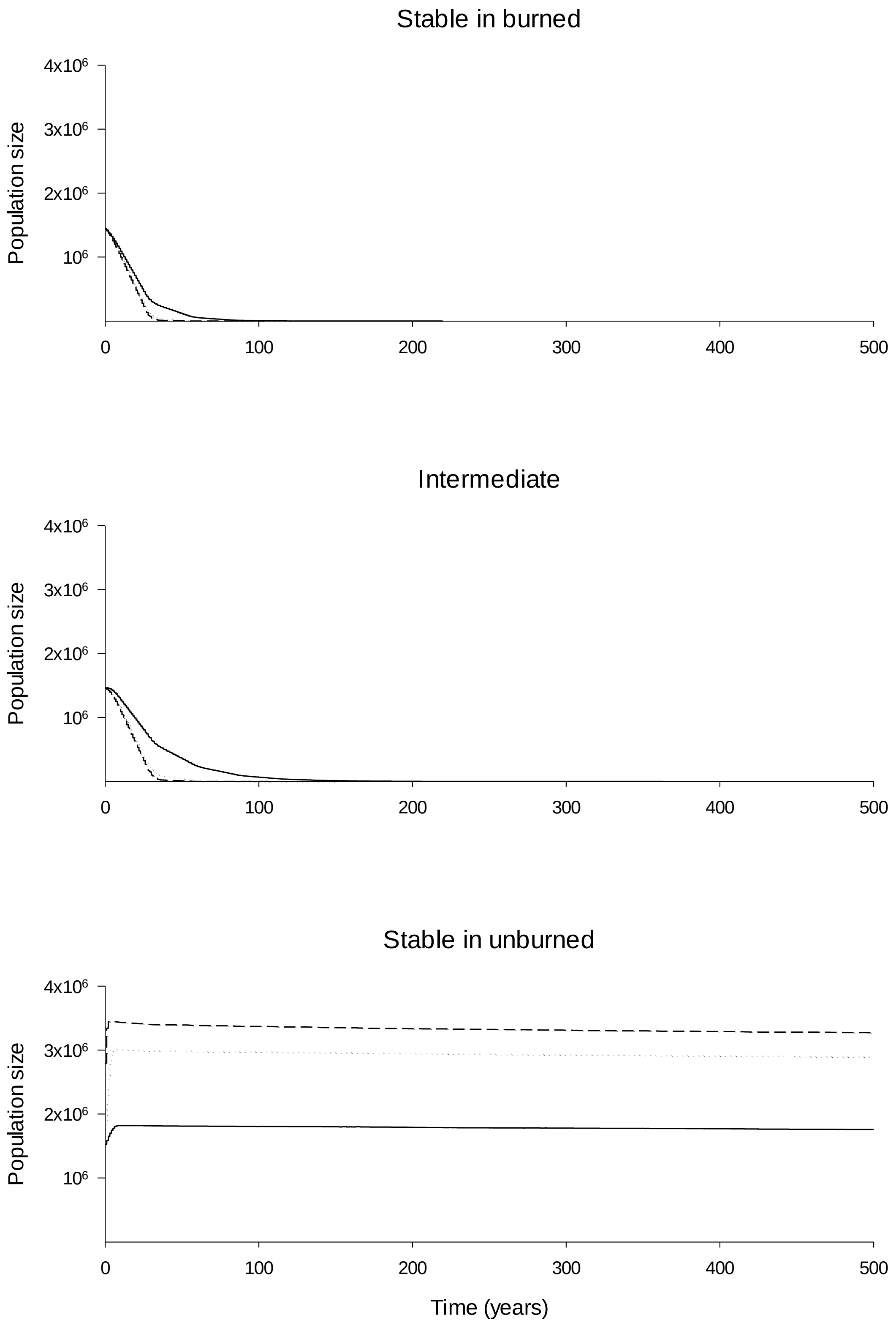


Figure 9.5. *Puya hamata* population size with three relative germination weights. Solid lines represent the germination 5 times (more likely in burned than in unburned). Dotted lines represent germination 25 times (more likely in burned than in unburned), and dashed lines represents germination 100 times (more likely in burned than in unburned) in 'rare fires' regime.

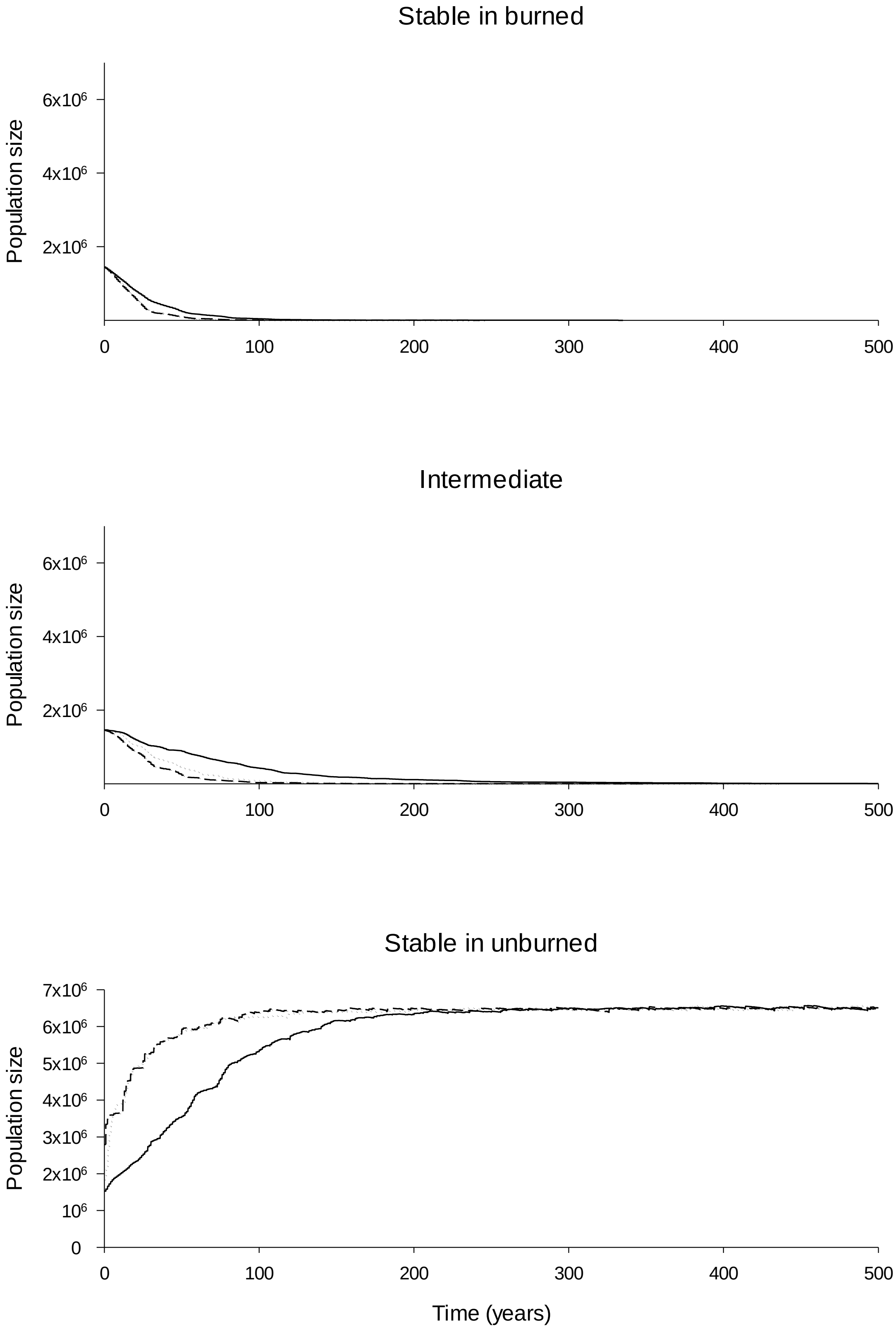


Figure 9.6. *Puya hamata* population size with three relative germination weights. Solid lines represent the germination 5 times (more likely in burned than in unburned). Dotted lines represent germination 25 times (more likely in burned than in unburned), and dashed lines represents germination 100 times (more likely in burned than in unburned) in 'occasional fire' regime.

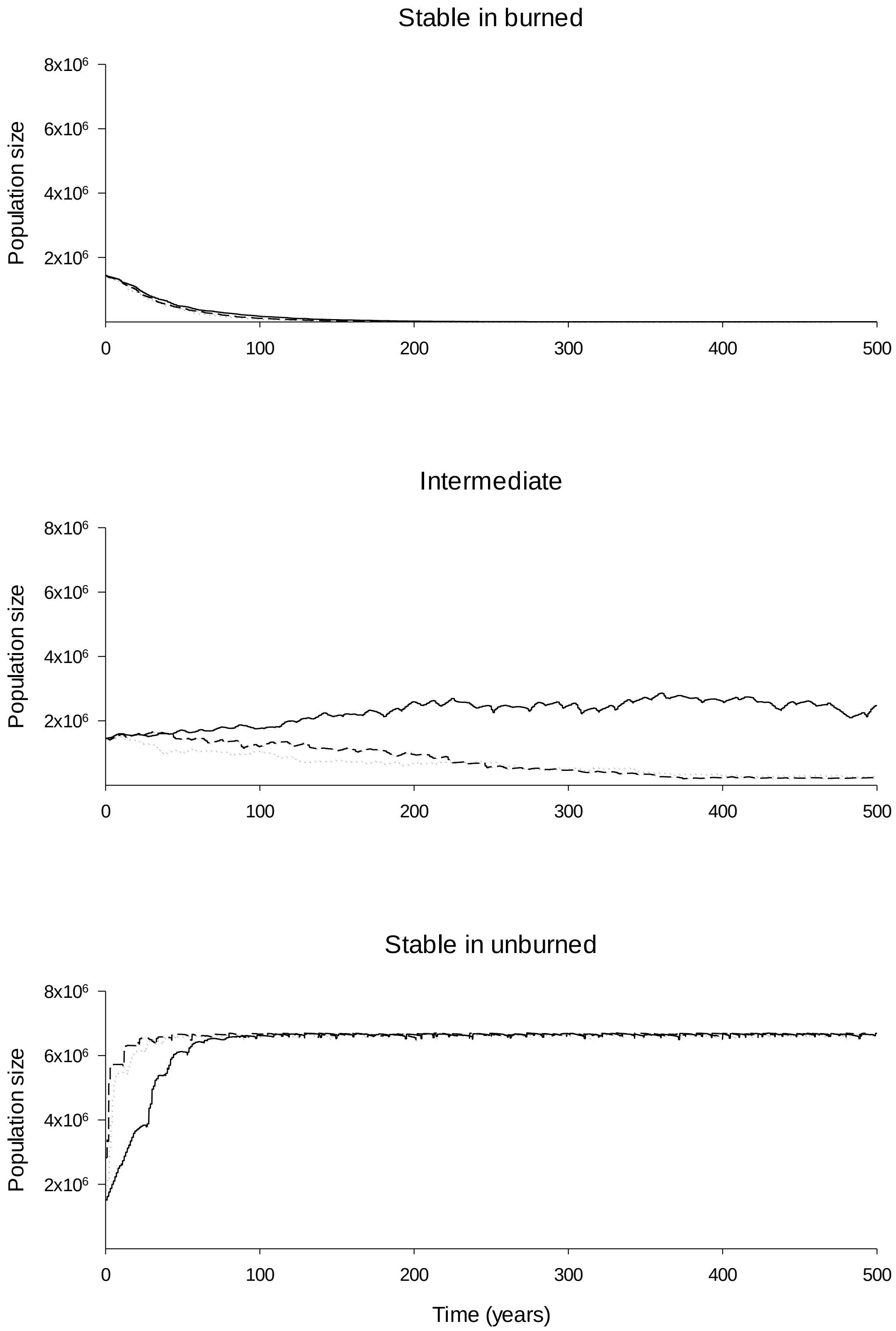
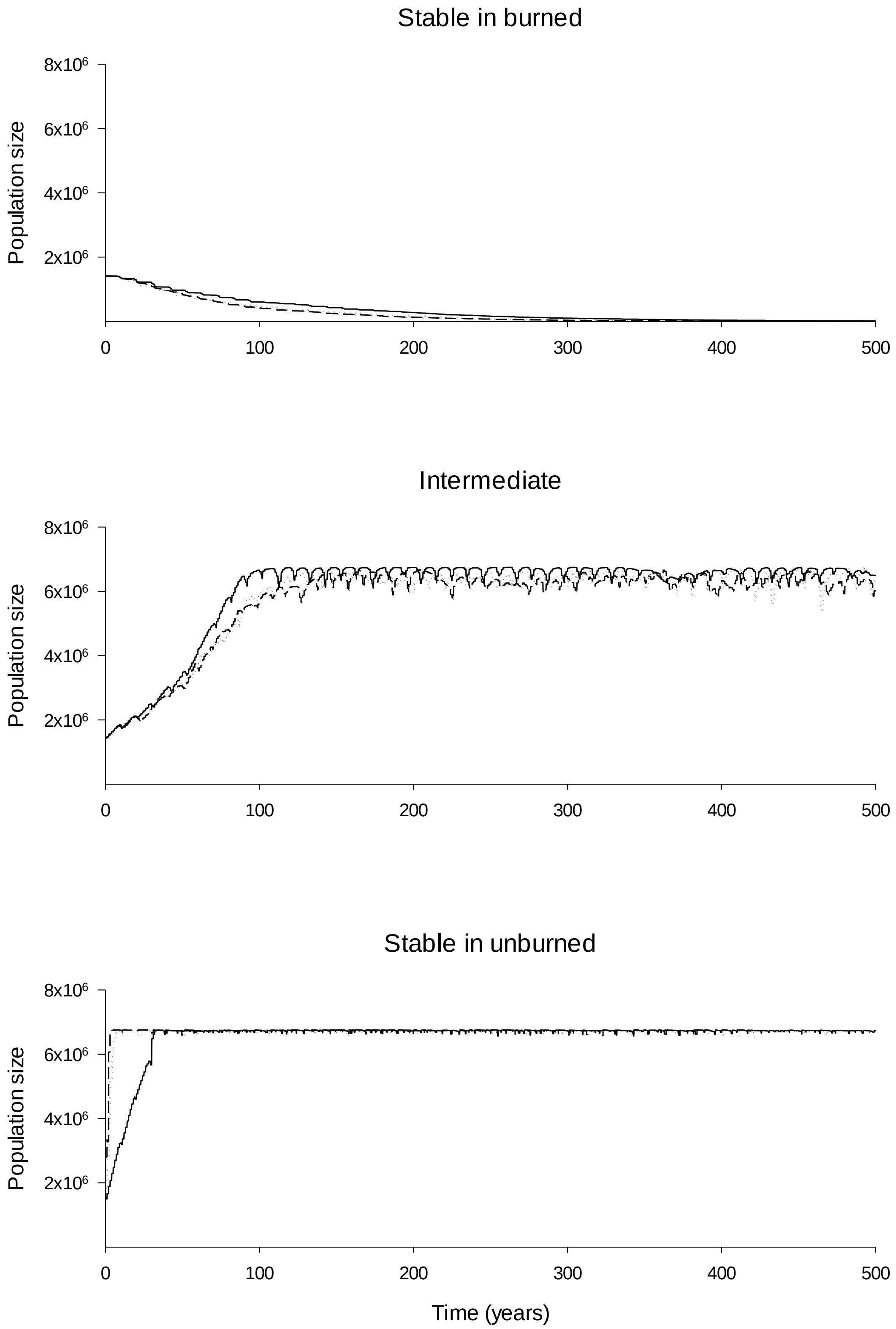


Figure 9.7. *Puya hamata* population size with three relative germination weights. Solid lines represent the germination 5 times (more likely in burned than in unburned). Dotted lines represent germination 25 times (more likely in burned than in unburned), and dashed lines represents germination 100 times (more likely in burned than in unburned) in 'frequent fires' regime.



Discussion

LandBaSE-P simulated the fire mosaic patterns observed in the páramos of the REEA. Fire spread probability was more influential than the fire start probability in determining fire regime. However, the exact combinations required to achieve different fire regimes varied according to the cell size used in the model, because of the complex interactions between these variables at different scales.

In Ecuadorian páramos, fires every 4–5 years have been reported by Valdospinos-Navas (2008) and 1–2 by Bader (2007). However, 19-25 years was the most frequent obtained in the model. Without virtual farmers deliberately starting fires in cells as soon as they have recovered from burning, and restarting fires if they go out, this probabilistic model is unable to match the fire frequency of some heavily managed páramos. Heavily managed páramos like REEA have changed in vegetation composition as it was mentioned by Moscol Olivera and Cleef (2009). Páramos of REEA had a floristic composition that suggests disturbance mainly appearing after burning and grazing of bunchgrass páramo. Some taxa found in REEA are propagated by wind, man and animals. Road, mule tracks and paths are causing an important diaspora input.

Long-distance seed dispersal was not important for the maintenance of populations in our simulated scenarios. Maximum distances from 10 to 5000 m shared similar outcomes. This effect was unexpected. It has been observed in other models that long seed dispersal has an important effect in the population dynamics using kernels able to simulate long distances (Baker, 1992). For example, Dyer (2012) showed the importance of long seed dispersal in the context of projected climate change. Similarly, Shigesada *et al*. (1996) and Higgins and Richardson

(1999) concluded that long seed dispersal events must be taken into account to make accurate predictions of the rate of biological invasions. However, the particular interactions between semelparous seed production, long-distance seed dispersal, fire regime and its effects on seed germination might combine to produce a different outcome for *Puya* in the páramo. At present, the model is based on limited data on seed dispersal patterns, and the further work on long-distance seed dispersal and subsequent modelling would be needed to confirm the patterns observed here. Of course, there are significant difficulties in observing rare long-distance dispersal events. A combination of genetics techniques and modelling offer the most promising approaches to explore this difficult challenge (Krauss *et al.*, 2009).

As observed in Chapter 7, the germination of *Puya hamata* in the field was very low but the proportion of seeds that germinate in different circumstances is unknown. Different probabilities of germination in burned and unburned areas had obvious effects on *Puya hamata* population sizes, as a result of changes in availability of germination sites according to fire regime. This is consistent with the literature, Fenner & Thompson (2005) recognised that in most plant communities with a closed vegetation, establishment of seedlings generally requires at least some degree of disturbance to provide areas free of existing vegetation. Open areas created by any activity in vegetation can be considered ‘competitor-free spaces’ that provide opportunities for germination and establishment (Booy *et al.*, 2000). Germination and establishment are crucial in the population dynamics of any plant. These processes could promote important changes in sizes of populations.

Depending on the interaction between fire regime and differential germination probabilities, modelled populations were driven to extinction, remained stable or increased rapidly. The significance of germination rates in different vegetation densities highlights the need for better data from the field to support the model. In particular, good estimates of germination after fires and in unburned areas would help to narrow down the wide range of potential values.

The simulations shown in this chapter illustrate some of the potential questions that can be tested and explored with LandBaSE-P. One of the main objectives of this programme was to explore landscape scales over long periods of time, and the results support Turner's (1989) conclusion that it is at these scales where very important processes happen.

'No fires', 'rare', 'occasional' and 'frequent' fires' regimes were run with long-distance seed dispersal and the relative germination rates. Frequency of fire increased the simulation time, even when simulations were run in a high performance machine capable of running several multi-threading cores simultaneously. LandBaSE-P is not optimized for multi-core processing yet and uses just one processor to make the calculations. It is able to take full advantage of the capabilities modern desktop computers but it performs as a cascade of calculation rather than a multi calculation process. For this reason, it can take several hours or even days to run a single simulation. The LandBaSE-P programme would benefit from a re-programming for multi-core processing and/or cluster workload distribution, to improve running times as well as allowing simulations at larger scales than 9 km^2.

10 General discussion

High-altitude grasslands in the northern Andes, or páramos, have a history of natural and anthropogenic fires (Cochrane, 2009), which influence biodiversity and ecosystem services (Myers, 2006). The impact of fires on páramo biodiversity has been reported across the northern Andes (and the puna region of the central and southern Andes) (Herzog *et al.*, 2011), but few detailed studies have been conducted elsewhere in the region. Partly, this is because of the isolated nature of these habitats and the challenging working environment, but also it is difficult to discover or record fire history in such remote places. Nonetheless, during the 3-5 million year existence of the Andean páramos (Hofstede *et al.*, 2003; Van der Hammen, 2000), occasional fires would have been a natural occurrence (Cochrane *et al.*, 2009); indeed, the arrival of humans has been linked to a dramatic increase in fire frequency (Cochrane *et al.*, 2009) and some authors have even suggested that páramos are anthropogenic in origin, maintained by the clearance of native forest by regular burning (Lægaard, 1992). However, recent studies have suggested that páramos were extensive in the northern Andes even before the arrival of people (Di Pasquale *et al.*, 2008).

Millions of Andean people depend on the páramo ecosystem (Anderson *et al.*, 2011). Several key ecosystem services, such as the provision of water, may be adversely affected by frequent burning (Anderson *et al.*, 2011) but the lack of good-quality information on páramos fire history reduces our ability to understand how ecosystem service provision is affected by anthropogenic fire. The lack of an adequate understanding of ecological processes, and how fire impacts, is an obstacle to the development of effective management strategies for the conservation of biodiversity and the protection of ecosystem services. One problem is the complexity of these systems, and the urgency of the challenge to manage páramos in times of rapid land use and climate change. One potential solution is to use indicators that act as surrogates for more complex changes. The search for, and the evaluation of, sensitive indicators for monitoring changes in ecosystems has become an important issue (Abreu *et al.*, 2009). Some species may be particularly suited as indicators because they respond measurably to environmental change and control key aspects of ecosystem function (Grabherr & Pauli, 2004).

This study used *Puya hamata* as an indicator species to provide information about the impact of fire on ecological processes in the páramo of the Reserva Ecológica El Ángel (REEA). Although specific to REEA páramos, my findings are of wider interest because *Puya hamata* is a species common to páramos in Colombia, Ecuador and Perú (Tropicos, 2011), and the genus is widespread throughout the Andes and mountains of southern Central America (Benzing, 2000). *Puya* is a flagship plant, well-known to the general public in Ecuador, and one which plays a key role in a number of ecological processes, such as a food source for hummingbirds, bears and invertebrates, a habitat for various invertebrates, and one which dominates habitats at the expense of other plants (Miller & Silander, 1991).

Response of *Puya hamata* populations to fire is relatively well known: plants survive because of their rosetophilic form (Woods *et al.*, 1998), and readily establish afterwards from seed (Miller & Silander, 1991). Other studies show similar response to fires within this genus (Brunschön *et al.*, 2010). However, some of these studies are limited in scale, while others provide partial information across a range of species and aspects of their ecology (Cano *et al.*, 2000; Miller & Silander, 1991; Mora *et al.*, 2007; Varadarajan, 1990). The studies reported in this thesis integrate key ecological processes with the dynamics of *Puya hamata* populations and fire. The next section discusses *Puya*'s lifecycle as a guide to understand the effect of fires in each ecological process.

An important finding (Chapter 5) was that *Puya* plants in the centre of large aggregations had lower reproductive output (in terms of seed viability and germination) compared with more isolated plants. Also, plants in the centre of aggregations had lower reproductive output than plants at the edge. Many studies have investigated how the aggregation of individuals or flowers affects the number of fruits and seeds produced (Alexandersson & Ågren, 1996; García-Meneses, 2004; Sih & Baltus, 1987; Tirado & Pugnaire, 2003), but relatively few have examined the impact of aggregation on seed viability or germination (Fowler, 1984; Oliveira *et al.*, 2011; Tirado & Pugnaire, 2003).

Generally plant aggregation studies consider patch size alone without consideration of the importance of position inside groups (Goulson, 2000). In many situations, within-patch position may be irrelevant to reproductive output because of the pollinator vector. However, in circumstances where plant aggregations are mostly composed of siblings, territorial pollinators reduce the chance of outcrossing in larger patches. As a consequence, seed viability and germination rates would also be expected to decrease for plants within such a patch. Non-territorial pollinators might be expected to have occasional access to plants at the patch edge, increasing the probability of outcrossing. Territorial behaviour has been observed for hummingbirds feeding on *Puya hamata* inflorescences in larger patches (Paul M. Ramsay, unpublished), but trap-lining hummingbirds which promote outcrossing are typical of isolated *Puya* plants, and they may also steal nectar from *Puya* plants at the edges of larger patches (Woods & Ramsay, 2001) . Results in Chapter 5, clearly demonstrate that the spatial context of a plant can affect reproductive output in these circumstances in line with expectations. Some additional studies on hummingbird behaviour around *Puya* plants in different spatial contexts have already been conducted, demonstrating the restriction in pollinator access caused by territorial birds (Paul M. Ramsay, unpublished). However, a better understanding of how this behaviour affects the genetic structure of *Puya* in relation to spatial context (and reproductive output) would be valuable.

No previous studies have been published on seed dispersal in *Puya*. Anecdotally, it has been reported that the majority of *Puya* seeds fall near to the parent plant (Miller, 1988), and the present study confirmed this pattern for *Puya hamata*—although this was based on a small study carried out for a time-limited period. Seed dispersal observations in the field are difficult to interpret (Cain *et al.*, 2000) because it is impossible to be sure about the origins of individual seeds, especially in a landscape with many reproductive adults within potential range. Also, rare long-distance seed dispersal events may be important for species with normally short-distance seed dispersal (Jones & Muller-Landau, 2008), Nonetheless, the very low probability of such an event may make practical observations in the field impossible, especially when combined with the difficulties in identifying seed origin. Therefore, in the model of *Puya hamata* dynamics, seed dispersal was considered mostly short-distance, but the importance of long-distance seed dispersal was evaluated for simulated populations. In these simulations, long-distance seed dispersal did not affect *Puya hamata* population dynamics. However, these simulations started with an existing, well-dispersed population of plants; perhaps long-distance seed dispersal is only important in situations where colonisation of new territory is important. Further simulations starting with small, spatially restricted populations may demonstrate a more important role for long-distance dispersal in certain circumstances.

Following dispersal, germination of *Puya hamata* seeds was low in the field experiments where only one seedling appeared across all treatments (Chapter 7), and seedlings were also found rarely in the detailed demographic studies of Chapter 8 (only nine seedlings in 8000 m^2 over two years of observations). Germination rates in the wile are often very low (Körner, 2003). Nevertheless, conditions for germination should have been acceptable and occasionally high germination and recruitment rates conditions occur and maintain *Puya* populations.

Experiments under controlled conditions clearly demonstrated the significance of temperature and light to the successful germination of *Puya hamata*. Both factors induce germination in many plants (Fenner & Thompson, 2005) and, given appropriate light and temperature, *Puya hamata* seeds germinated without the need for scarification, pre-burning or any chemical treatment. Interestingly, the temperature requirements for *P. hamata* germination were higher than the ambient daytime temperature typically experienced at soil level in the páramo. At high-altitudes in the tropics, the combination of cool air temperature and intense solar radiation combine to provide patchiness in soil temperatures according to vegetation cover (Grime, 2001): in dense shade, soil temperatures may be many degrees lower than in more open areas. The response of *Puya* to fires may be due to the fact that burning clears away vegetation allowing increased light penetration to the soil surface and elevated temperatures where germination can occur. A similar germination mechanism is reported for the Eurasia heathland species *Lobelia urens* (Dinsdale *et al.*, 2000).

Further studies on temperature and light profiles at fine scales in páramo vegetation could help to describe the potential for germination in different kinds of vegetation. The consequences of different fire management strategies on *Puya* could be modelled using this information. Similarly, broader-scale studies of temperature and light might explain the altitudinal limits of *Puya hamata*, as well as indicating potential responses to climate change. Similar germination studies could be conducted with a range of other plant species, to provide a better picture of how changes to fire regimes and climate might affect plant diversity in the páramo.

Once *Puya hamata* germinates, mortality is subsequently low. In the demographic study (Chapter 8), 93% of seedlings discovered during the first phase of survey were present one year later. Mortality was very low in juvenile and adult stages too (confirming the results of a smaller study by (Miller, 1988). This is expected for a semelparous plant and corroborates Young's (2010) conclusion that infrequent reproduction and low mortality rates may favour the evolution of semelparity. Only one other detailed demographic study of a long-lived semelparous plant has been published—*Lobelia telekii*, another giant rosette plant, from the tropical mountains of Kenya where very similar patterns of poor germination rates and low mortality at all life-history stages were reported (Young, 1985; Young, 2010; Young & Augspurger, 1991).

The rosette growth form is commonly associated with semelparity (*e.g., Lobelia, Agave*)(Young & Augspurger, 1991). In rosette species, the basal rosette thermally insulates meristems against low-temperatures, water-balance or fires (Simon *et al.*, 2009). The apical bud of *Puya hamata* has an elevated temperature compared with ambient air temperature on cold nights (Hedberg & Hedberg, 1979; Ramsay, 2001). The rosette form of the Bromeliaceae may have predisposed *Puya* to relatively low mortality and an evolutionary path to semelparity. The thermal properties of *Puya*'s basal rosette also functions as a protection against extreme temperatures (Lægaard, 1992). In Chapter 8, the survival of *Puya* rosettes at four fire intensities was assessed. Though some very small rosettes were killed by the high intensity fire, 97.1% of plants survived. After a low intensity fire, no *Puya* plants died.

In the simulated environments of LandBaSE-P (Chapter 9), sensitivity analyses were used to investigate the impact of fire regime on *Puya* populations. Some models have already been developed to explore the impact of fires on terrestrial environments (Shugart *et al.*, 1992) or the development of semelparity in plants (Childs *et al.*, 2004). LandBaSE-P combines population dynamics and fire regime into a spatially explicit individual-based model. The complexity of the model allows us to investigate relationships between different ecological processes, but also pushes the limits of desktop computing. The landscape scale of the simulation modelling was reduced to 9 km^2 because modelling larger landscape areas caused frequent computer crash. Nevertheless, 9 km^2 is an appropriate scale for such simulations, though smaller than the actual area of the real-world reserve.

Although some attempts to determine the history of fires in the REEA have been made (Bustos-Insuasti, 2008; Valdospinos-Navas, 2008), the extension and frequency of fires is still unknown. This is a classic problem for páramo research: fires are extremely important, but information about fire regimes is almost non-existent. Given the historical component of fire regimes, any attempt to collect data would take many years to produce meaningful results. Research in remote high altitude grasslands is often expensive, uncomfortable, and time-consuming, and especially so if projects are focused on landscape scales over long periods of time. Simulation modelling provides a good complement to direct observational research, especially for work at large scales and long time periods. Nevertheless, simulation modelling needs good-quality field and laboratory data to support it (Bravo de la Parra & Poggiale, 2005), but provides an alternative to explore the role of fires on *Puya* population dynamics.

Of course, landscape size effects the interaction between fire spread and fire start probabilities. Large landscapes means connectivity of processes. In particular, fire spread was a crucial parameter for generating virtual fire regime scenarios, while fire start probabilities had little effect. The model could not simulate fire return intervals of 4–5 years using fire spread and fire start probabilities—local farmers in real páramos with very short fire return intervals often start many fires simultaneously to overcome the patchiness than would form as a result of natural fire spread. This is an indicator that fire regimes in REEA are not natural and the cycle of fires is more frequent that the can be accounted for simply by fire spread from single starting points. On the other hand, in virtual scenarios of infrequent fires, burning was catastrophic because so much fuel had accumulated that fire spread was limiting. Dead versus live biomass ratios are higher in páramo plants than lower-altitude temperate regions (Pérez, 1992), contributing to the susceptibility of these grasslands to fire. In grassland, *Puya* disappears without burning, but can occupy all available space following a grassland fire. Interestingly, *Puya* can persist in páramo bogs in the absence of fire (pers. obs., Augspurger, 1985).

In summary, *Puya hamata* germinates much more frequently after fires, can form large aggregations of single recruitment cohorts, suffers very low mortality (with and without fires) once established, and lives up to 30 years. *Puya* would be expected to disappear from unburned páramo within 100–130 years, but thrives in burned grassland. Using information on its population structure, *Puya* could be used as an indicator of recent fire regime. Within the lifespan of *Puya* plants, pulses of recruitment would normally indicate the signatures of past fires, and their timings could be estimated using *Puya hamata* growth. The size of *Puya* aggregations might reflect longer-term fire history, but this will require additional field observations and simulation modelling to calibrate.

The REEA páramo —in combination with adjoined Volcán Chiles—is one of 14 intervention sites for Proyecto Páramo Andino, (Proyecto Páramo Andino, 2011). These areas were chosen for research into the conservation of biodiversity and ecosystem services, as well as a variety of land use and human *cultural* diversity. REEA was a suitable study site for *Puya hamata* research because it offers a range of burning regimes, but one of the objectives of studies in the 14 intervention sites was to trial approaches that could be used elsewhere. With some simple additional observations, the same approach could be used in other páramos with *Puya hamata*, or with other long-lived *Puya* species in Central and South American mountain grasslands (for example, *Puya goudotiana, Puya dasylirioides, Puya raimondii*). The use of flagship species like *Puya* (Sgorbati *et al.*, 2004), and efforts to manage their populations, might promote wider conservation efforts as a consequence.

The research presented in this thesis has important implications for páramo management. Fire history is very important for the conservation of biodiversity and ecosystem services, but poorly understood for páramo grasslands (Verweij & Budde, 1992). *Puya hamata* populations could be used to estimate fire intervals in different areas. It would be useful if the managers of REEA and other páramo reserves recorded fire outlines on maps, with dates, for more certain interpretations in the future. In the meantime, though, maps derived from *Puya* would form the basis for relating species composition to fire dynamics. Some species, like *Puya*, increase in numbers as fire frequency increases, but other species like woody plants are killed by burning (Moscol Olivera & Cleef, 2009). Some plant species return during the process of post-fire recovery, but others may disappear permanently. Efforts to determine the responses of individual species have been limited by poor knowledge of fire history and post-fire succession in páramo grasslands. Using *Puya*, a better characterisation of the response to fire of a wide range of species would be possible.

Effective conservation needs to connect fire ecology with fire management (Myers, 2006). Currently, most attempts at fire management in the páramo are concerned with controlling fire start probabilities, by prohibiting fires. However, there are two problems with this approach: fires are started anyway, and even without fires for many years, catastrophic fires of high intensity become more likely (as shown in the simulation modelling). It would be more realistic, and more effective, to manage fire spread probabilities. These are limited by the interaction of fuel build-up (which is related to the time since the last fire), natural barriers (like cliffs, rivers, bogs) and the fire mosaic pattern at the landscape scale (where a fire is stopped when it meets an area burned too recently for fire to spread). The identification of areas sensitive to burning, and the use of prescribed fires around them, could be more effective at protecting biodiversity than ineffective bans on burning. Furthermore, the maintenance of mosaics of different time of recovery increases structural variability, microclimates and biodiversity (Sklenár & Ramsay, 2001). This would be preferable to infrequent but intense landscape-wide fires.

More generally, there is a need for comprehensive work on fire ecology and its effects at realistic spatial and temporal scales. There are some important approaches on this subject in some ecosystems. For example, Groeneveld *et al.,* (2002) developed a spatially explicit, rule-based model for three co-occurring *Banksia* species to investigate coexistence mediating processes in a fire-prone shrub land. They found that fire regime (patchiness and frequency) is a key factor in mediating coexistence of the three studied species. Their model predicted the temporal and spatial fire regimes under which coexistence is possible for a given parameterization of demographic and seed production attributes of the three species. It provided new insights into the key factors mediating coexistence, and for management and conservation, where manipulation of fire intensity and frequency is a powerful management tool.

A better understanding of the impact of climate change on fire ecology is important because changes in climate could alter vegetation, fuel characteristics and fire regime, along with the strategies required to meet management objectives (Falk *et al.*, 2011; McKenzie *et al.*, 2011). Such fire management strategies should reflect the size of land units for which managers are responsible and the landscape scales across which fires spread (McKenzie *et al.*, 2011). They should be regularly monitored and adjusted to take account of changing fire regimes and their ecological effects to reduce undesirable effects on ecosystem composition, structure and function (Millar *et al.*, 2007).

Managing changing fire regimes represents a major challenge in the face of climate change, but made easier by the use of simulation models with appropriate temporal and spatial scaling. LandBaSE-P is a good example of such a simulation model, supported with good-quality evidence that can be used as a research tool for population dynamics and fire regimes that works at large spatio-temporal scales. The same model could be used, for other semelparous species in fire prone ecosystems (*e.g., Agave cupreata* in semi-deciduous dry forest in México), and could be adapted relatively easily for other species with different life histories.

Although simulation modelling, as illustrated by *Puya hamata* and LandBaSE-P, has an important role in ecology, biodiversity conservation and sustainable land management, it should be used to complement field and laboratory studies rather than replace them. This thesis shows how detailed fieldwork, combined with selected laboratory studies and simulation modelling, can provide a good understanding of the complex dynamics of real-world populations, and generate ideas for management and future research.

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