# Super-performance in a palm species

**Merel Jansen**

**Thesis committee**

**Promotors**
Prof. Dr N.P.R. Anten
Professor of Crop and Weed Ecology
Wageningen University

Prof. Dr P.A. Zuidema
Personal chair at the Forest Ecology and Forest Management Group
Wageningen University

**Co-promotors**
Prof. Dr F.J.J.M. Bongers
Personal chair at the Forest Ecology and Forest Management Group
Wageningen University

Prof. Dr M. Martínez-Ramos
Professor of Population and Community Ecology
National Autonomous University of Mexico

**Other members**
Prof. Dr T.R. van Andel, Wageningen University and Naturalis Biodiversity Center
Prof Dr F. Berendse, Wageningen University
Dr E. Jongejans, Radboud University Nijmegen
Dr Y. Vindenes, University of Oslo, Norway

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# Chapter 1

## Introduction

Merel Jansen

The world is changing rapidly due to anthropogenic disturbance, effects include: global warming (Houghton *et al.* 2001), pollution (Smith 2013), a changed global nitrogen cycling (Fowler *et al.* 2013), land-use change (Schmitz *et al.* 2014), and spread of exotic species (Vitousek *et al.* 1996; Paini *et al.* 2016). This has a tremendous impact on both natural and agricultural systems. As a result, tropical forests are disappearing rapidly (Hansen *et al.* 2013), biodiversity is threatened at such a rate that this may cause a sixth mas-extinction, (Ceballos *et al.* 2015), and global food security is at risk as agricultural systems are affected by these global changes (Wheeler & Von Braun 2013). To understand the effects of global changes on natural and agricultural systems, predict how these systems will be affected in the future, and design best management practices to divert the negative changes, a very good understanding of the ecological systems and underlying drivers is fundamental.

Ecological systems can be studied at many different levels of aggregation, ranging from the molecular level (*e.g.* De Meaux & Mitchell-Olds 2003) to worldwide patterns (*e.g.* Cramer *et al.* 2001). At all levels, systems are influenced by external drivers like the environment or human-induced global changes. Furthermore, different levels of aggregation influence each other. For example, molecular processes influence organelles, and organelles influence cellular processes. Therefore, to understand processes that play at a certain level of aggregation, it is necessary to understand processes at lower levels, including the external drivers of this level. For example, large-scale changes in vegetation patterns, are a product of demographic processes of the individual species. These demographic processes could in their turn be heavily influenced by environmental variation. The relation between different levels, external drivers, and their consequences is illustrated in Fig. 1.1.

A level of aggregation of particular interest is that of the population, so populations of plants or animals. Many important ecological processes occur at the population level, like adaptation, extinction, and invasion, which are all processes that tend to be accelerating under the current, global environmental change (Vitousek *et al.* 1996; Matesanz, Gianoli & Valladares 2010; Ceballos *et al.* 2015). The common way to study natural populations of plants or animals is by calculating the mean vital rate in a population. So, the mean growth rate, survival probability of reproductive output of a group of plants or animals. These mean vital rates are then used to describe the dynamics of populations. By doing so the influence of possible differences in these demographic rates between individuals are ignored. This may constitute an important drawback as some individuals may produce much more offspring than others, or grow faster, or live longer. Although ecologists are increasingly recognizing that individuals do matter when studying population level processes (Zuidema, Brienen & During 2009; Bolnick *et al.* 2011; Vindenes & Langangen 2015; Snyder *et al.* 2016), the exact relations between individual heterogeneity, the external drivers of it, and population level processes are not yet always well understood.

The general objective of this thesis is to understand how individual-level processes, and the external drivers of it, contribute to population-level processes. For this, I specifically focus on differences between individuals, the central theme of this thesis. Throughout the thesis, several terms are used to describe this (see box 1 for a list of terms used in this thesis), but

they all fall under the umbrella of individual heterogeneity. What this entails exactly, will be explained in the next section.
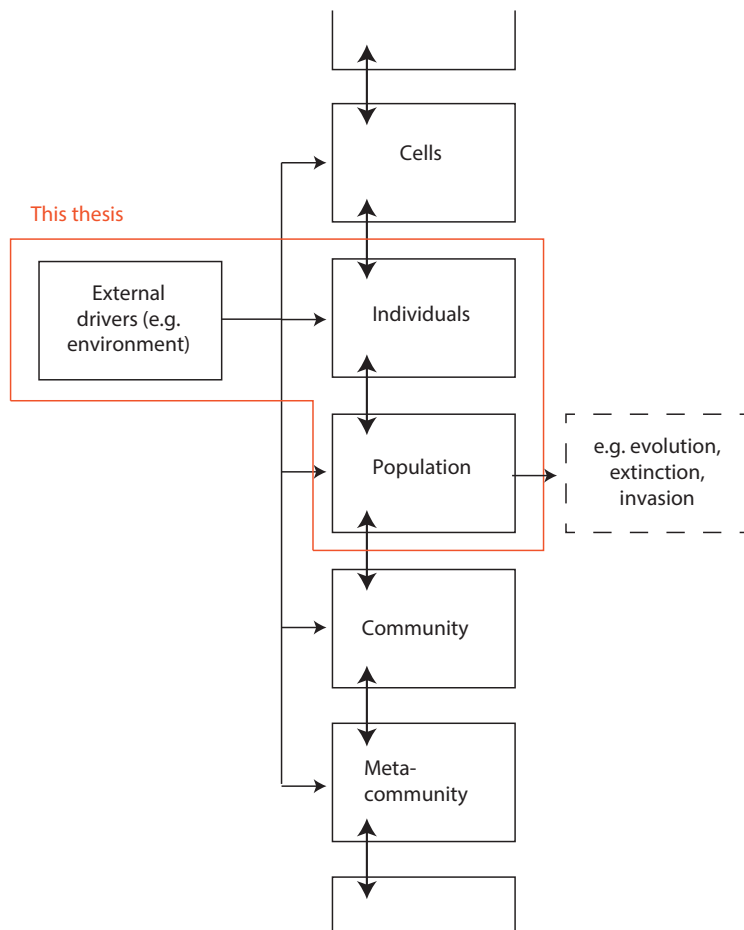


**Figure 1.1**. Ecological systems can be studied at different levels of aggregation, ranging from the cellular level to the global level. All levels are influenced by external drivers like the environment, and different levels also influence each other. In this thesis, I focus on the relation between individual heterogeneity in performance, their external drivers, and population level processes. A better understanding of how these elements interact will provide insights into the regulators of population level processes like invasion, selection and population management.

Box 1. Terminology used to describe differences between individuals within populations

**Individual heterogeneity** (*e.g.* Vindenes & Langangen 2015)
Performance differences between individuals, at any temporal scale.

**Short-term performance differences**
Performance differences between individuals seen over a temporal scale that is one or more orders of magnitude shorter than the expected lifespan.

**Long-term performance differences**
Performance differences between individuals seen over a temporal scale that is less than one order of magnitude shorter than the expected lifespan.

**Lifetime performance differences** or **Differences in life-output**
Differences in total life performance, e.*g.* differences in cumulative reproductive output seen over the whole lifetime, or (for trees) stem diameter at time of death.

**Super-performance** (Jansen *et al.* 2012)
Some individuals persistently perform better than the population mean. A super-performer is therefore an individual with such persistent above-average performance.

**Stochastic individual heterogeneity** or **individual stochasticity** (Caswell 2009)
Performance differences between individuals that randomly (*i.e.* stochastically) fluctuate over time.

**Dynamic individual heterogeneity** (Tuljapurkar, Steiner & Orzack 2009; Paini *et al.* 2016)
Performance differences between individuals that are time-varying, but not stochastic (*i.e.* differences are auto-correlated over time).

**Fixed individual heterogeneity** (*e.g.* Plard *et al.* 2012)
Performance differences between individuals that are fixed over time.

*Individual heterogeneity*

Not all individuals perform equally well. Within populations of the same species, some individuals grow faster, reproduce at higher rates or have lower mortality risks than others (Sarukhán *et al.* 1984; Lomnicki 1988; Pfister & Stevens 2002). Performance differences are well documented for animals (Pfister & Stevens 2002; Pelletier *et al.* 2007; Tuljapurkar, Steiner & Orzack 2009). Think for example of the many studies describing the higher reproductive success of alpha males in primate species (*e.g.* Berard *et al.* 1993; Pusey, Williams & Goodall 1997; Jack & Fedigan 2006), or of studies that describe differences in life reproductive success in birds (*e.g.* Annett & Pierotti 1999; Steiner, Tuljapurkar & Orzack 2010). In plants, however, these differences between individuals have received much less

attention. For plants, we know that in a given year one individual might grow faster or produce more seeds than another individual (*e.g.* Greenberg 2000). But what is not always clear is whether the same individuals grow faster or reproduce more every year. So, do such differences between individuals persist over time, making that some individuals are more successful in life than others?

In short-lived plants (*e.g.* annuals or biennials) this is relatively easy to determine as observation of the complete life cycle is relatively easy. For example, individual lifetime fitness has been quantified in wild radish (*Raphanus raphanistrum*, Conner, Rush & Jennetten 1996). However, for long-lived species (both plants and animals) this is much harder. Many tree species, for example, can easily live for up to several hundreds of years (Martinez-Ramos & Alvarez-Buylla 1998; Fichtler, Clark & Worbes 2003), and so do some animals (Nielsen *et al.* 2016). It is impossible to observe the complete life cycle of such long-lived species in the timespan of a researcher's career. Some species however, have the advantage that they leave a visible trace of their growth history. A good example of this are trees. Many temperate and some tropical tree species are known to produce annual rings in their wood formation (Fichtler, Clark & Worbes 2003; Groenendijk *et al.* 2014). Several studies have been performed in which these tree rings were used to reconstruct complete growth histories of the individual trees (*e.g.* Nowacki & Abrams 1997; Brienen 2005). Also, many fish species produce annual growth rings in their bones that offer the possibility to reconstruct growth histories (*e.g.* Adams 1942; Le Cren 1947; Okamura & Semba 2009). Furthermore, internodes, leaf scars on the trunks of some trees (like *Cecropia* spp., Zalamea *et al.* 2008), and papaya (*Carica papaya*, Ackerly 1999) and palms provide information on growth histories, although internode formation is usually not annual. Another option that can provide information about long-term growth differences is isotope analysis: with this method ages of individuals can be determined (Kerr *et al.* 2006), and by comparing this with sizes, information on average growth differences between individuals can be obtained. Such studies have shown that long-term growth differences can be very large and very persistent. For example, Brienen & Zuidema (2006) showed that trees of 60cm diameter of the same species vary two- to three-fold in age, and Brienen, Zuidema & During (2006) showed that in some species differences in growth rate between individual trees persist for more than 20 years. These studies provided the first proof of the extent to which individuals within populations of long-lived plant species persistently differ in terms of growth rate.

The methods mentioned so far offer the possibility to observe growth differences between individuals over their entire life. However, they generally do not provide information on differences in reproduction. Indeed, for long-lived plant species much less is known about long-term differences in reproduction than about long-term differences in growth. Simulation models might offer the opportunity to obtain some estimations of long-term differences in reproductive output. Models have been shown to be able to predict well long-term differences in reproductive output in animals. For example, simulation models were able to predict quite well differences in life-reproduction in mute swans (Tuljapurkar, Steiner & Orzack 2009), and in roe deer (Plard *et al.* 2012). This approach has however not often been used to estimate differences in reproduction in long-lived plant species.

In conclusion, short-term differences in both growth and reproduction have been shown to be common in both short- and long-lived species, and in both plants and animals. For long-lived species, it is known that long-term differences in reproduction are large in animals, and in growth in some plants.

*The causes of individual heterogeneity*

Even though we know now for several long-lived plant species that performance differences can be strong and persistent, there is often little understanding of the causes of this individual heterogeneity. Spatial variation in biotic and abiotic conditions are both known to strongly influence plant short-term performance. For example, spatial variation in light levels may cause growth differences between plants (Chazdon 1986). And spatial heterogeneity in habitat quality can influence reproductive success in animals (Lambrechts *et al.* 2004). With short-term performance, I refer to performance over a time span that is one or more orders of magnitude smaller than the expected life span of a species (Box 1), so short-term performance differences for a tree, for example, could be annual differences in growth rate. A whole body of plant ecological research has focused on dose-response experiments that have shown the effects of environmental variation on short-term performance (see Poorter *et al.* 2010). What is much less investigated and has thus remained unclear, is to what extent environmental factors that cause short-term performance differences are the same factors that cause long-term performance differences between individuals. Possibly, a factor that has a strong effect on short-term performance, but is highly variable over time (*e.g.* many short-term diseases, or light availability for an understorey palm), does not strongly contribute to long-term performance differences. Likewise, it is possible that an environmental effect that has a weak effect on short-term performance can be determining for long-term performance differences if it persistently provides an advantage to some individuals throughout their whole lifetime. This could, for example, be soil texture (Russo *et al.* 2005), maternal effects (Mousseau & Fox 1998), or diet choice (Annett & Pierotti 1999). Which environmental factors are most important for long-term performance differences will differ between functional types. For example, in many plant species, fast growth means higher light availability and overshadowing competitors, which allows even faster growth (Weiner 1986). Therefore, in many plant species, light availability would probably be the main determinant of long-term growth differences. However, shade-tolerant forest understory plants growth responses to changes in light availability tend to be less pronounced than in canopy tree species (Chazdon 1992; Martínez-Ramos, Anten & Ackerly 2009), and edaphic factors and biotic interactions could play a comparatively larger role in explaining persistent growth differences. In this thesis, I will quantify the contribution of several environmental factors to individual heterogeneity in a forest understorey species.

Long-term variation in performance among individuals can also be partly genetically determined. Especially in agricultural research, the relation between genetic variation and performance has been studied extensively; it is the basis of plant and animal breeding (Allard & Bradshaw 1964; Bourdon & Bourbon 1997). The relation between genetic variation and

performance has been studied relatively less for long-lived species, probably because their long life-span makes experiments much more time consuming. Studies have been performed, however, for long-lived cultivated species like *Populus spp*. (*e.g.* Heilman & Stettler 1985; Stevens, Waller & Lindroth 2007), oil palm (*e.g.* Hardon, Corley & Ool 1972) and peach palm (*e.g.* Clement 1995) and most of them found a clear relation between genetic variation and performance. Breeding studies are however very different from studies in natural populations. In breeding studies, different genotypes are grown under similar conditions because of which the genetic component is clearly visible. In natural populations, however, the environment is much more heterogeneous, and therefore the environmental and genetic effects are not so easily separated. This is even harder to separate when strong interactions between genotype and environment (*i.e.* GxE interaction) are present. For example, maybe the genotypes that perform best in *e.g.* high nutrient conditions or without the stress of leaf loss, are not the same genotypes that perform best in low nutrient conditions or with the stress of leaf loss. Especially in situations where local environment is characterized by large spatial heterogeneity, this type of trade-offs would maintain within population genetic diversity (Stearns 1992), and would, therefore, make a genetic basis for individual heterogeneity in performance more likely. Both studies that analyze the relation between genetic variation and performance, and studies that address GxE interactions, are often performed with individuals from different populations to maximize the genetic variation (*e.g.* Poorter *et al.* 2005), therefore not providing much information on within-population variation. More studies on the relation between within-population genetic variation and performance differences, and within population GxE interactions and trade-offs, would help to determine to what extent individual heterogeneity is governed by genetic variation. In this thesis, I will study the extent to which genetic variation can cause growth differences in a natural population of a long-lived palm species, and if there is a trade-off between growth and tolerance to leaf loss in this population.

*Population consequences*

As mentioned above, ecologists and demographers are increasingly recognizing the importance of individual heterogeneity for population processes (Zuidema, Brienen & During 2009; Bolnick *et al.* 2011; Steiner & Tuljapurkar 2012; Vindenes & Langangen 2015; Snyder *et al.* 2016). For example, demographic studies have shown for tropical canopy trees, that fast-growing juveniles contribute twice as much to population growth compared to slow growers (Zuidema, Brienen & During 2009). Furthermore, several population characteristics, including population growth rate (Pfister & Stevens 2003), optimum flowering size (Rees 2000) and mortality (Vaupel, Manton & Stallard 1979), have been shown to be influenced strongly by individual heterogeneity.

So why is population mean performance not always an adequate predictor of population level processes? Bolnick *et al.* (2011) explain that there are six different mechanisms by which ecological processes are influenced by trait variation (like variation in vital rates). Obviously, genetic variation plays an important role in several of these processes because it allows for genetic selection and evolution to take place. But also if individual heterogeneity does not have a genetic basis it can strongly influence ecological processes in general and population

processes in specific. This is primarily based on Jensen's inequality (Ruel & Ayres 1999), referring to a simple mathematical rule that when a process non-linearly depends on a trait, the process at the mean trait value, is not a good predictor of the population mean process. This emphasizes the need for (plant) demography to consider and quantify the contributions of individuals that differ in performance. To be able to quantify population level processes, it is necessary to understand individual-level processes (Fig. 1.1).

To be able to fully understand and analyze the influence of individual heterogeneity on population processes, it is first of all necessary to quantify the extent to which individuals differ. But also knowledge of the environmental and genetic drivers of individual heterogeneity is essential for this. Because super-performing individuals (*i.e.* individuals that persistently grow faster and reproduce more than others) may contribute more to population growth (Zuidema, Brienen & During 2009), they may also contribute more to future generations. The environmental causes of super-performance are therefore the conditions individuals should be adapted to, and populations evolve to the genetic characteristics of super-performers. Furthermore, super-performing individuals, possibly play an important role in the resistance and resilience of populations to disturbance (*i.e.* maintaining and recovering population growth rate under stress, Harrison 1979), because super-performers potentially contribute more to the recovery of the population. However, this depends on the relative tolerance to disturbance of super-performers compared to under-performers. A positive relation between performance and tolerance would make super-performers more important, while a negative relation would make them less important. Many types of disturbances entail leaf loss, which results in losses of resources and reductions in photosynthesis and future growth. But plants can mitigate the potential negative impacts of these losses through compensatory growth (Anten, Martínez-Ramos & Ackerly 2003), which makes them more tolerant. Compensatory growth entails either allocating more new assimilates to leaves, allocating new assimilates more efficiently to leaf area (*i.e.* by increasing specific leaf area), or growing faster with existing leaf area (*i.e.* by increasing net assimilation rate, Anten, Martínez-Ramos & Ackerly 2003). Generally, fast-growing plants exhibit greater compensatory growth as faster growth entails a faster recovery of losses (Bryant & et al. 1983). But compensatory growth capacity also depends on the presence of other growth limiting factors (*e.g.* water availability). Genetic variation in tolerance and compensatory responses would allow populations to adapt to changes in disturbance events that entail leaf loss (Lande & Shannon 1996). Thus, to understand the population consequences of individual heterogeneity, quantification, and knowledge of the underlying drivers is necessary.

The most commonly used tool to analyze demographic processes are demographic models. Most of these models do however not take individual heterogeneity into account but are based on population mean estimates of vital rates. The importance of individual heterogeneity for population processes makes it essential that the current focus in demographic modeling on performance of the average individual should shift towards one that explicitly accounts for these individual differences. New demographic modeling tools, in particular, Integral Projection Models (IPMs), offer this possibility (Zuidema *et al.* 2010; Rees, Childs & Ellner 2014; Ellner, Childs & Rees 2016). Integral projection models are based on regression results

of relations between vital rates and state variables like size and age. For analysis, they are usually approximated by discretizing the model, which allows analysis with standard matrix algebra. An important characteristic of this model is that differences between individuals can be taken into account. In the standard version of an IPM (Easterling, Ellner & Dixon 2000), variance around vital rate means are taken into account, but variation between individuals does not persist over time. Later methods, however, do offer this possibility (Ellner & Rees 2006) and are therefore a great tool to analyze the role of individual heterogeneity in population processes. In this thesis, I will use IPMs to analyze the role of individual heterogeneity in population processes.

*Management consequences*

Plant and animal population are exploited with a variety of management forms, that range from simple resource harvesting to sophisticated active management to restore resource availability. The simplest management system is the mere harvest of animals or (parts of) plants from completely natural populations. Globally a large number of species in natural populations are exploited for a variety of products, providing income to millions of people and an economic incentive for nature conservation (Iqbal 1993). Important products include for example timber, bushmeat, fruits, fish, and leaves. Individual heterogeneity could play an important role in the management of such natural plant populations. The disproportionate contribution of some individuals to population growth could entail a disproportionate importance in producing future yields (Brienen & Zuidema 2007), and when harvesting entails the removal of plant parts (*e.g.* leaves, or resins), differential response of individuals to harvesting could influence this importance. Possibly, knowledge of this disproportionate contribution could be used to improve harvesting practices, by sparing those individuals that contribute most to the growth of the population (by producing more offspring than others). This could make the population more resistant to harvesting practices (*i.e.* a smaller reduction in population growth rate). In the exploitation of animal populations selective hunting is quite common practice (Milner, Nilsen & Andreassen 2007), but the potential of selective harvesting in natural plant populations, has not yet been studied. In this Ph.D. thesis, I will explore the potential of sparing individuals to improve harvesting practices of a tropical forest plant species.

In some cases, the underlying causes of individual heterogeneity are used to actively manage the natural populations to promote productivity. For example, when the main environmental drivers of high performance are known, these type of conditions can be promoted. An example of this is liana cutting, which provides more light to trees and therefore promotes timber production (Pérez-Salicrup & Barker 2000). Natural populations can also be enriched by adding new individuals, for example, valuable timber species in logging areas (Ådjers *et al.* 1995). In this, a first selection could already be made of which genotypes are preferred if information on the relation between genetic variation and performance are available. In these type of management practices, identification of the causes of individual heterogeneity can provide insight into which management choices would be most effective.

In agricultural practices, populations are managed much more intensively; especially in modern agriculture in which both genetic setup and environmental conditions are shaped to maximize productivity (Machado 2009). In agricultural practices, differences between individuals, or actually the genetic variation underlying phenotypic differences, are clearly used in animal and plant breeding practices (Bourdon & Bourbon 1997; Allard 1999). However, in modern agricultural systems, usually, just one genotype is selected, which tends to make these systems vulnerable to disturbances like pest outbreaks, and therefore highly dependent on external input like pesticides (Horrigan, Lawrence & Walker 2002). Fortunately, the advantages of genetic and functional heterogeneity for more resilient agricultural systems is starting to be re-discovered (Horrigan, Lawrence & Walker 2002) and understanding the drivers of these effects is gaining much interest among crop ecologists.

*Objectives*

The main objectives of this thesis can be divided into four main questions that I will address:

1. To what extent do individuals differ in performance? (Chapter 2,4)
2. What causes individual heterogeneity in performance? (Chapter 3,4)
3. What are the demographic and evolutionary consequences of individual heterogeneity? (Chapter 2,3)
4. Can individual heterogeneity be used to improve the management of populations? (Chapter 3,4,5)
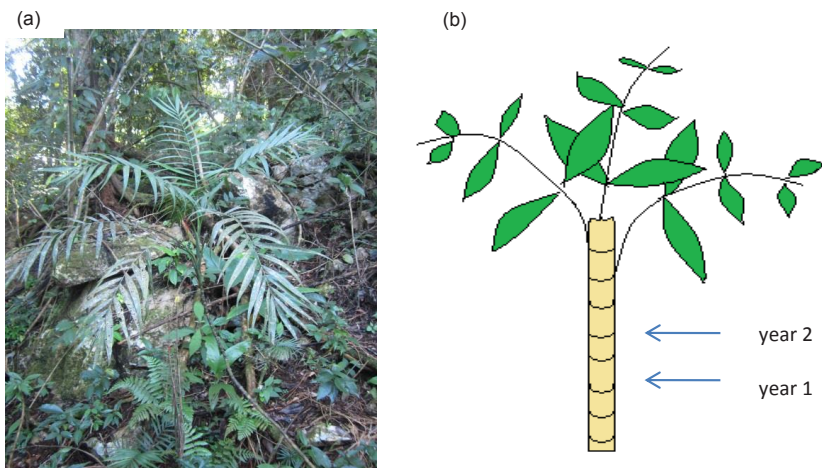


**Figure 1.2**. (a) *Chamaedorea elegans* in its natural habitat. (b) Illustration of growth history reconstruction from internodes. The length between two nodes represents stem growth in between the production of two leaves. If the average leaf production of an individual is two, then the length of two internodes (as illustrated in the figure) is representative of the growth in a year. In this way, the complete growth history of the individual can be reconstructed

*General approach*

I aim to answer these questions using the understorey palm *Chamaedorea elegans* as a study species (Fig. 1.2a). This is a dioecious species that naturally occurs on karstic outcrops in rain forest in Mexico, Guatemala, and Belize. It can reach a maximum height of 1.5 m, is unbranched, single stemmed and produces one single cluster of leaves. The advantage of this species is that, just as trees, it leaves a visible track of its growth history. These are not tree-rings though, but nodes, the scars on the trunk left after the production of a leaf. Measuring all internodes (the distance between the nodes) enables reconstructing the complete growth histories of individuals, allowing quantification of the degree to which individuals differ in growth rate. The process of internode reconstruction is illustrated in Fig. 1.2b. The leaves of *C. elegans* are widely harvested as a non-Timber Forest Product (NTFP, Hodel 1992), and are used in the floral industry worldwide. *Chamaedorea* leaves are one of the most important NTFPs in central-America. The leaves of *C. elegans*, *Chamaedorea oblongata* and *Chamaedorea ernesti augustii*, are together known as "*Xate*". Leaves are usually harvested from natural populations by local people known as *xateros* (Sol-Sánchez *et al.* 2007), but *C. elegans* is also planted in forest for enrichment (Trauernicht & Ticktin 2005).

My thesis is part of a larger research effort lead by Miguel Martínez-Ramos of the National Autonomous University of Mexico. This research effort aims to understand the ecology and management of *Chamaedorea* leaf harvesting practices, and has been running for more than a decade. Many scientific studies have already been published (*e.g.* Anten, Martínez-Ramos & Ackerly 2003; Martínez-Ramos, Anten & Ackerly 2009; Hernández-Barrios *et al.* 2012; Jansen *et al.* 2012; Lopez-Toledo *et al.* 2012; van Lent *et al.* 2014; Hernández-Barrios, Anten & Martínez-Ramos 2015).



**Figure 1.3**. Location of the research site, indicated by the red dot. The research site is located in the Montes Azules biosphere reserve in the state of Chiapas, Mexico.

Most data that we used in this thesis was collected in two adjacent plots that were constructed in the Montes Azules Biosphere Reserve in Chiapas, Mexico. The plots were located close to the Chajul Biological station (16°06' N, 90°56' W, see Fig. 1.3). This area is characterized by lowland evergreen tropical forest (Ibarra-Manríquez & Martínez-Ramos 2002) and annual rainfall is around 3000 mm, with a dry season from January to April. The first plot was constructed in March 1997 and demographic data of 814 adult individuals were collected twice a year until February 2000. In addition to this, data on seedling growth and survival were collected. More details are described in Martínez-Ramos, Anten & Ackerly (2009) and in Chapter 2. In March 2010 we measured the lengths of all internodes of all remaining female individuals in this plot (187 female individuals in total). With this data, we were able to determine the level of individual heterogeneity in this population and to analyze the demographic consequences of this. However, data on the environmental causes of individual heterogeneity were not collected. Therefore, in November 2012, we constructed a second plot (of 0.7ha), where we mapped and tagged all individuals larger than 10cm stem length (830 individuals in total). In November 2013, we measured several biotic and abiotic factors in this plot at the individual plant level. The two factors that we found most determining for plant performance (which were light availability and soil pH), we measured again in November 2014 (for the same individuals at the same location) to be able to quantify temporal changes in these factors. Furthermore, we applied twice a year a two-third defoliation treatment to half of the randomly selected individuals to simulate the effect of leaf harvesting. Photo images of the research site and of an individual that was subjected to the defoliation treatment are shown in Fig. 1.4.

To analyze if individual heterogeneity had a genetic component, we performed a second experiment. We collected all seeds of all female individuals in the newest of the two plots in November 2012, and the seeds of several reproductive females in the other plot. We transported the seeds to the Netherlands and grew the seeds of the different half-sib families (*i.e.* seeds of different mothers) up to seedlings of twelve months of age in the Unifarm greenhouse facilities of Wageningen University. From age six months, we applied a two-third defoliation treatment to half of the seedlings from each family. By performing this experiment, we were able to analyze variation within and between families, for several growth parameters, and response to defoliation. Using a quantitative genetic approach, this provided us with information about the heritability of growth parameters and response to defoliation. Strong heritability would suggest that genetic variation within our study population could importantly contribute to individual heterogeneity.

*Thesis outline*

Throughout the chapters of this thesis, I cover the four main objectives mentioned above. The general theme, individual heterogeneity, is central in all chapters. In Chapters 2 and 3, I quantified long-term variation in growth rate from internode reconstructions. In Chapter 3 I also estimated long-term variation in reproductive output. I used a simulation approach for this because internode reconstruction only provides information on growth history and not reproduction. In Chapters 4 and 5, I analyzed if individuals differ in their response to leaf

loss. The environmental causes of individual heterogeneity are analyzed in Chapter 3, and the genetic causes in Chapter 4. I address the demographic consequences of individual heterogeneity in Chapter 2, for which I determined how much individuals differ in their contribution to population growth, and in Chapter 5, in which I used these different contributions to design smarter harvest schemes by developing different criteria for sparing high performing individuals. The logic of this thesis is shown in Fig. 1.5.



**Figure 1.4**. Left: Photo image of the research site. The white-orange tubes were used to delineate the transect boundaries. Right: Photo image of a *C. elegans* individual in the research plot, that was subjected to a defoliation treatment. Newly produced leaves were marked with colored tape, and plants were labeled.

All chapters contain three major elements: empirical data (field and experiment), statistical analysis and simulation models. Models are a central tool in this thesis. In Chapters 2, 3 and 5 we used approaches similar to each other. There, I first performed regression analysis between vital rates and predictive variables (stem length and past growth rate in Chapters 2 and 5 and stem length and environmental variables in Chapter 3), based on field measurements. Based on these statistical models, I then performed simulations to analyze population processes (Chapter 2 and 5). I did this by constructing Integral Projection Models (IPMs, Easterling, Ellner & Dixon 2000; Ellner & Rees 2006). I specifically incorporated the persistence of performance differences in these models, which allowed me to evaluate the effect of individual heterogeneity on population processes. In Chapter 3 I used a model with a similar structure, but instead of analyzing population processes, I used it for individual-based simulations, which allowed me to quantify the effect of environmental variation on long-term individual heterogeneity.

In Chapter 4 I used a different approach. Based on the data that we collected in the greenhouse experiment, I estimated several growth parameters, using an iterative growth model that specifically takes the timing of leaf loss into account. Further statistical analyses were then performed, on the by the model estimated parameters, with which I estimated if there is a genetic basis for individual heterogeneity in terms of growth and response to leaf loss in our study population.
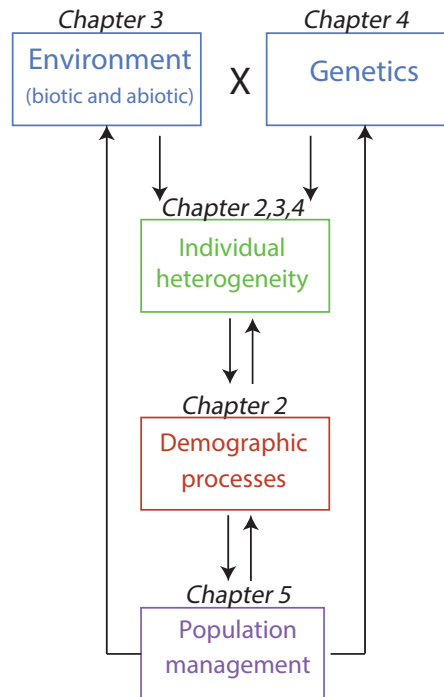


**Figure 1.5**. Graphical overview of the structure of this thesis. This thesis covers four main questions (indicated by the different colors in the scheme): (1) To what extent do individuals differ in performance? (green) (2) What causes individual heterogeneity? (blue) (3) What are the demographic consequences of individual heterogeneity? (red) (4) Can individual differences be used to improve the management of populations? (purple). The answers to these questions are all related, as indicated by the black arrows in the scheme. Most of the relations indicated by the gray arrows are discussed in Chapter 6 but do not fall under the main objectives of this thesis. Some questions are covered in multiple chapters of this thesis. Which chapters these are is written in black.
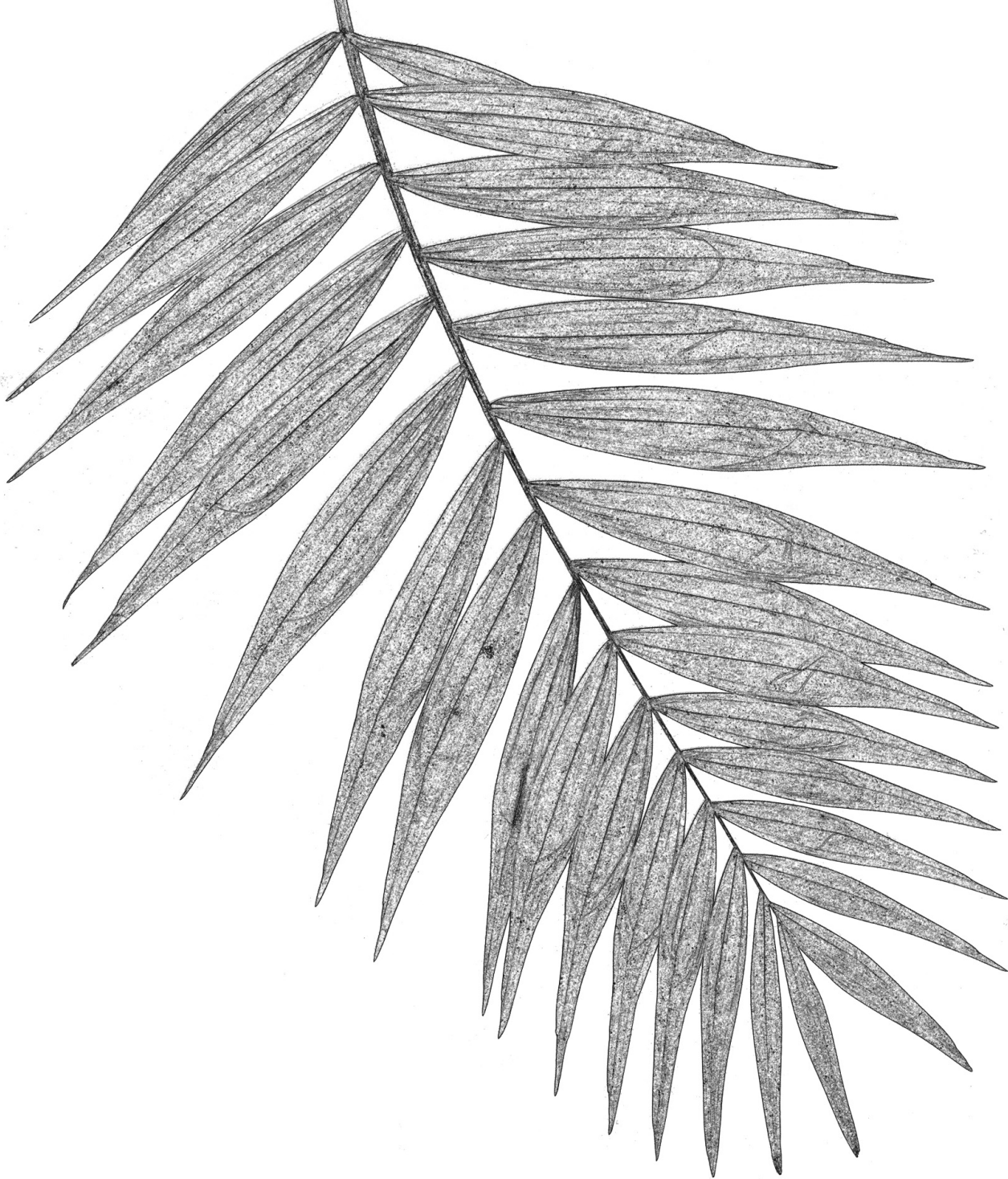
# Chapter 2

Strong persistent growth differences govern individual performance
and population dynamics in a tropical forest understorey palm

Merel Jansen, Pieter A. Zuidema, Niels P.R. Anten and Miguel Martínez-Ramos

## Abstract

1. Persistent variation in growth rate between individual plants can have strong effects on population dynamics as fast growers reach the reproductive size at an earlier age, and thus potentially contribute more to population growth than slow growers. In tropical forests, such persistent growth differences have so far been documented for canopy tree species, where they are primarily associated with forest gap dynamics, but not for forest understorey species which are less responsive to gaps. Here we study persistent growth differences and their demographic consequences for a tropical forest understorey palm, *Chamaedorea elegans*.

2. We measured internodes along stems and annual leaf production rates to reconstruct lifetime growth trajectories. Using regression analysis we determined the relative effect of stem length and past growth rate on vital rates (survival, growth and reproduction). We then simulated population dynamics using Integral Projection Models (IPMs), in which individuals were categorized by both stem length and lifetime past growth rate.

3. Stem growth differences among individual palms persisted over most of their lifetime. Past growth rate averaged over the palm's lifetime proved to be a very good predictor of growth, reproduction probability and seed production, often much better than stem length or age. The effects of past growth rate were positive, indicating that fast growers maintain high rates of growth and reproduction.

4. Projected population growth rate ($\lambda$) was 1.056 and stable stage distributions closely resembled observed population structures. Separating individuals with above-median and below-median past growth rates in IPMs revealed substantial differences in elasticity values. The 50% fastest growers had a 1.8 times higher elasticity, and thus a 1.8 times higher contribution to population growth, compared to slow growers.

5. *Synthesis.* Strong and persistent growth differences that are probably associated with environmental (edaphic) and/or genetic factors, govern individual performance and population dynamics of a tropical forest understorey palm. Overall, our study shows that strong inter-individual growth variation is not limited to canopy trees and that it can be generated by other factors than canopy dynamics. It is likely that persistently fast growing 'super performers' govern population growth of many long-lived species.

**Key-words:**

## Introduction

Not all individuals survive, grow, and reproduce at the same rate within a population (Sarukhán, Martínez-Ramos & Piñero 1984). Some grow faster than others and such growth differences can be maintained for some time or even for a substantial part of the total lifetime. Persistent differences have been documented for some time in animals (*e.g.* De Leo & Gatto 1995; Pfister & Stevens 2002; Pelletier *et al.* 2007; Tuljapurkar, Steiner & Orzack 2009), but they have received relatively little attention in plants. Studies in plants that did cover persistent growth differences were mostly restricted to tree species (Kohyama & Hara 1989; Clark and Clark 1992; Terborgh *et al.* 1997; Brienen, Zuidema & During 2006). Persistent growth variation in trees is likely caused by growth spurts ('releases') of juvenile trees that can be sustained over several years or decades (Lusk and Smith 1998; Brienen and Zuidema 2006). These growth spurts occur when juvenile trees growing in the forest understorey suddenly receive more light after the creation of canopy gaps.

While variation in light is an obvious driver for persistent growth differences of canopy trees, many understorey plant species complete their life cycle under low-light conditions, and these tend to exhibit much weaker growth responses to light compared to canopy tree species (*e.g.* Chazdon 1992; Svenning 2002; Martínez-Ramos, Anten & Ackerly 2009). As a result, differences in growth rate among individuals in understorey species might be smaller than in canopy species. Nevertheless, for forest understorey species, spatial variation in soil fertility, soil texture and water availability as well as genetic variation between individuals may cause growth differences. These factors may be more permanent than light availability (Ceccon, Huante & Rincón 2006) and, as a result, growth differences in understorey species might persist over longer time spans than those in canopy species. However, until now this issue has been poorly explored.

Temporal autocorrelation of growth and persistent variation in growth rate strongly determine population dynamics (Zuidema & Franco 2001; Pfister & Stevens 2003; Pelletier *et al.* 2007; Vindenes, Engen & Saether 2008; Tuljapurkar, Steiner & Orzack 2009; Zuidema, Brienen & During 2009). Fast growers can have a disproportionate contribution to population growth because they reach reproductive size at an earlier age and have a higher probability of reaching that size (Zuidema, Brienen & During 2009). This suggests that environmental or genetic factors underlying variation in growth may have a more profound impact on population dynamics than previously assumed. For example, if fast-growing individuals are more sensitive to climate change or harvest regimes, this will have a disproportionately large influence on population growth. The magnitude of this effect will depend on the strength and persistence of growth differences, but also on possible positive or negative trade-offs between growth, survival and reproduction. Negative trade-offs between growth and other vital rates (*e.g.* Martorell, Vega & Ezcurra 2006), may offset the higher contribution of fast growers to population growth. Positive trade-offs increase this contribution (Van Noordwijk & De Jong 1986). Such trade-offs have hardly been studied so far (Zuidema, Brienen & During 2009) and not at all in forest understorey species.

We studied the magnitude and consequences of persistent growth differences in the tropical forest understorey palm *Chamaedorea elegans*. We choose this long-lived understorey species as a study system because the growth history of individual palms can be easily reconstructed from internode lengths (Lugo & Rivera Batlle 1987; Pinard 1993) and because demography of a large set of individuals has been monitored over several years (Martínez-Ramos, Anten & Ackerly 2009). This enables us, on the one hand, to investigate functions that relate growth, survival and reproduction to stem length and past growth rate and, on the other hand, to assess the influence of persistent inter-individual growth variation on population dynamics, by adapting an age-size dependent Integral Projection Model (IPM) (Childs *et al.* 2003; Ellner & Rees 2006). Specifically, we addressed the following questions: (i) Do growth differences among individuals persist over time and, if so, for how long? (ii) To what extent are historical growth differences related to current individual growth and reproduction? (iii) What are the consequences of persistent growth differences for population dynamics in a long-lived rainforest understorey plant?

## Materials and methods

*Study site and species*

Data were collected at the Chajul Biological Field Station (16°06' N, 90°56' W) in the Montes Azules Biosphere Reserve (MABR), Chiapas, Mexico. The dominant vegetation type in the area is lowland evergreen tropical forest (Ibarra-Manríquez & Martínez-Ramos 2002). Annual mean precipitation is around 3000 mm with a dry season (monthly rainfall < 100 mm) from January to April. The mean annual temperature is about 25 °C. Precipitation can vary substantially, among others in relation to El Niño southern oscillation events (Martínez-Ramos, Anten & Ackerly 2009).

*Chamaedorea elegans* is a dioecious understorey palm found in tropical rain forests in Mexico, Guatemala and Belize (Hodel 1992). In MABR *C. elegans* occurs on karst-range sites, which are topographically irregular mountain chain areas (300–700 m a.s.l), where the soil is basically composed of a thin layer of organic matter, with masses of limestone rocks exposed over karst topography. Light levels vary between 0.5 % and 33 % of natural day light (average light level is 4.5 %), and soil depth varies between 0 cm and 40 cm (average soil depth is 21.5 cm; NPRA and MMR, unpublished data). *Chamaedorea elegans* reaches a maximum height of 1.5 m, is unbranched, single-stemmed and produces one single cluster of leaves. Species with these characteristics are very suitable for reconstructing growth histories by measuring internodes (Pinard 1993). The leaves of *C. elegans* are harvested and sold nationally and internationally (USA and Europe) in the floral industry. As such they are an important non-timber forest product (NTFP) providing income to many people (Oyama 1992). The population of this species is in decline due to habitat loss, and leaf, seed and whole plant extraction (Biodiversitas 2003).

*Data collection*

In March 1997, a 100 m x 112 m plot was established in which 353 individuals of *C. elegans* (including males and females) were mapped and tagged. From then until 2000, plant height, stem length, number of leaves, reproductive status, reproductive activity (inflorescence, infructescence and fruit production), mortality, length of the most fully extended leaf and relative light intensity above each plant were measured annually for all individuals. Additionally, in March 1997 a number of seedling plots were established with a total surface area of 135 m$^2$. In this area, all individuals shorter than 10 cm in height were mapped and tagged. In March 1998, 1999 and 2000 the new seedling cohorts were also identified, and each time the survival and height of all individuals in all cohorts was measured. More details about the study plots, methodology, and demographic attributes of the studied population can be found elsewhere (Martínez-Ramos, Anten & Ackerly 2009).

In March 2010 all internodes of each of the individual palms within the plot that were still alive (187 plants in total) were counted and their length was measured. In most palms including *C. elegans*, this is easy as leaf scars clearly mark individual internodes (Tomlinson 1990). The length of the internode represents the stem growth of the individual palm due to the production of two leaves.

*Statistical analysis*

To estimate lifetime past growth rates, we calculated the average annual leaf production over the period March 1997 to March 2000 per individual. Combining this information with internode length, we could reconstruct the age of a palm at any stem length. This method assumes that leaf production per individual is approximately constant within a stem. This assumption likely overestimates the differences in stem growth rates among individuals, because leaf production of an individual is unlikely to be constant over time (see Results). To estimate the sensitivity of our results to assumptions on variation in leaf production among individuals, we performed a robustness test. All statistical and modelling analyses were also performed under the assumption that all individuals had equal leaf production. In this case, the differences in lifetime past growth rates between individuals are only based on differences in internode length. This way of calculating certainly underestimates persistent growth differences among individuals, as leaf production rates do vary among individuals (Martinez-Ramos *et al.* 2009), but it provides a lower-bound estimate of the importance of past growth on individual performance and population growth.

We investigated the persistence of growth differences between individuals over ages using Spearman rank correlations. We correlated growth rates at each age with growth rate at subsequent ages.

We analysed the combined effects of stem length, age and past growth rate on vital rates (growth, survival, reproduction probability and seed production) over the period March 1997 to March 2000. We included only female palms in the statistical analyses of vital rates. In the case of survival we could not identify a relation to past growth or age, as the internodes of plants that had already died could no longer be measured. Therefore in the analyses of

survival we used all female palms (142 individuals), and in the analysis of growth rate, reproduction chance and seed production we used all female palms for which we were able to collect internode data in 2010 (68 individuals). Determinants of the mean annual growth rate and of the mean annual seed production were evaluated using multiple (stepwise backward) linear regressions. Determinants of the three-year probability of survival and the probability of reproduction (per year) were evaluated using multiple (stepwise backward) logistic regressions. In all regression analyses we tested for the effect of size, age and lifetime past growth rate (i.e. size/age) on vital rates (age was also added as age$^2$). Regression analyses were performed in R and were also performed for the robustness test.

*Construction of a size-past growth model*

To evaluate the effect of persistently fast growers on population growth, an Integral Projection Model (IPM) was constructed that included past growth. The basis for this model was an age- and size-dependent IPM (Childs *et al.* 2003; Ellner & Rees 2006), which was adapted such that population dynamics depended on size (stem length) and past growth rate (in stem length). In an age-size IPM population dynamics are described as (Ellner and Rees 2006):

$$n_0(y, t+1) = \sum_{a=0}^{m} \int_{\Omega} F_a(x,y) n_a(x,t) dx \qquad a = 0 \qquad \text{eqn 2.1a}$$

$$n_a(y, t+1) = \int_{\Omega} P_{a-1}(x,y) n_{a-1}(x,t) dx \qquad a > 0 \qquad \text{eqn 2.1b}$$

in which $x$ is size at time $t$, $y$ is size at time $t+1$ and $\Omega$ the set of all possible sizes. The probability density function $n_a(y,t)$ describes the state of the population of individuals of age $a$. $F_a(x,y)$ and $P_a(x,y)$ are the fecundity and survival-growth function respectively and m is the maximum age. Applying the midpoint rule (Easterling, Ellner & Dixon 2000), this model can be transformed into a set of large transition matrixes (one transition matrix per age), where $\Omega$ is now divided into very narrow size classes. In an age-size IPM the functions $F_a(x,y)$ and $P_a(x,y)$ are based on continuous functions that relate vital rates (growth, survival and reproduction) to both size and age. Lifetime past growth rate ($p$) can be expressed as a function of size ($x$) and age ($a$) as $p = \frac{x}{a}$. Therefore, in a linear example case, vital rate ($v$) can be related to size and past growth as:

$$v = \alpha + \beta * x + \gamma * \frac{x}{a} \qquad \text{eqn 2.2}$$

where $\alpha$, $\beta$ and $\gamma$ are regression coefficients. Note that an age-term ($\delta*a$) can be added to eqn 2.2 in case age *per se* explains (additional) variation in vital rate $v$. As eqn 2.2 is a function of size and age, incorporating such a function in $F_a(x,y)$ and $P_a(x,y)$, allows applying the analyses outlined by Ellner and Rees (2006). A detailed explanation and R code is included in Appendix S2.1 in the Supporting Information.

We used regression equations for vital rates to construct $F_a(x,y)$ and $P_a(x,y)$. We assumed no pollen limitation, and therefore we based the model on female palms only. As we lacked data on the influence of past growth rate on the performance of seedlings and individuals < 10 cm stem length, these size classes were not included. New stemmed individuals entered the model with a size distribution based on the growth rate distribution of individuals smaller than 10 cm, which was determined from the internode data, see Appendix S2.1. To construct $F_a(x,y)$ we averaged values of the three annual reproduction probability functions, multiplied this by the seed production function and by the average number of seedlings per seed. We applied a normal distribution in $P_a(x,y)$ to describe the variation in growth rate. As growth variation was independent of stem length or past growth rate, we used mean variation. As we did not find a significant contribution of size to survival (see Results), we used the average adult survival in $P_a(x,y)$. Maximum size in the model was 1.1 times the maximum observed stem length, minimum size 0.9 times the minimum observed stem length. The maximum age was taken to be 30 years, as very few individuals exceed this age. All individuals smaller than 11 cm were considered to be non-reproductive, as we did not observe any smaller individual with flowers or fruits. Two hundred points were used when applying the midpoint rule to construct the transition matrix. To verify if including persistent growth differences in IPMs changes population growth rate, we also constructed IPMs based on regression equations with only size as an explanatory variable.

*Demographic analyses*

An age-size-dependent IPM has a dominant eigenvalue, which represents the population growth rate ($\lambda$) and a right and left dominant eigenvector, which represent the stable size-age distribution and the reproductive value, respectively. To determine the relative contribution to population growth of fast growers, we conducted elasticity analysis (Ellner & Rees 2006). Elasticity values quantify the effect of a proportional change in a given transition probability or a certain size or age category, on population growth rate ($\lambda$; see Childs *et al.* 2003; Ellner & Rees 2006). The proportion of elasticity values accounted for by persistent fast growers therefore provides information on their contribution to $\lambda$. We distinguished fast and slow growers using quantiles in the age distribution per size class (where 50% is the median age): fast growers are the individuals below quantile age. Quantile ages were obtained from the stable age distribution of the corresponding size class. The total contribution of the fast growers was then calculated as the sum of the elasticity values per size class over all ages below quantile age (the fast growers), summed over all size classes. The same analysis was performed for the robustness test. The R-script is included in Appendix S2.1.

## Results

*Persistent growth differences*

Lifetime growth trajectories showed strong and persistent growth differences between individuals, which was first indicated by the width of the 'fan shape' and relatively few

crossings of the growth trajectories (Fig. 2.1a). A formal proof of persistent growth differences was obtained from rank correlations (Fig. 2.1b). The rank order of individuals with regard to growth rate at a particular age was almost always significantly correlated to that of the next and further age classes. These rank correlations were high (> 0.8) if growth rates were compared with the next age class and gradually decreased when comparing to further age classes (Fig. 2.1b). The correlations were significant up to a 26-year age difference (Fig. 2.1b). The rank correlation results indicate that growth rank at one age is a good predictor for growth rank at older ages and therefore differences in growth rate are persistent and long lasting.
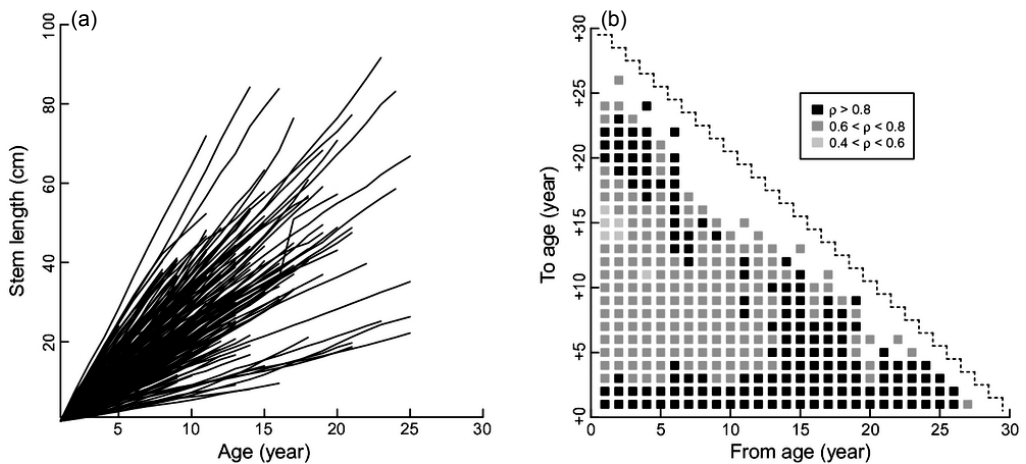


**Figure 2.1**. (a) Reconstructed lifetime growth trajectories of 187 individuals of *Chamaedorea elegans* in a Mexican tropical rain forest. Each line represents one individual. The width of the fan shape and few 'crossings' of lines indicate the magnitude of the persistent growth differences among individuals. (b) Spearman rank correlations of growth rate between subsequent ages. Significant rank correlations ($P < 0.05$) are shown and indicate that the rank order of individuals based on their stem growth rates at one age is maintained in the next or following ages. The dashed line delimits the ages for which correlations were conducted.

Leaf production rates were autocorrelated in time. For example, leaf production rates during the second and third year were significantly correlated ($r = 0.45$, $P < 0.001$). This suggests that variation in leaf production among individuals persists over time, at least to some extent. Furthermore, mean leaf production rates were also correlated with average lifetime internode length ($r = 0.32$, $P < 0.001$). This relation indicates that fast growing individuals in terms of stem length (per leaf) also tend to produce more leaves per year. These results suggest that assuming constant leaf production rate over the lifetime of individuals is probably quite realistic. Nevertheless, it is useful to test how sensitive results are to changing leaf production rates to an equal value for all individuals. The results of this robustness test are included in Appendix S2.2.

**Table 2.1.** Results of regression analyses to explain variation in vital rates of *Chamaedorea elegans* in a Mexican forest. Estimated coefficients, significance, and amount of variation explained: $R^2$ (Nagelkerke for logistic, Nagelkerke 1991) are shown. Age did not appear in any of the regression equations and is therefore not shown. Sample sizes are 142 individuals for survival chance and 68 individuals for growth, reproduction probability in year 1, 2 and 3 and seed production.

| | Intercept | P | Stem length (cm) | P | Past growth rate (cm year$^{-1}$) | P | $R^2$ |
|---|---|---|---|---|---|---|---|
| *Stem growth rate (cm year$^{-1}$)* | 0.413 | ** | 1.033 | *** | 0.443 | *** | 0.842 |
| *Survival chance (individual individual$^{-1}$ 3-year$^{-1}$)* | 2.382 | *** | -0.006 | ns | na | | 0.002 |
| *Reproduction probability year 1 (individual individual$^{-1}$ year$^{-1}$)* | -2.146 | *** | | ns | 0.480 | * | 0.125 |
| *Reproduction probability year 2 (individual individual$^{-1}$ year$^{-1}$)* | -2.830 | *** | | ns | 0.687 | ** | 0.220 |
| *Reproduction probability year 3 (individual individual$^{-1}$ year$^{-1}$)* | -0.249 | ns | | ns | 1.094 | * | 0.209 |
| *Seed production (seeds individual$^{-1}$ year$^{-1}$)* | 5.651 | ns | | ns | 7.675 | *** | 0.285 |

Significance levels are * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; ns, non-significant; na, the variable was not included in the analysis.
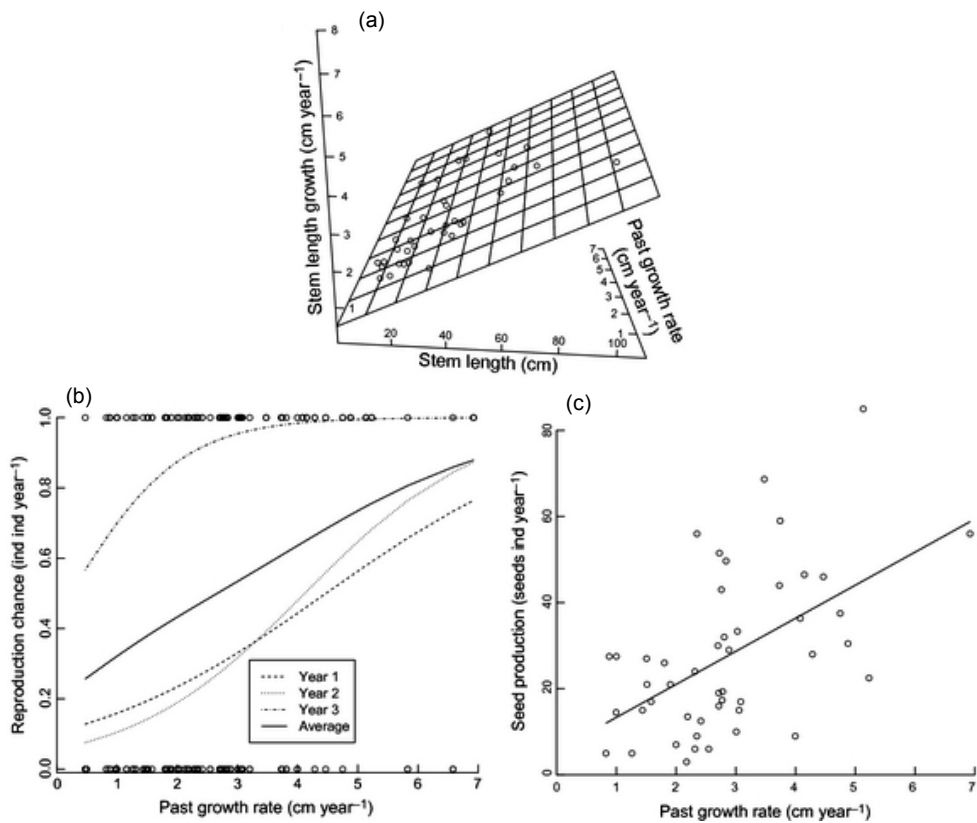
**Figure 2.2.** Results of multiple regression analyses in which vital rates growth (a), reproduction probability (b) and seed production (c), were related to stem length and past growth rate of *Chamaedorea elegans* in a Mexican tropical rain forest. Past growth rate strongly influenced current growth, reproduction probability and seed production. Regression results are included in Table 2.1. Note that sample sizes in 2b are larger as most individuals are represented by three dots, one for each year.

*Effect of persistent growth differences on individual fitness*

The results of the multiple regression analyses for vital rates are shown in Table 2.1 and functions are illustrated in Fig. 2.2. Age (or age$^2$) did not enter in any of the regression models and therefore was not a good predictor of vital rates. Stem growth rate was positively related to both stem length and past growth rate. Survival probability was not significantly related to stem length. For reproduction probability and seed production, past growth rate (*i.e.* size/age) explained most variation (positive relation) while current stem length did not appear in the regression equations. In all, these results suggest that past growth rate is a better predictor of these vital rates than stem length or age. Furthermore the relationships between growth, probability of reproduction and seed production with past growth were strongly positive. Thus, fast growers kept on growing fast (and therefore reached the reproductive size at an earlier age), had a higher probability of reproducing, and produced more seeds.

*Effect of persistent growth differences on population dynamics*
There was good correspondence between the stable population size structure predicted by the IPM and the structure observed in the field (Fig. 2.3a). This indicates that the dynamics simulated by the kernel are representative of the past dynamics of the population. The population growth rate (λ) projected by the model was 1.056, suggesting modest population growth. This value was very close to the value (1.059) obtained with a model that was based on size only. Elasticity values calculated for our IPM could be grouped by size or by past growth rates. The latter option allowed us to separate contributions of those individuals that have reached high lifetime growth rates vs. those that were slow growers. This separation showed that fast growers contributed considerably more to population dynamics than slow growers (Figs 2.3b, c and 2.4). For example, when we summed the elasticity values of the 10% fastest growing individuals over all size classes, we found that these accounted for 17% of the elasticity. Similarly, the 20% fastest growers contributed 29% to the elasticity (Fig. 2.4). When the population was divided in half, with fast and slow growers each representing 50% of the population, fast growers accounted for 64% of the elasticity. Thus, the fastest-growing 50% of the population contributed 1.8 fold more to population growth compared to the slow growers. This is also illustrated by the size-age distributions of elasticity values, showing the highest values for individuals in age classes of below-median age (Figs 2.3b and c).
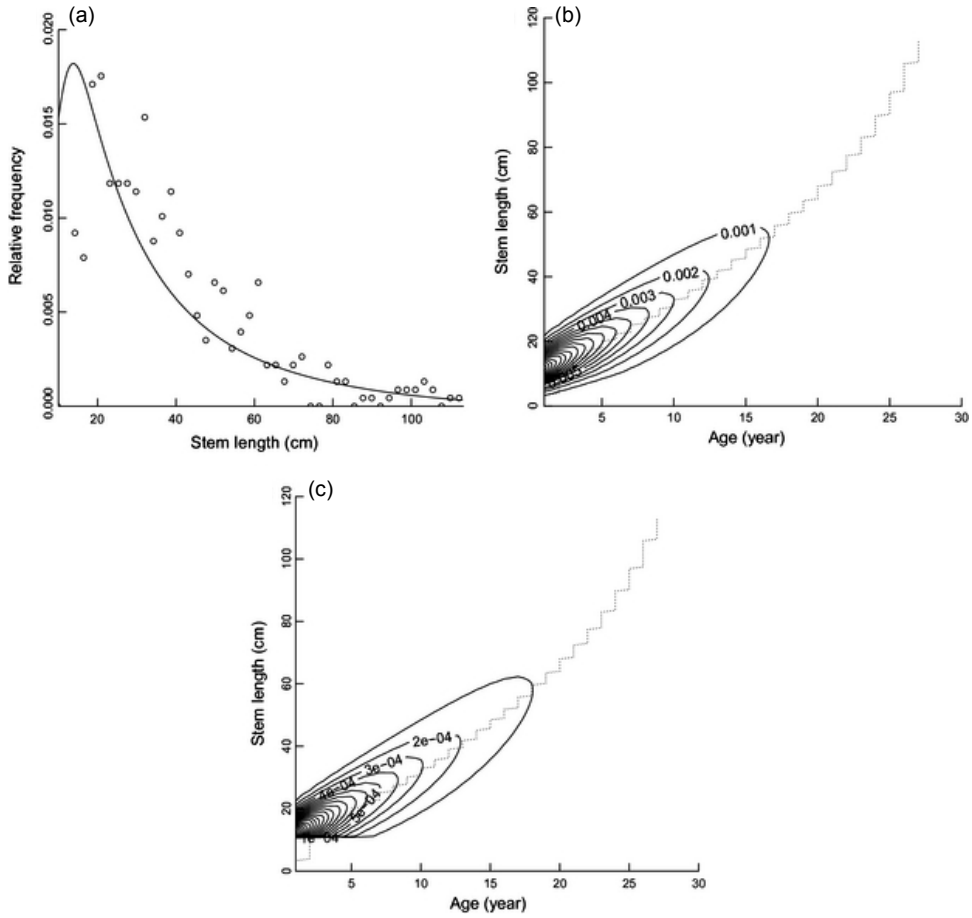
**Figure 2.3.** (a) A comparison of observed population structure (symbols; category width=2.23 cm) and predicted stable size distribution (line) of the Integral Projection Model for *Chamaedorea elegans* in a Mexican tropical rain forest. (b) Contour plot showing the distribution of elasticities for survival and growth (representing 82% of total elasticity) over size and age classes. High values indicate a large contribution to population growth. The dotted line represents median age per size class. For most size classes, elasticity values tend to be highest for below-median ages, i.e. persistent fast growers. (c) Idem for fecundity elasticities (18% of total elasticity)
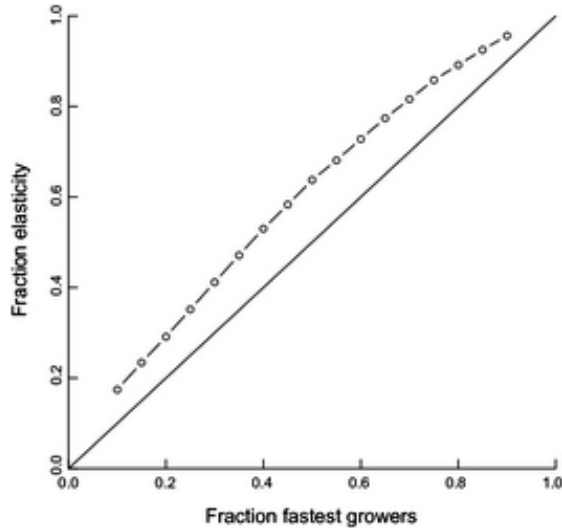
**Figure 2.4.** Relative contribution of fast growers to population growth for the understorey palm species *Chamaedorea elegans* in a Mexican tropical rain forest. The y=x line represents the situation in which fast growers would proportionally contribute to population growth. The left-most dot indicates that 10% of the fastest growers (i.e. 10% youngest individuals per narrow size class) account for 19% of the elasticity and therefore contribute disproportionately to population growth.

## Discussion

*Lifetime persistence of growth differences*

We measured internodes along stems and combined this information with annual leaf production rates to reconstruct lifetime growth trajectories for individuals of the tropical understorey palm *C. elegans*. We then showed that differences in growth rate between individuals persisted for long periods of time (up to 26 years). This strong persistent growth variation was also maintained in a robustness test, under the assumption of equal leaf production for all individuals (see Appendix S2.2). As only few individuals live longer than 30 years, our results imply that growth differences among individuals of understorey palm *C. elegans* persist over a substantial part of its lifespan.

Intriguingly, we found higher rank correlations for our study species compared to those obtained for large-stature tree species (Brienen, Zuidema & During 2006; Rozendaal & Zuidema 2011; Zuidema, Vlam & Chien 2011) and we found such correlations for a larger part of the life of individuals of our study species. The stronger persistence of growth differences in this understorey palm compared to canopy tree species studied before may reflect different causes of inter-individual variation in these groups of species. It has been proposed that growth variation in juvenile individuals of canopy tree species is determined by

gap dynamics, which lead to strong spatial and temporal variation in light availability ( Pfister & Stevens 2002; Brienen & Zuidema 2006). Growth of understorey palm species, on the other hand, is relatively insensitive to light variation (Chazdon 1992), as was also documented for *C. elegans* (Anten, Martinez-Ramos & Ackerly 2003; Martínez-Ramos *et al.* 2009). Inter-individual growth differences in these species could be more closely associated with edaphic condition or genetic variation, which are more permanent than gap-induced shifts in light availability (Ceccon, Huante & Rincón 2006), potentially leading to more persistent growth differences. In accordance with this idea, growth differences among *Cedrela odorata* trees were found to be more persistent in a dry forest than in a wet forest (Brienen, Zuidema & Martinez-Ramos 2010), likely because they were caused by long-term spatial variation in water availability in the dry forest and by shorter-term spatial variation in light conditions in the wet forest. It is likely that other factors than light availability drive strong and persistent inter-individual growth differences in *C. elegans* and related understorey (palm) species. Therefore, overall, we would expect more persistent growth differences if these are mainly caused by relatively permanent conditions like soil water and/or nutrient availability or by genetic differences among individuals.

*Past growth drives current palm performance*

Past growth rate and stem length importantly govern current growth in *C. elegans*. Several studies on canopy tree species found similarly large contributions of past growth rates on current growth rates (Brienen, Zuidema & During 2006; Rozendaal & Zuidema 2011; Zuidema, Vlam & Chien 2011). Intriguingly, in *C. elegans* seed production and reproduction probability are chiefly determined by past growth rate, without a significant effect of stem length. The strong positive correlation of stem growth and reproduction suggests that both are constrained by a third factor or combination of factors that allow the individual palm to both grow faster and reproduce more than others for long periods of time (Van Noordwijk & De Jong 1986). Palm age did not contribute significantly to explaining variation in any of the vital rates in our study species, in contradiction to what has been found for many plant species (*e.g.* Van Dijk 2009). This suggests that individual performance of *C. elegans* is not governed by age.

*Super performers within populations: what causes inter-individual differences in vital rates?*

We showed that inter-individual growth differences among individuals can persist for long periods of time and that these fast growers reproduce more than slow growers. This suggests the existence of super performers in our study species. Although the causes of these persistent differences in growth and reproduction are unknown, we suspect that they are associated with a combination of environmental factors (soil and topographic heterogeneity) and/or genetic differences. Most differences among individuals in animals are due to genetic differences (*e.g.* Coltman, Pilkington & Pemberton 2003), although examples of variation attributed to neutral processes are also found (Steiner & Tuljapurkar 2012). However, in plants this is likely to be different. As animals are generally able to move between (micro-)sites and search for optimal resource conditions, local variation in habitat does not necessarily lead to variation in vital

rates. In contrast, sessile plants depend on the resources available at the micro-site where they grow; therefore spatial environmental variation is more important in creating variation in individual performance for plants compared to animals (Harper 1977). Nevertheless, there are examples of genetic differences that clearly influence individual performance. For instance, in the tropical rain forest understorey palm (*Astrocaryum mexicanum*), strong variation in growth rates could be explained by genetic differences among individuals, with heterozygous individuals growing faster than homozygous ones (Eguiarte, Pérez-Naser & Piñero 1992). Furthermore, for the same species it was found that palms with higher reproductive rates were spatially aggregated in spots of the forest with more light (Piñero & Sarukhán 1982), which indicates that both genetic variation and environmental factors may contribute to variation in vital rates. The role of genetic differences can relatively easily be tested using quantitative genetic experiments, in which (seeds of) fast and slow growers are grown under similar conditions. However, there is reason to assume that genetic differences are not very important in explaining persistent growth differences, as heritable traits that would allow plants to make more efficient use of the available resources would be readily selected for and lead to faster (average) growth and likely reduced variation.

In our study species, variation in light availability and soil depth explain 8% of the variation in stem growth, but there is no relation between these variables and reproductive output (Martínez-Ramos, Anten & Ackerly 2009). Thus, other factors, including soil nutrient or water availability, are probably responsible for the observed persistent growth differences. One potential factor is the presence of karst-range sites in the study area: growth and survival of canopy trees growing at these sites is much more sensitive to changes in annual rainfall than those growing on alluvial soils where soil nutrients and water availability is higher (M. Martinez-Ramos, unpubl. data). If the differences are indeed caused by environmental factors, the spatial heterogeneity in growth conditions, possibly in association with dispersal patterns, may play an important role in regulating population dynamics (Svenning 2002). This in turn implies that changes in this spatial pattern may strongly affect population growth. For example, if super performers require certain growing conditions, they may be relatively vulnerable to changes in those conditions due to habitat loss or climate change.

*The importance of fast growers for population growth*

When some individuals persistently grow faster than others, they may have a disproportional contribution to population growth. Compared to slow growers, fast growers reach the reproductive size at a younger age and have a higher probability of doing so. This fast-growth effect can be larger if fast-growing individuals also produce more seeds – which was the case in our study species. For *C. elegans*, we estimated that the contribution of fast growers (individuals below median age of a certain size) to population growth is 1.8 times higher than that of slow growers (individuals above median age of a certain size). A similar difference in the importance of fast and slow growers was found for the tropical forest canopy tree species *Cedrela odorata* (Zuidema, Brienen & During 2009). Using loop analyses in an age-size classified matrix model, they found that fast-growing juvenile individuals contributed two times more to population growth compared to slow growers.

The fast-growth effect we presented for *C. elegans* may have been slightly overestimated as we assumed that observed differences in leaf production rates among individuals measured during a couple of years are representative of lifetime differences in leaf production. However, our main conclusion was maintained in a rigorous robustness analysis that showed, even under the most conservative assumption of all plants having equal leaf production rates, faster growers still contributed 30% more to population growth than slow growers (Appendix S2.2). On the other hand, the fast-growth effect of the original model may also have been an underestimate, if past growth rate is positively related to survival probability. We lacked data to test this, but such relations were recently found for many tropical tree species (Rüger *et al.* 2011). In all, our results show that population growth is disproportionately governed by fast-growing individuals that attain high rates of reproduction.

*Implications for conservation and management*

If fast growers contribute more to population growth than slow growers, it would be effective to target conservation and management efforts at this group (Zuidema, Brienen & During 2009). Differentially exploiting (leaves, fruits, entire individual) of fast and slow growers may be beneficial for the survival and recovery of harvested populations, and may increase yields in the long run. Clearly, an important condition to put such recommendations in practice is the identification of these fast growers. The internodes of understorey palms allow for relatively straightforward recognition of fast growers. Thus, understorey palms are a very suitable group to test the effects of protecting fast growers to improve sustainability of harvesting practices.

## Acknowledgements

**SUPPORTING INFORMATION**

**Appendix S2.1** *Methods and R script for a size and past growth rate dependent IPM and for the analysis of the relative importance of fast growers.*

**Appendix S2.2** *Results of a robustness test to evaluate the effect of leaf production rates on model output.*

**Appendix S2.1** *Methods and R script for a size and past growth rate dependent IPM and for the analysis of the relative importance of fast growers.*

# Here we explain how an IPM that is based on size and past growth rate can be constructed, using results of regression analysis that relate vital rates to size (i.e. stem length) and past growth rate, based on the methods for age-size IPMs (Childs et al., 2003; Ellner and Rees, 2006). Furthermore, we explain how this model can be used to determine the contribution of fast growers to population growth compared to that of slow growers. To illustrate this, the text below can be run as an R script. This will give a figure similar to Fig. 2.4 as output. It also gives the absolute and relative contribution of fast growers to population growth.

################# R script for a size and past growth rate dependent IPM #################

#======================= Coefficients from regression analysis =======================#

## Results regression analyses that relate vital rates to size and past growth rate

```
# growth
gc1<- 0.4131985059816964          # intercept
gc2<- 1.033254415549539           # size dependence
gc3<- 0.442829296121639           # past growth rate dependence

# growth variation
gvc1<- 0.2155738219794835         # there was no size or past growth rate dependence, so the mean
variation was used
gvc2<- 0                          # therefore the size dependence is zero
gvc3<- 0                          # as is the past growth rate dependence

# reproduction chance
# year 1
rc11<- -2.145710269344375         # intercept
rc21<- 0                          # size dependence
rc31<- 0.4798402528402234         # past growth rate dependence
# year 2
rc12<- -2.829649961946504         # intercept
rc22<- 0                          # size dependence
rc32<- 0.686957001800037          # past growth rate dependence
# year 3
rc13<- -0.2486487301357424        # intercept
rc23<- 0                          # size dependence
rc33<- 1.0938414583993847         # past growth rate dependence

# seed production
spc1<- 5.650516863253285          # intercept
spc2<- 0                          # size dependence
spc3<- 7.67529145518755           # past growth rate dependence
```

#======================= Other necessary coefficients =======================#

# because we did not find size dependent survival rates we used average survival
```
sa<-  0.96610716933178            # adult survival
```

# number of female seedlings per seed

fsdl<- 0.017676076015

# to determine how many of the produced female seedlings become adults per year we used average seedling survival rates, average initial seedling size and average seedling growth rates

```
ss<- 0.8103254                    # seedling survival
is<- 3.75                         # average initial seedling size
sg<- 1.759437751004016            # average seedling growth rate
```

# the average time till adulthood (10 cm stem length) is then:
```
time<- ((10-is)/sg)
```

# and the number of new adults:
```
nna<- ss^time
```

# the size distribution of new adults is based on the growth rate distribution of individuals smaller than 10cm, which was determined from the internode data. Average growth rates per individual were multiplied by the average time spend as seedling. The result is representative of the size distribution after 3.552271 years of growth(which is after the average time spend as seedling). This distribution is therefore representative of the measured variation in growth rate.
```
mu<- 10.18524157838404            # mean
sig2<- 18.22828004325677          # variation
```

#============================== Formulas ==============================#

### Here the results from the regression analysis (functions of size and past growth rate) are translated into functions of size (x in the formula) and age, by expressing past growth rate as size/age. For more explanation of the general form of the formulas, see Ellner and Rees (2006).
# NOTE: We added a correction factor to the age (+time-1) because here new individuals enter the model not at age 1, but at age 3.552271. This is because we do not have data of the influence of past growth on the vital rates of seedlings. Any model in which individuals enter at age 1 does therefore not need any age correction factor.

# Growth function

```
gxya<-function(x,y,age) {
        sigmax2<-gvc1+gvc2*x+gvc3*(x/(age+time-1)) ;
        sigmax<-sqrt(sigmax2) ;
        mux<-gc1+gc2*x+gc3*(x/(age+time-1));
        fac1<-sqrt(2*pi)*sigmax;
        fac2<-((y-mux)^2)/(2*sigmax2);
        return(exp(-fac2)/fac1);
}
```

# function of growth and survival together

```
pxya<-function(x,y,age) { return(sa*gxya(x,y,age)) }
```

# Fecundity function.  The ifelse function makes that there are no reproductive individuals below the size of 11 cm

```
fxya<-function(x,y,age) {
        rx1<-(exp(rc11+rc21*x+rc31*(x/(age+time-1))))/(1+(exp(rc11+rc21*x+rc31*(x/(age+time-1)))));
```

```
        rx2<-(exp(rc12+rc22*x+rc32*(x/(age+time-1))))/(1+(exp(rc12+rc22*x+rc32*(x/(age+time-1)))));
        rx3<-(exp(rc13+rc23*x+rc33*(x/(age+time-1))))/(1+(exp(rc13+rc23*x+rc33*(x/(age+time-1)))));
        nkids<-fsdl*(spc1+spc2*x+spc3*(x/(age+time-1)))*((rx1+rx2+rx3)/3);
        n.adults<-nna

        sig<-sqrt(sig2);
        fac1<-sqrt(2*pi)*sig;
        fac2<-((y-mu)^2)/(2*sig2);
        f<-nkids*n.adults*exp(-fac2)/fac1;

        return(ifelse(x<11,0,f));
}
#================================= IPM =================================#
```

### The above formulas are now functions of size and age. Therefore the same methods as for the age-size IPM can be used to convert the functions to an IPM. The part of the script below can be used which is copied from the supplementary material from Ellner and Rees (2006). We added it here so that this script can be run in R. Explanation of this part of the script can also be found here. Output of this is model elasticity and stable age-size distribution, which will be used in the next part of the script to determine the contribution of fast growers to population growth compared to slow growers.

```
matrix.image=function(x,y,A,col=topo.colors(100),...) {
        nx=length(x); ny=length(y);
        x1=c(1.5*x[1]-0.5*x[2],1.5*x[nx]-0.5*x[nx-1]);
        y1=c(1.5*y[1]-0.5*y[2],1.5*y[ny]-0.5*y[ny-1]);
        image(list(x=x,y=y,z=t(A)),xlim=x1,ylim=rev(y1),col=col,bty="u",...);
}
n.big.matrix = 200; n.age = 30;
P<-array(NA,dim=c(n.big.matrix,n.big.matrix,n.age)) #P[j,i,a] will be h*P_{a-1}(x_j,x_i)
B<-array(NA,dim=c(n.big.matrix,n.big.matrix,n.age)) #B[j,i,a] will be h*F_{a-1}(x_j,x_i)
minsize=2.186013; maxsize=103; L= 0.9*minsize; U= 1.1*maxsize; n = n.big.matrix
b = L+c(0:n)*(U-L)/n; y = 0.5*(b[1:n]+b[2:(n+1)]);
h = y[2]-y[1]
for (age in 1:n.age) {
        P[,,age]<-h*t(outer(y,y,pxya,age=age))
        B[,,age]<-h*t(outer(y,y,fxya,age=age))
}
tP=P; tB=B;
for(age in 1:n.age) {tP[,,age]=t(P[,,age]); tB[,,age]=t(B[,,age]);}
Nt=matrix(0,n.big.matrix,n.age); Nt1=Nt; # population now and next year
iteration=function(Nt) {
        for(age in 2:n.age) {Nt1[,age]=P[,,age-1]%*%Nt[,age-1]}
        Nt1[,1]=0;
        for(age in 1:n.age) {Nt1[,1]=Nt1[,1]+B[,,age]%*%Nt[,age]}
        return(Nt1)
}
iteration.t=function(Nt) {
        Nt1[,n.age]=tB[,,age]%*%Nt[,1]
        for(age in 1:(n.age-1)) {Nt1[,age]=tB[,,age]%*%Nt[,1] + tP[,,age]%*%Nt[,age+1]}
        return(Nt1)
}
Nt=matrix(1,n.big.matrix,n.age);
```

```
qmax=1000; lam=1; tol=1.e-8;
while(qmax>tol) {
        Nt1=iteration(Nt);
        qmax=sum(abs(Nt1-lam*Nt));
        lam=sum(Nt1);
        Nt=Nt1/lam;
        cat(lam,qmax,"\n");
}
stable.dist=Nt/sum(Nt); lam.stable=lam;                    # Here is the stable size-age distribution
Nt=matrix(1,n.big.matrix,n.age);
qmax=1000; lam=1; tol=1.e-8;
while(qmax>tol) {
        Nt1=iteration.t(Nt);
        qmax=sum(abs(Nt1-lam*Nt));
        lam=sum(Nt1);
        Nt=Nt1/lam;
        cat(lam,qmax,"\n");
}
repro.val=Nt/sum(Nt); lam.stable.t=lam;
Psens=array(0,dim=c(n.big.matrix,n.big.matrix,n.age))
for(age in 1:(n.age-1)) {
        Psens[,,age]=outer(repro.val[,age+1],stable.dist[,age])
}
v.dot.w = h*sum(repro.val*stable.dist);
Psens=Psens/v.dot.w;
Pelas=Psens*(P/h)/lam;                                     # Here is the size-age elasticity distribution for
growth-survival
rm(Psens) ;
Bsens=array(0,dim=c(n.big.matrix,n.big.matrix,n.age))
        for(age in 1:n.age) {
                Bsens[,,age]=outer(repro.val[,1],stable.dist[,age]);
        }
Bsens=Bsens/v.dot.w;
Belas=Bsens*(B/h)/lam;                                     # Here is the size-age elasticity distribution for
fecundity
rm(Bsens);
```

#========= Contribution fast growers to population growth compared to slow growers =========#

### In this part of the script the relative contribution of fast growers to population growth is determined using model elasticity. To do this, fast and slow growers first need to be identified. This is done using the stable size-age distribution. The stable size-age distribution gives the stable age distribution per size class. For each size class it is determined what the age is below which individuals are considered fast growers (palms of a certain size that are young grew faster than palms of the same size that are old). When this age is the median age, the size class is divided into the 50 % fastest and the 50 % slowest growers. Using quantile ages, it can also be divided into *e.g.* the 10 % fastest and the 90 % slowest growers (i.e., the 10% youngest and the 90% oldest individuals, respectively). When the division between fast and slow growers is made, their contribution to elasticity can be summed separately to obtain the total contributions.

## A matrix is created that gives the quantile age per size class for each of the fractions in line 1 (this includes the 50% case of the median age). First, per size class, the fractional stable age distribution is transformed to a non-fractional form as it is not possible to calculate the quantile age of a population of "fractional

individuals"(stablevec, lines 4-5). This non-fractional distribution can be used to create a vector of 10000 hypothetical individuals of different ages representative for the stable age distribution of this size class (stableagemat, lines 6-17). From this vector the desired quantile age can be determined using the quantile function (line 18). All quantile ages per size class probability are then stored in a matrix (stall, lines 20-21).

```
probvec<-c(0.1,0.15,0.2,0.25,0.3,0.35,0.4,0.45,0.5,0.55,0.6,0.65,0.7,0.75,0.8,0.85,0.9)    #(1)
stall<-matrix(0,n.big.matrix,17);                                                          #(2)
fall<-function(n){                                                                         #(3)
        stablevec<-(stable.dist[n,]/sum(stable.dist[n,])*10000);                           #(4)
        stablevec<-round(stablevec);                                                       #(5)
        m<-matrix(0,30,2)                                                                  #(6)
        m[,1]<-as.vector(stablevec);                                                       #(7)
        m[,2]<-as.vector(c(1:30));                                                         #(8)
        m<-m[stablevec>0,];                                                                #(9)
        stableagemat<-matrix(0,11000,1);                                                   #(10)
        stableagemat[(1:m[1,1]),]<-rep(m[1,2],m[1,1])                                      #(11)
        for(i in 2:length(m[,2])){                                                         #(12)
                lim1<-sum(m[1:(i-1),1])                                                    #(13)
                lim2<-sum(m[1:i,1])                                                        #(14)

                stableagemat[((lim1+1):lim2),]<-rep(m[i,2],m[i,1])                         #(15)
        }                                                                                  #(16)
        stableagemat<-stableagemat[stableagemat>0,]                                        #(17)
        return(quantile(stableagemat,prob=probvec))                                        #(18)
}                                                                                          #(29)
for(i in 1:n.big.matrix){                                                                  #(20)
        stall[i,]<-fall(i);                                                                #(21)

}                                                                                          #(22)
```

## Once it is determined per size class which ages represent fast growers, this can be translated into contribution of these fast growers to elasticity. This is done by using the elasticity distribution. This distribution is a distribution per size class and per age, so per size class it can be divided into the part below quantile age and above quantile age (and therefore fast and slow growers) (lines 5 to 9). Then this is summed over all size classes, leading to the total contribution of fast and slow growers to population growth separately (lines 11 to 14).

```
elas.combined<-Pelas+Belas;                                                                #(1)
percentage.elas.mat<-matrix(0,17,2);                                                       #(2)
for(k in 1:17){                                                                            #(3)
elas.mat<-matrix(0,n.big.matrix,2);                                                        #(4)
for(i in 1:n.big.matrix){                                                                  #(5)
fast<-ifelse((stall[i,k]-1)<1,0,sum(elas.combined[,i,1:(stall[i,k]-1)]))+    (0.5*sum(elas.combined[,i,stall[i,k]]));
                                                                                           #(6)
slow<-ifelse((stall[i,k]+1)>30,0,sum(elas.combined[,i,(stall[i,k]+1):30]))+
(0.5*sum(elas.combined[,i,stall[i,k]]));                                                    #(7)
        elas.mat[i,1]<-fast;                                                               #(8)
        elas.mat[i,2]<-slow;                                                               #(9)
}                                                                                          #(10)
fasttotal<-sum(h*h*elas.mat[,1]);                                                          #(11)
slowtotal<-sum(h*h*elas.mat[,2]);                                                          #(12)
percentage.elas.mat[k,1]<-fasttotal;                                                       #(13)
percentage.elas.mat[k,2]<-slowtotal;                                                       #(14)
```

} #(15)

# Graphical display of relative contribution of fast growers to population growth compared to slow growers for several fractions.

```
par(mfrow=c(1,1));
plot(probvec,percentage.elas.mat[,1], xlim=c(0,1), ylim=c(0,1), type="b", cex.axis=1.3, cex.lab=1.3,
xlab="Fraction fastest growers", ylab="Fraction elasticity",axes=F,xaxs="i",yaxs="i")
axis(1,tck=0.02,cex=1.4)
axis(2,tck=0.02,cex=1.4)
lines(c(0,1),c(0,1))          # adding the line which indicates when the contribution of fast and slow growers
would be equal
```

## The population can be divided in half, in the 50% fastest growers and the 50% slowest growers (individuals below and above median age respectively). In this case the relative contribution of fast growers compared to slow growers is:

```
percentage.elas.mat[9,1]/percentage.elas.mat[9,2]
```

**Appendix S2.2.** *Results of a robustness test to evaluate the effect of leaf production rates on model output.*

As expected, the application of equal leaf production rates for all individuals reduced the magnitude and degree of persistence of growth differences among individuals (Fig S2.1). Nevertheless, growth ranks were still correlated over up to 23 years age difference, albeit with lower correlation coefficients (Fig. S2.1). Thus, even under the most conservative assumption of equal leaf production, growth differences between individuals persist over time.

Results of the statistical tests of how vital rates relate to size, age and past growth were similar under the assumption of equal leaf production. The major difference was a lack of significant effect of past growth on the probability of reproduction in two of the three years (Table S2.1 and Fig. S2.2). Thus, also under the assumption of equal leaf production, variation in past growth rates between individuals remain sufficiently large to explain variation in growth, seed production and – to a lesser extent – reproduction probability.

The output of the Integral Projection Model changed relatively little when equal leaf production rates were assumed for all individuals. The population growth rate was comparable ($\lambda$=1.060) and the results of the elasticity analyses changed slightly: the relative contribution of fast growers to population growth rate was slightly lower (Fig. S2.4). Nevertheless, even in the extreme situation of equal leaf production, the 50 % fastest growers in this case still contributed 1.3 times more to population growth compared to the slow growers. Finally, the stable size distribution differed more from the observed distribution (Fig. S2.3), which suggests that the original model better represented the actual population dynamics.
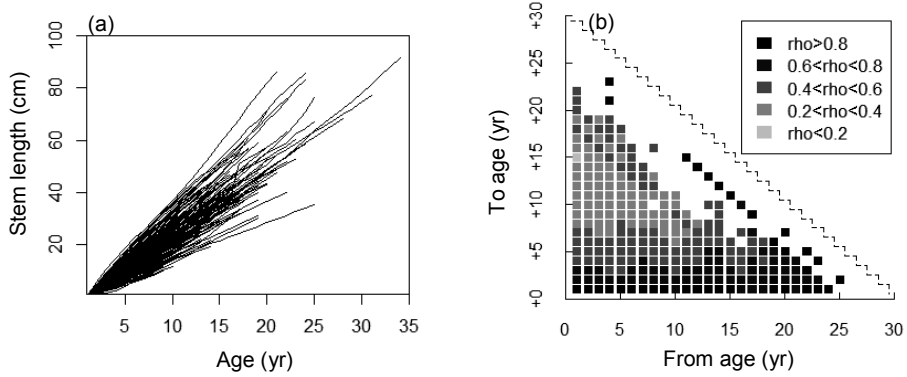
**Figure S2.1.** (a) Reconstructed lifetime growth trajectories of 187 individuals of *Chamaedorea elegans* in a Mexican tropical rainforest, under the assumption that all individuals have equal rates of leaf production. Each line represents one individual. The width of the fan shape and few 'crossings' of lines indicate the magnitude of the persistent growth differences among individuals. (b) Spearman rank correlations of growth rate between subsequent ages. Significant rank correlations ($P<0.05$) are shown and indicate that the rank order of individuals based on their stem growth rates at one age is maintained in the next or following ages. The dashed line delimits the ages for which correlations were conducted.
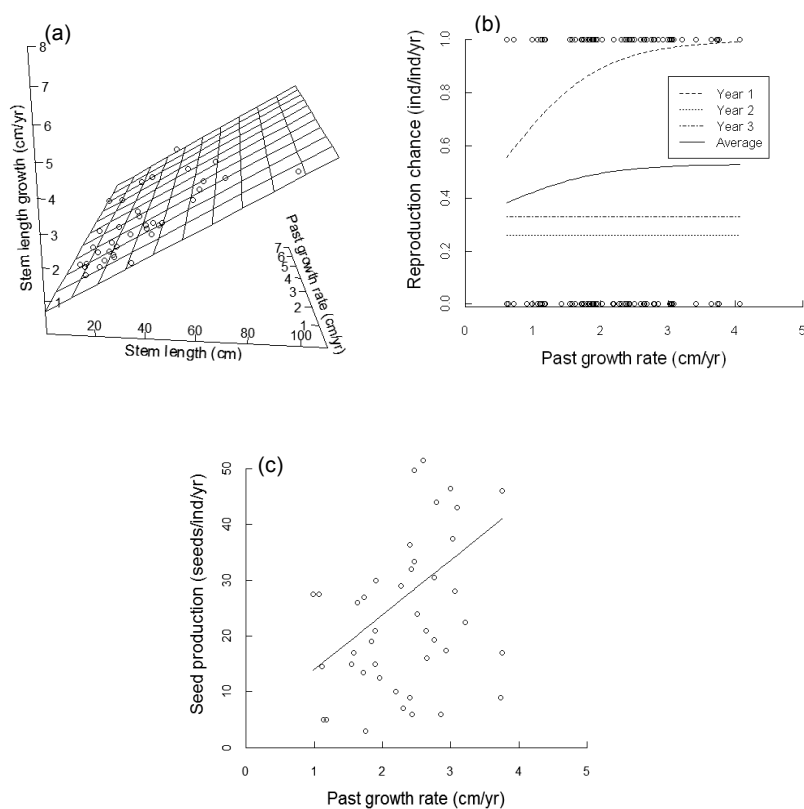
**Figure S2.2.** In the multiple regression analyses the vital rates growth (a), reproduction chance (b) and seed production (c), were related to stem length and past growth rate. Even under the assumption of equal leaf production past growth rate strongly influenced current growth and seed production, but influenced reproduction chance significantly only in one of the three years.
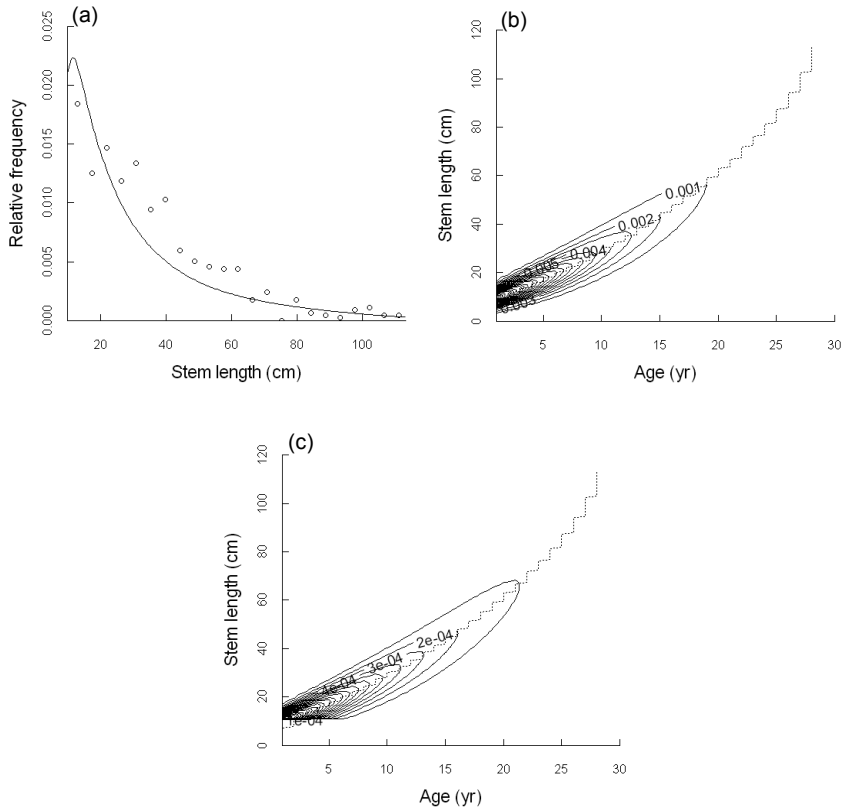
**Figure S2.3.** (a) Comparison of observed population structure (symbols) and predicted stable stage distribution (line). The observed population size distribution is displayed using size categories with a width of 4.45 cm in stem length. b,c) Results of elasticity analyses for survival-growth (91 % of total elasticity) (b) and fecundity (9 % of total elasticity) (c). The elasticity distribution indicates for which transitions there would be a large effect on population growth rate if the transition (*i.e.* vital rates for the belonging size class) would change. The dotted line indicates what the median age in each size class is and therefore shows that even under the assumption of equal leaf production the majority of the elasticity is in the lower- below median age size classes.
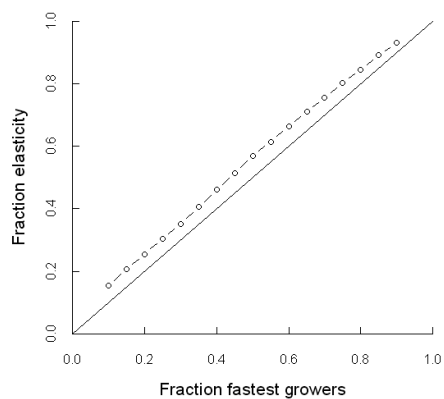
**Figure S2.4.** The left-most dot indicates that 10% of the fastest growers (i.e. 10% youngest individuals per narrow size class) account for 15% of the elasticity. The solid y=x line represents the situation in which fast growers would proportionally contribute to population growth. As all dots are located above this line, this figure illustrates that even under the assumption of equal leaf production fast growers contribute disproportionately to population growth.

**Table S2.1.** Estimated coefficients, significance and amount of variation explained: $R^2$ (Nagelkerke for logistic) are shown. Significance levels are *$P<0.05$, **$P<0.01$, ***$P<0.001$, ns non-significant. Na indicates that the variable was not included in the analysis. Age did not appear in any of the regression equations and is therefore not shown. Past growth rates were calculated under the assumption that all individuals had equal leaf production rates.

| | Intercept | P | Stem length (cm) | P | Past growth rate (cm/yr) | P | $R^2$ |
|---|---|---|---|---|---|---|---|
| *Growth (cm/yr)* | 0.685 | ** | 1.041 | *** | 0.298 | * | 0.649 |
| *Reproduction chance year 1 (ind/ind/yr)* | | ns | | ns | | ns | na |
| *Reproduction chance year 2 (ind/ind/yr)* | -2.182 | * | | ns | 0.560 | ns | 0.058 |
| *Reproduction chance year 3 (ind/ind/yr)* | -0.606 | ns | | ns | 1.352 | * | 0.190 |
| *Seed production (seeds/ind/yr)* | 4.148 | ns | | ns | 9.827 | *** | 0.149 |

# Chapter 3

Explaining long-term inter-individual performance variation in plant populations: persistence of abiotic factors matters

Merel Jansen, Niels P.R. Anten, Frans Bongers, Miguel Martínez-Ramos, Mayra E. Gavito, Pieter A. Zuidema

# Abstract

Short-term effects of environmental (biotic and abiotic) variation on individual performance (survival, growth, and reproduction) have been quantified for many organisms. Within natural populations, high levels of long-term inter-individual performance variation are often observed, which suggests that environmental differences among individuals persist over time. To date, the extent to which the combined effects of different environmental factors on plant performance persist over time has not been assessed. Here, we analyze the extent to which temporal persistence of spatial environmental heterogeneity can contribute to long-term inter-individual variation in performance in a tropical palm species. We studied 830 individuals of the long-lived tropical understorey palm *Chamaedorea elegans* in a natural population. We first related spatial environmental heterogeneity in light availability, soil variables (pH, moisture content, N- and P-availability) and leaf damage, to differences in palm performance, during two years. For the two most significant abiotic factors (light and pH), we quantified changes in their spatial heterogeneity over time. We then performed individual-based simulations of growth and reproduction trajectories, in which we varied (i) the strength of the effect of the environmental factor on performance and (ii) the temporal persistence of the environmental factor, and compared these.

Short-term variation in stem length growth and reproduction were strongly driven by light availability, while soil variables and leaf damage had smaller effects. Both light availability and soil pH were autocorrelated over time, and including this autocorrelation greatly increased simulated variation in stem length growth among 20-year old palms with 110% (light) and 5% (pH), to levels similar to observed variation. At the same time, variation in cumulative reproductive output increased with 126% due to auto-correlation in light and pH. Analysis in which we varied both the strength of the effect of environmental variation on performance and the temporal persistence of the environmental factor, revealed a pattern showing that a large fraction of observed long-term performance differences is explained, as long as one of these effects is high. This implies that environmental factors that are relatively unimportant for short-term plant performance, can still drive long-term performance differences between plants when the variation in the environmental factor is sufficiently persistent over time. Knowing the relative importance of different environmental factors for long-term variation in plant performance will provide better insights into plant environmental adaptations.

**Keywords**

*Chamaedorea elegans*, individual heterogeneity, life history, life-long fitness, plant population dynamics, spatial- and temporal variation, super-performance, tropical forests, forest understorey

## Introduction

The biotic and abiotic environmental factors that drive performance of individuals (*i.e.* growth, survival, and reproduction) in natural populations have been studied for many plants and animals in dose-response experiments (see Poorter *et al.* 2010). Soil nutrients, water, and light availability, as well as herbivory, are important drivers of individual plant performance (*e.g.* West & Coombs 1981; Kleb & Wilson 1997; Van Der Wal *et al.* 2000; Berry *et al.* 2008; Van Nguyen *et al.* 2015), and large inter-individual variation in performance within populations can result from spatial heterogeneity of such factors. For example, large annual differences in growth or survival of understory plants (Chazdon 1986; Chazdon 1988) result from spatial variation in light availability in the tropical rainforest understory due to canopy gap dynamics (*e.g.* Chazdon & Fetcher 1984b; Nicotra, Chazdon & Iriarte 1999; Poorter & Arets 2003).

An unanswered question in ecology is whether the environmental factors driving short-term individual performance also determine the large inter-individual differences in performance in the long run. Such long-term performance differences have been documented in natural populations for a wide variety of plant and animal species. For example, coetaneous individuals have been shown to differ in lifetime reproductive output (*e.g.* Steiner, Tuljapurkar & Orzack 2010; Plard *et al.* 2012) and growth (*e.g.* Brienen & Zuidema 2006; Jansen *et al.* 2012). The extent to which environmental factors generate long-term inter-individual variation depends not only on the strength of short-term dose-response relations but also on the degree to which differences in the environmental factors affecting individual's performance persist over time, *i.e.* whether the environmental variation is temporally autocorrelated. Returning to the example of tropical rainforest understory plants, a short-term strong effect of light availability on plant growth may not contribute to explaining long-term inter-individual differences if this factor varies importantly over time (*i.e.*, is weakly autocorrelated in time). And vice versa, an environmental factor that only weakly influences short-term performance can be an important determinant of long-term inter-individual differences if such influence persists over time (*i.e.* is highly autocorrelated in time); in the long-term such small influence can produce a significant advantage for some individuals over others. This latter case could be of particular importance in sessile organisms like most plants, for which temporal fluctuations in soil and micro-topographic conditions are highly autocorrelated over time.

In this paper, we address the following questions: (1) To what extent can temporal persistence of environmental heterogeneity explain long-term inter-individual variation in performance, and (2) how is this related to the strength of the influence of the environmental factors on short-term performance?

We used the understorey palm *Chamaedorea elegans* as a study system. The particular growth form of most palms like *C. elegans* (*i.e.*, production of clear internodes along a single stem) makes them ideal for the reconstruction of lifetime growth histories and, thus, for the quantification of long-term inter-individual differences (Jansen *et al.* 2012). We collected two years of performance data, related this to environmental heterogeneity, and quantified

autocorrelation in environmental heterogeneity over time. We were able to extrapolate these results to longer time spans by using robust individual based simulations of growth and reproduction trajectories, in which we varied (i) the strength of the effect of the environmental factors on performance and (ii) the temporal persistence of the environmental factor. We validated model outputs by comparing simulated- to observed long-term performance variation. We expected that both the persistence of environmental variation and the strength of the effect of environmental variation on short-term performance would importantly contribute to long-term performance differences, and that observed long-term variation in stem length growth could only be explained when persistence of environmental variation was taken into account.

## Materials and methods

*Species and site*

*Chamaedorea elegans* is a dioecious understorey palm species that occurs naturally in lowland tropical rain forest in Mexico, Guatemala and Belize (Hodel 1992). It is single-stemmed and produces a single cluster of leaves, which makes this species very suitable for the reconstruction of growth histories (Pinard 1993). *C. elegans* is relatively small (maximum height 1.5 m, Hodel 1992), because of which local environmental conditions can relatively easily be measured per individual. It mainly occurs on karstic soils characterized by a strong heterogeneity in light availability (i.e. due to gap occurence, Chazdon 1988; Bongers *et al.* 2001), soil conditions (*e.g.* Crowther 1982; Dubbin, Penn & Hodson 2006) and level of herbivory (*e.g.* Matos 2000).

The research was performed in the Montes Azules Biosphere Reserve, close to the Chajul Biological Station, in the state of Chiapas, Southern Mexico (16°06′ N, 90°56′ W). Annual rainfall at this site is around 3000 mm with a distinctive dry season (rainfall <100 mm per month) between January and April. Mean annual temperature is around 25 °C (Martínez-Ramos, Anten & Ackerly 2009). The study site is located within an irregular karst-range area (300–700 m a.s.l.), locally known as 'Cordon Chaquistero', where the soil is basically composed of a thin layer of organic matter; vegetation in the study site is tropical rainforest with a maximum average (± SE) canopy height of 35 ± 4 m and 1.2-1.5% of the area in gaps (Ibarra-Manríquez & Martínez-Ramos 2002).

*Plot setup*

A 0.7 ha research plot was established where all individuals with a stem length larger than 10 cm (830 individuals in total) were mapped and tagged in November 2012, and the length of all internodes of each individual was measured. The number of newly produced leaves was counted and survival was recorded in November 2013 and November 2014. Newly produced inflorescences and young fruits were counted in June 2014 and June 2015, when male inflorescences have not yet died off, abortion of very young fruits has already taken place, but

mature fruits have not yet fallen off (M. Jansen, personal observation). In November 2014 the length of all newly produced internodes was measured for each individual.

In the study plot an experiment was set-up in which a defoliation treatment was applied. The effect of this treatment on palm performance is not part of the questions addressed in this study, but it was taken into account by including defoliation treatment (and interactions) as co-variables in all regression analyses where the effect of environmental factors on palm performance was analyzed. In the defoliation treatment, two out of every three newly produced leaves were removed of half of the (randomly selected) individuals, and this was repeated two times per year during two years. The other half was not defoliated.

*Measurement of biotic and abiotic factors*

Relative light availability was measured in October-November 2013 for 101 individuals and October-December 2014 for 255 individuals which were selected based on their mean internode length so that measured individuals were well distributed over the observed mean internode lengths, and therefore over growth performance levels (Jansen *et al.* 2012). Light availability was measured using Hobo pendant light loggers (Onset Computer Corporation, Bourne, MA, USA; loggers measure wavelengths between 150 and 1200 nm), placed right above the center of the crown of the individuals, which measured light intensity once every minute for a week. One hobo was placed in full daylight to be able to calculate relative light availability. Relative light availability was calculated by dividing the sum of the measured values above a plant by the sum of the values measured at full daylight in the same period. Both years of data were used in the analyses.

Soil samples were taken well distributed over the plot in November 2013 for 370 individuals, with a soil drill of approximately 30-cm length and 2-cm diameter on three sides of the roots of each plant at approximately 5-cm from the center of the plant's rooting point. The drill was entered into the soil at a 45-degree angle until a depth of 20 cm, and soils samples thus taken were dried the same day in a stove at $\sim 70\ ^{\circ}$C. Soil pH was measured in all samples with an Accumet AB15+ Basic pH meter (Fisher Scientific, Waltham, MA, USA) after shaking a 1:5 soil:water suspension for 30 min. In January 2015, 100 soil samples were collected in a similar way (where individuals were selected based on their mean internode length for good representation over different growth performance levels), but these samples were kept cooled and without drying until they were analyzed in the laboratory. We measured the following soil characteristics: pH (as mentioned above), texture by particle sedimentation (Kroetsch & Wang 2008), ammonium and nitrate as available N forms extracted with KCl 2N and available P extracted with Mehlich 3 solution (Mehlich 1984). Both N and P available forms were measured after color development (Murphy & Riley 1962; Robertson *et al.* 1999) in a Bran-Luebbe III AutoAnalyzer. Data of both years were used in analyses.

Soil water content was measured directly in the field for all individuals in the plot with a Frequency Domain (FD) soil moisture meter (Theta probe, Delta-t, Cambridge UK) at three sides of the roots (approximately 5cm from the center) of each individual plant in November 2013 (wet season) and March 2014 (dry season). Soil depth to bedrock was measured in

November 2013 also for all individuals in the plot with an iron rod, which was inserted into the soil next to the base of the stem. Soils deeper than 74.5 cm (the length of the rod) were recorded as 74.5 cm (which was the case for 4% of the measured individuals).

In November 2013, leaf damage (mostly caused by herbivory) was estimated for leaves that one year before had been marked as the third fully developed leaf (counting from the apex). These leaves were chosen because they were exposed to herbivore damage for enough time to be recorded. Leaf damage was estimated for all individuals in the plot where the third fully developed leaf was present (599 individuals in total). With an average leaf production of almost two leaves per year (1.86, SD=0.71), leaves were therefore approximately 2 years old at the moment of measurement. Photos were taken of the leaf and analyzed for percentage of damage (part of the leaf that was missing, as in *e.g.* Škaloudová, Křivan & Zemek, (2006)) using Image J software.

*Relating short-term performance to local environment*

Individual (short-term) performance was expressed as the vital rates growth (stem length elongation), survivorship, probability of reproduction, and seed production. Stem length growth was estimated for every individual by multiplying the number of newly produced leaves in a year by the mean length of the internodes produced by that individual between November 2012 and November 2014. The presence/absence of newly produced inflorescences in female palms was used to estimate the probability of reproduction per year. Seed production per year was quantified as the number of newly produced fruits per plant (in this species fruits carry one seed). Survival was quantified over a two-year period (from November 2012 to November 2014), because in *C. elegans* mortality is a relatively rare event in individuals larger than 10 cm height.

Vital rates were related to the measured environmental factors per census year. As sample sizes differ between environmental factors (see Table S3.1 in the Supporting Information), and to avoid correlations between independent variables, we carried out separate analysis for each of the environmental variables and for each year the environmental factor was measured, using all-subset multiple regression [dredge function from MuMIn package (Barton 2015) for R software (R Development Core Team 2014)]. Stem length, defoliation treatment and the interactions between these factors were included to account for ontogenetic and leaf area loss effects; we included non-linear terms if visual inspection of the data suggested non-linearity. The best model was selected based on AIC. All environmental variables included in the best model of the all-subset regressions, were then combined in one large all-subset regression. In this regression, all interactions between environmental variables were also included and corrections for ontogenetic and treatment effects were again incorporated. The best combined model was selected based on AIC values. Logistic regression was used in the analysis of probabilities of reproduction and survival. Linear regression was used in the analysis of seed production instead of Poisson regression, as seed production exhibited a close to normal distribution. Linear regression was also used in the analysis of stem length growth.

Note that data on environmental factors was collected at the end of each census year. Some environmental variables were recorded in both years and others in only one year (see Table S3.1). Therefore, some environmental variables were included in the analysis of only one of the two census years. Furthermore, as simulations were only performed for the two environmental factors that most strongly influenced palm performance (see below), all subset regression analyses were performed again with just relative light availability and soil pH as explaining environmental variables. As both light and soil pH were measured in both census years, the analysis of both census years were for growth, probability of reproduction and seed production combined in (general) mixed effect models, in which year (and interactions of light and pH with year) were included as fixed effects, and individual as a random effect. Survival probability was analyzed using standard logistic regression since this vital rate was already analyzed over two years (see above).

*Modeling temporal persistence of spatial variation in environment*

When spatial heterogeneity in environment persists over time, spatial environmental variation in a given year will be significantly correlated with spatial environmental variation in the next year (*i.e.* will be temporally autocorrelated). We modeled this temporal auto-correlation of spatial environmental heterogeneity for the two factors that most strongly influenced performance (soil pH and relative light availability, see results section and Table S3.2). Using regression analysis, we related local environment in the first census year to that in the second census year (where each individual for which data was available was a data point). Then, we used the resulting relationships, in combination with the residual variance, to construct a probability density function describing transitions from the local environment in year t to the local environment in year t+1. For soil pH, this can mathematically be described as:

$$P_{i,t+1} \sim N(m(P_{i,t}), \sigma^2) \hspace{4cm} \text{eqn 3.1}$$

where pH of individual i at time t+1 ($P_{i,t+1}$) is sampled from a normal distribution (N) with variance $\sigma^2$ and with mean m which depends on pH of that individual being simulated at time t ($P_{i,t}$). In simulating the soil pH trajectories that an individual can experience, each year a pH value is drawn from this distribution.

Variation in light is strongly driven by canopy dynamics, which are not always a gradual process (Van der Meer & Bongers 1996; Sterck *et al.* 1999). Although most individuals will probably experience gradual changes in their light environment, our data shows that some experience large and abrupt changes. For example, formation of a canopy gap entails a sudden increase in light (Chazdon & Fetcher 1984a). To model this, studied palms were split into those enduring large and those enduring small changes in relative light intensity (*i.e.* percentage of full daylight) between census years. We defined a large change as that equal to or larger than 1.5% of light level outside the forest. This assumption was based on visual inspection of data. Regression analysis between local light level in census year 1 and census year 2 was performed for both data subsets. The resulting relationships were combined, by determining the relative contribution of each of the two functions with respect to occurrence of data points. The relative contribution was first determined for eight equally sized intervals

of light levels, set between the minimum and maximum observed light values, by considering the number of data points. Then, these points were smoothed using non-linear regression analysis. From these relationships the probability density function for transition from light level at time t ($L_{i,t}$) to that at time t+1 ($L_{i,t+1}$) was constructed using the residuals of both light transition models. Mathematically the full model can be described as:

$$L_{i,t+1} \sim (1-c(L_{i,t}))*N(m_s(L_{i,t}), \sigma_s^2) + c(L_{i,t})*N(m_l(L_{i,t}), \sigma_l^2) \qquad \text{eqn 3.2}$$

Where $L_{i,t+1}$ is sampled from the combination of the two normal distributions with relative contributions c (which depends on $L_{i,t}$) and 1-c (*i.e.* c is the fraction of plants experiencing large changes in light and 1-c the fraction of plants experiencing small changes). The normal distributions have means and variances ($m_s$ and $\sigma_s^2$ for small change and $m_l$ and $\sigma_l^2$ for large change), in which $m_s$ is a function of $L_{i,t}$.

When spatial environmental heterogeneity is not temporally autocorrelated, an individual will experience an environment that varies randomly and does not depend on previous states. We simulated such an environment by randomly selecting a value from the stable state distributions from equations 3.1 and 3.2.

*Simulating long-term performance trajectories*

Variance in life growth and reproduction trajectories was quantified using individual-based simulations. For this, we used the above-described relationships between vital rates (stem growth, survivorship, probability of reproduction, and seed production), stem length and environmental factors (light availability and soil pH), as well as the transition probabilities for year-to-year changes in environmental conditions (equations 3.1 and 3.2). For each of the two census years, the relationships between vital rates, stem length, light availability and soil pH were transformed into probability density functions. For growth and seed production we used a normal distribution with mean value predicted by the statistical model and variance equal to the residual variance from this model. Survivorship and probability of reproduction (whether or not an individual reproduced in year t) were described using a binomial distribution. This can mathematically be described as:

$$X_{i,t+1} \sim N(m_g(X_{i,t}, L_{i,t}, P_{i,t}), \sigma_g^2) \qquad \text{eqn 3.3a}$$

$$S_{i,t} \sim B(1, p_s(X_{i,t}, L_{i,t}, P_{i,t})) \qquad \text{eqn 3.3b}$$

$$R_{i,t} \sim B(1, p_r(X_{i,t}, L_{i,t}, P_{i,t})) \qquad \text{eqn 3.3c}$$

$$F_{i,t} \sim N(m_f(X_{i,t}, L_{i,t}, P_{i,t}), \sigma_f^2) \qquad \text{eqn 3.3d}$$

Where size X at time t+1 and number of produced seeds F at time t are sampled from normal distributions with means $m_g$ and $m_f$ that depend on size, light level and pH at time t, and variance $\sigma_g^2$ and $\sigma_f^2$ . Whether or not an individual survived and/or reproduced is sampled from the binomial distribution, with probabilities $p_s$ and $p_r$ that depend on stem length, light level and pH at time t. To facilitate numerical analysis of the model, the total model was discretized within the observed size, light and pH ranges using n=500 stem length classes, and

o=45 classes per environmental variable, following numerical methods described in Ellner and Rees (2006).

With this model, individual-based simulations were performed to determine frequencies of possible growth and reproduction trajectories. Each simulation starts at stem length 10 cm (which is the stem length from which demographic data were available), and with a relative light and soil pH level that are randomly selected from the stable light and pH distributions of the respective persistence model (equations 3.1 and 3.2). Growth, reproduction, and survival of the individual in consecutive time steps are simulated using the model from equation 3.3. The environmental trajectories that individuals experience are modelled in two ways: stochastically by randomly drawing from the stable state distributions of equations 3.1-3.2 (in which soil pH and light values that an individual experiences are therefore each time step randomly determined) or temporally autocorrelated by using equations 3.1 and 3.2 (in which environmental variation persists over time). To be able to analyse the separate contributions of the persistence of the spatial heterogeneity in the different environmental variables, we analysed in total four scenarios: a completely stochastic scenario, a scenario in which pH is persistent over time (equation 3.1), a scenario in which light is persistent over time (equation 3.2), and a scenario in which light and pH are both persistent (equations 3.1 and 3.2). In each time step of the simulations, it was randomly determined which of the two versions of equation 3.3 (*i.e.* which census year) was selected. For each scenario, 10,000 simulations were performed for 20 time steps (we chose this number of time steps because we only have few observations above the estimated age of 20 years, determined from internode reconstructions).

From the individual based simulations, we quantified the contributions of temporal persistence in environmental variation to long-term performance differences. We did this for long-term differences in growth by quantifying variance in stem length at different ages (based on the 10,000 simulated individual trajectories), for each of the four scenarios. Differences between scenarios indicate the added contribution of the modeled temporal autocorrelation in environmental variation. Long-term differences in reproductive output were analyzed in a similar manner, in which variance in cumulative reproductive output at different ages was quantified for each of the four scenarios. Persistence of differences in growth and reproduction in each of the four scenarios was quantified using Spearman rank correlations between growth rate/reproductive output at all possible combinations of ages, and then averaging correlation coefficients per time lag. See Appendix S3.1 for R-script of the simulations.

*Validating simulations: Comparing simulated to observed long-term inter-individual growth differences*

The growth histories of all 830 individuals in the research plot were reconstructed using internode lengths following the approach of Jansen *et al.* (2012). First, the relationship between leaf production and stem length was analyzed using regression analysis. This relationship was used to estimate the annual leaf production over the entire life of a plant, starting at stem length and age 0, and assigning the corresponding number of internodes (and

therefore stem length) to that year/age. This process was continued until all internodes had been assigned to an age. Long-term differences in stem growth trajectories and the persistence of differences in stem length growth over time were quantified as for the simulated trajectories.

*Analyzing the full potential range of temporal persistence in environment, and strength of environmental effects on performance*

We further analysed the effect of the two main aspects of spatial environmental heterogeneity influencing long-term performance differences (the strength of the effect on performance, SE, and temporal auto-correlation, PE) in an analysis in which we used similar methods as described above, but where we virtually changed the slopes, intercepts and residual variances of the soil pH and light availability temporal persistence, and stem growth relations that we obtained with regression analysis. A more detailed description of the methods that we used is provided in Appendix S3.2.

# Results

*Vital rates and environmental factors*

Screening of all environmental factors

There was large variation between individuals in growth trajectories, with trajectories fanning out widely (Fig. 3.1), suggesting great differences in plant performances over time. All subset multiple regression analyses carried out to assess effects of environmental factors on vital rates showed that in both studied years, stem growth rate was largely explained by light availability, although the effect was much stronger in the first than in the second sampling year (Fig. 3.2 and Table S3.2). Growth was also significantly influenced by soil nutrient availability ($PO_4$, $NH_4$), soil pH, leaf damage, and soil moisture content (in dry and wet season). The probability of reproduction (in female palms) was also strongly determined by relative light availability and, to a lesser degree, by soil pH (only in the first year), leaf damage, soil N-availability ($NO_3$ and $NH_4$), and soil clay content. In the first year, seed production was strongly influenced by light availability, soil pH, soil moisture content (in the dry season), and leaf damage. In the second year, seed production was only influenced by soil pH. Survival probability was influenced only by leaf loss. The other measured soil factors (depth to bedrock, and silt and sand content) did not significantly contribute to any of the measured performance indicators.

Combination of all significantly influencing environmental factors in one all subset regression per vital rate (Table S3.3) showed that these factors together explained a large part of the variation in growth rate in the first year ($R^2 = 0.72$), and a substantial part of the variation in the second year ($R^2 = 0.45$). Probability of reproduction was explained reasonably well ($R^2 = 0.40$ in year 1, and $R^2 = 0.42$ in year 2) and seed production very well ($R^2 = 0.92$ in year 1 and $R^2 = 0.63$ in year 2), although sample size for the analysis of seed production was very small

(N=11 in year 1 and N=12 in year 2). Differences in survival could only be explained to a small extent ($R^2$=0.16).

<u>The influence of relative light availability and soil pH</u>

When the combined effects of light availability and soil pH on vital rates were analyzed, both soil pH and light availability were included in the best regression models describing growth and seed production rates, but not in those describing probabilities of reproduction and survival (Table S3.4). Furthermore, the effect of light on growth and seed production was weaker in the second census year than in the first (as indicated by the negative interaction between light and year, Table S3.4). Positive stem length dependence appeared in the best models of all analyzed vital rates.

*Temporal persistence of spatial environmental heterogeneity*

Relative light levels in 2013 and 2014 were significantly related. However, there was a small probability that individuals in low light in a year experienced high light levels in the next year (Fig. 3.3a and Table S3.5). Furthermore, all individuals in high light (>6% of full daylight), experienced large reductions in relative light availability. Soil pH in 2013 and 2014 were also positively related (Fig. 3.3b and Table S3.5). The autocorrelation coefficient was 0.57 for relative light availability and 0.56 for soil pH for a time lag of one year (Fig. 3.3).
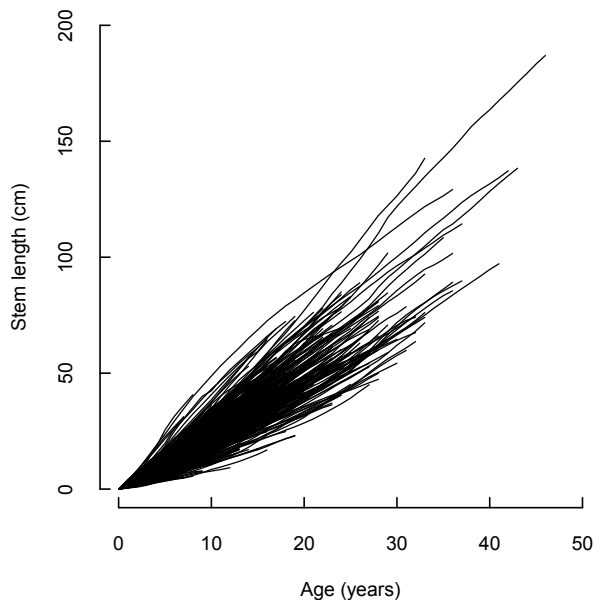


**Figure 3.1.** Reconstructed life growth histories from internodes of 830 individuals of *Chamaedorea elegans* in a Mexican tropical rain forest. Each line represents one individual. The width of the fan shape indicates large variation in life growth trajectories.
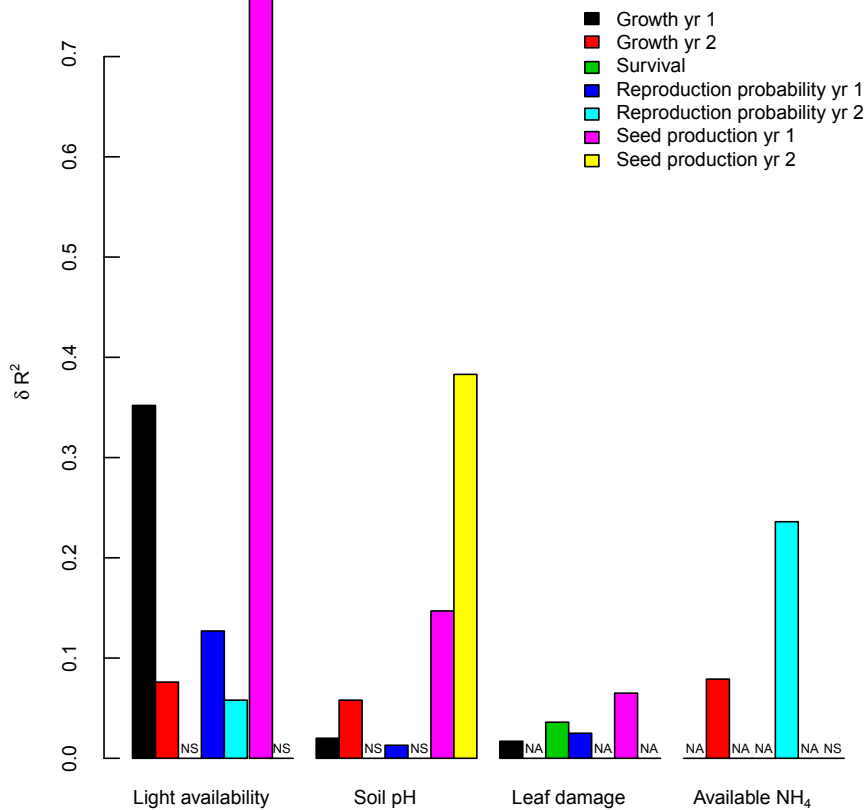
**Figure 3.2.** The four most important environmental factors influencing growth, survival and reproduction of *Chamaedorea elegans* palms in southern Mexico. $\delta R^2$ is the difference in $R^2$ between a regression model that includes the environmental factor and one that includes size and defoliation treatment only. NS: not included in the best model; NA: not tested.
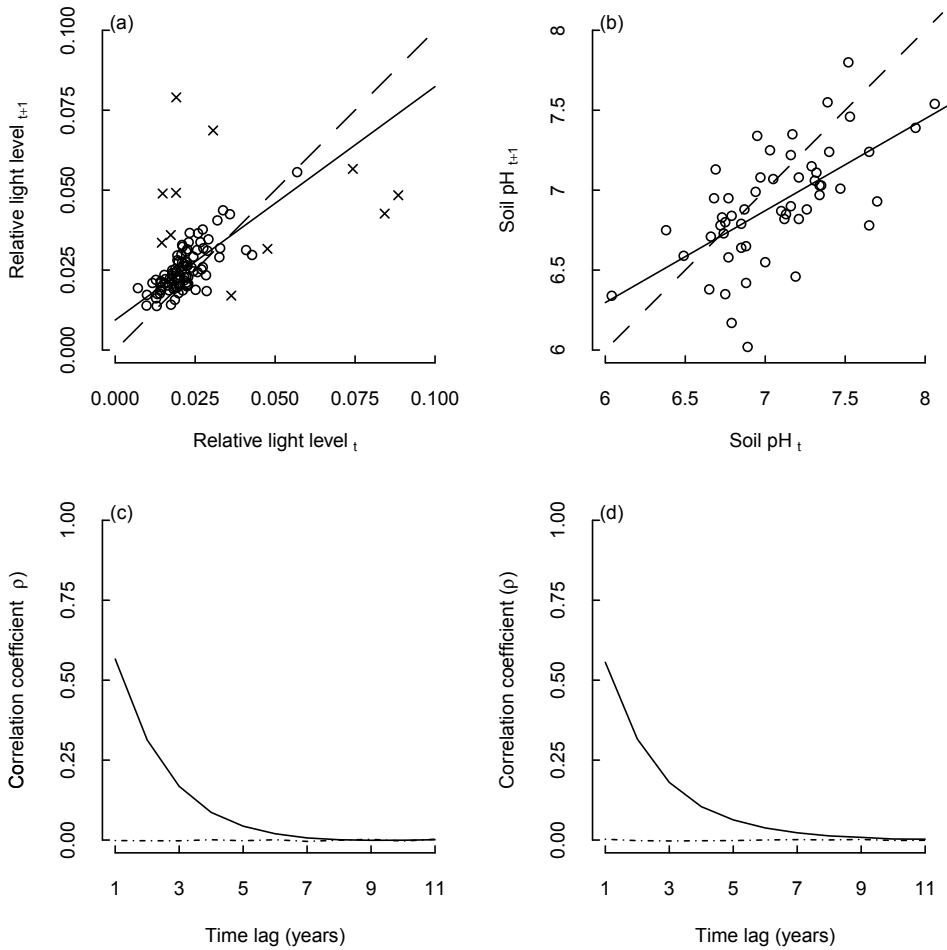
**Figure 3.3.** Temporal relationships of light availability (left) and soil pH (right) affecting *Chamaedorea elegans* individuals in southern Mexico. Results of regression analyses between relative light level in 2013 and 2014 [(a), continuous line], and between soil pH in 2013 and 2014 [(b), continuous line]; each data point represents one individual; dashed lines indicate 1:1 correspondence. Large changes in light level [a difference more than 1.5% of full daylight, indicated as crosses in panel (a)] resulted from forest gap dynamics and were modeled separately. Regression results are included in Table S3.5. Extrapolation of these relationships to longer time spans suggest quickly decreasing autocorrelation in relative light availability [(c), continuous line] and soil pH [(d), continuous line]; dashed lines indicate random variation in these two environmental conditions; shown correlation coefficients are mean Spearman rank correlation coefficients between simulated relative light level and soil pH at a given age and at consecutive ages.

*Effect of persistence in environmental variation on long-term performance differences*

Stem length growth

Simulations of growth trajectories of individuals in the four simulation scenarios (in which variation in light availability and soil pH were either stochastic or temporally autocorrelated) all showed a pattern of growth trajectories fanning out (Fig. 3.4a). As expected, the fan shape of growth trajectories was wider with higher auto-correlation in environmental conditions, and this was the pattern most similar to the observed one. Differences in width of the fan shape are the first indication of differences in contributions to variance in growth trajectories between the four scenarios. Quantification of these differences as variance in stem length at different ages for both the simulations and observed variance showed that completely stochastic variation can cause large variation in lifetime growth- and reproduction trajectories. Simulated long-term variation in stem length became much larger when variation in relative light environment was temporally autocorrelated, but the increase in variation due to the temporal autocorrelation of soil pH was only very small (Fig. 3.4b). For palms aged 20 (20 years after 10 cm stem length), stochastic variation explained 40% of the observed variation in stem length, slightly increased to 42% with pH temporal auto-correlation included, to 84% with light temporal auto-correlation included, and to 88% with both temporally autocorrelated (Fig. 3.4c). Spearman rank correlation coefficient (ρ) between growth rates at age t and age t+i determined from the reconstruction of internodes decreased from 0.89 to 0.40 in a period of the first 12 years and then stabilized, while in the most persistent simulated scenario (both light availability and pH temporally autocorrelated) ρ declined from 0.37 to 0.09 over the first 5 years (Fig. S3.1). Thus, overall, temporal persistence of observed growth differences was higher than the persistence of simulated growth differences.

Reproduction

Simulated reproduction trajectories showed that completely stochastic variation in environmental heterogeneity might cause large differences in lifetime reproductive output (Fig. 3.4c,d). However, when light availability and soil pH were not completely stochastic, but temporally autocorrelated, variation became much larger (Fig. 3.4c,d). Thus, after 20 years, the variation in cumulative reproductive output was 126% higher with temporal auto-correlation compared to the purely stochastic scenario. Furthermore, inter-individual differences in reproductive output were more persistent over time when light availability and pH were temporally autocorrelated: in this scenario, rho declined from 0.52 with a time lag of 1 year to 0.11 over a period of 5 years compared to a decline in rho from 0.11 to 0.06 in the completely stochastic scenario (Fig. S3.1). Note that for reproductive output we did not have observed data to reconstruct reproduction trajectories. Therefore, we only present the four simulated scenarios.
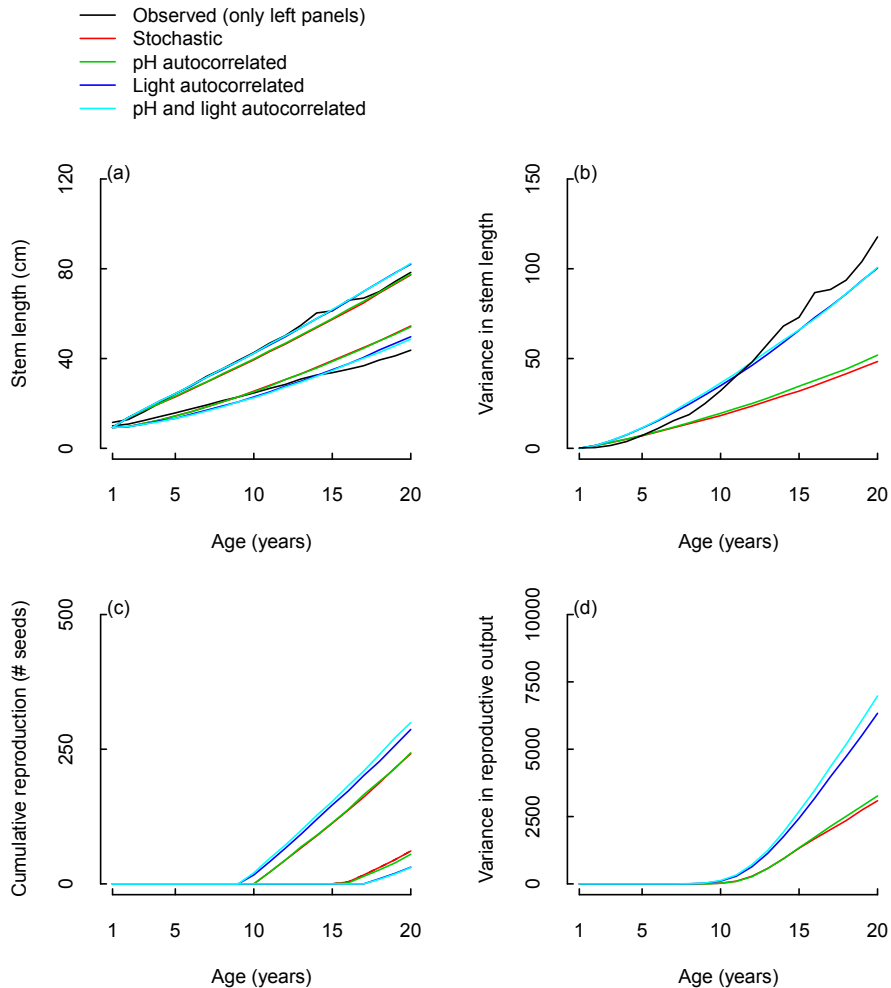
**Figure 3.4.** Ranges of observed and simulated lifetime trajectories for growth and reproduction of *Chamaedorea elegans* palms under four different environmental scenarios. (a) Quantiles (5 and 95%) of simulated growth trajectories, (b) change in the variance of trajectories in stem length with age, (c) quantiles of simulated reproduction trajectories (expressed as the cumulative number of produced seeds); and (d) variance in cumulative number of produced seeds. Age indicates time since reaching a stem length of 10 cm. Observed quantiles and variance in stem length determined from internode reconstruction of growth histories are also shown in the left panels. The relatively small distance of the dashed lines to the continuous line in panels (a,b) indicates that simulations that included temporal persistence of spatial variation in environment explained a large part of observed long-term growth differences. Wider width of fan shape in panels (a,c) and larger variance in panels (b,d) when environmental variation was auto-correlated indicates the influence of persistence in environmental variation on long-term performance differences.

*The full range of temporal persistence in environment, and strength of its effect on performance*

Analysing a wide range of values of persistence in environmental variation (PE) and the strength of the effect of environmental variation on performance (SE), for both light availability and soil pH, we found a pattern showing that a large fraction of observed variation in stem length at age 20 is being explained, as long as either SE or PE is high (Fig. 3.5).

With maximum SE of light (*i.e.* 100% of the residual variance in stem length growth explained), observed variance in stem length could already be explained with a PE of 0.2, indicating that an environmental factor that has a strong effect on short-term performance, can cause large variation in long-term performance, even though it is strongly time-varying (Fig 3.5b, *i.e*, the third grey square in the top row of Fig. 3.5b). On the contrary, when persistence of light availability was maximum (*i.e.* auto-correlation between consecutive years was 1), light only had to explain 0.4 of the residual variance in stem length growth in order to be able to explain observed long-term variation in stem length growth (*i.e.*, the third grey square from the bottom in the right column in Fig. 3.5b). This indicates that a factor with a relatively small effect on performance can still cause large long-term performance differences when it is persistent over time. With both high SE and high PE of light availability (*i.e.*, values most likely much higher than those at our site), explained variation became more than five times larger than observed long-term variation in stem length.

Because SE was expressed as fraction of residual variance in stem length growth (after accounting for the other environmental factor), results were slightly different for soil pH (Fig. 3.5d). Maximum SE of pH could only explain observed long-term variation with a PE of 0.7. With maximum PE, a SE of 0.4 was necessary. Furthermore, with both high SE and PE, explained variation still became more than five times larger than observed long-term variation in stem length, also for soil pH.

Even though results between light availability and soil pH slightly differed, these results clearly show that both SE and PE should be considered when assessing the importance of an environmental factor for long-term performance differences.
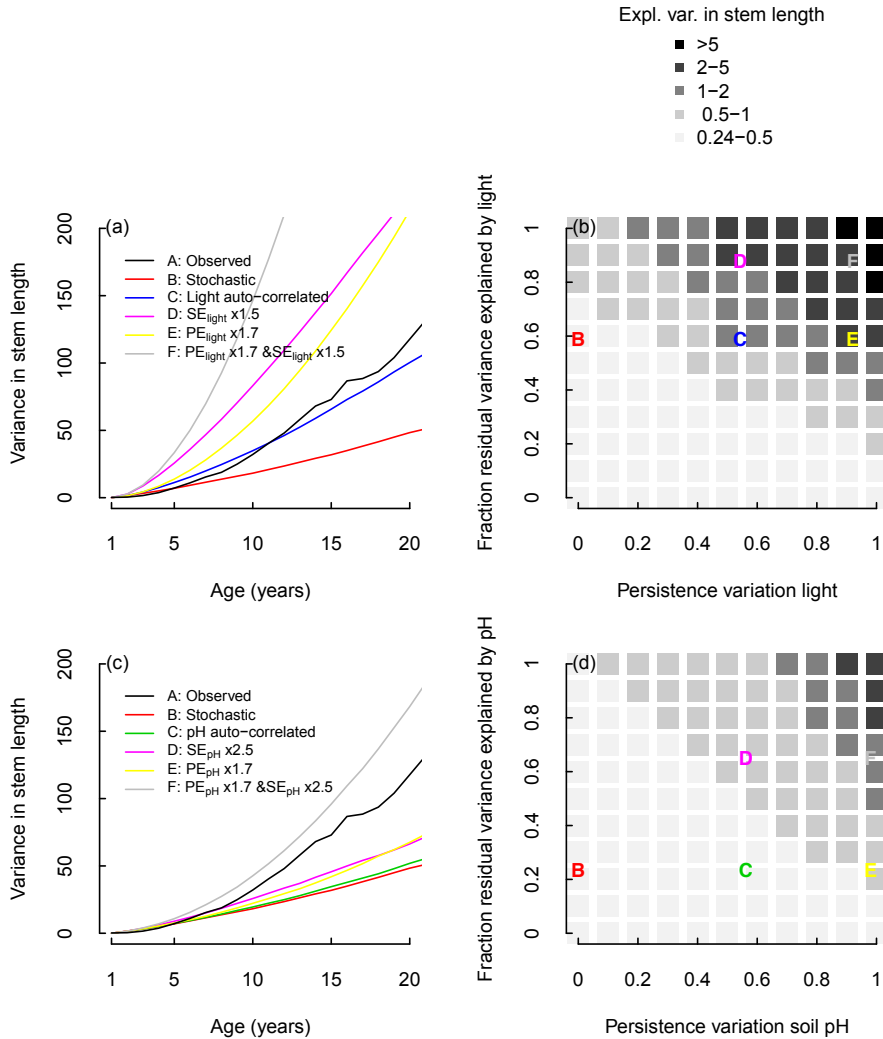
**Figure 3.5.** The combined effects of the persistence of environmental variation (PE) and the strength of the effect of the environmental factors light availability (upper panels) and soil pH (lower panels) on performance (SE) on long-term differences in stem growth of *Chamaedorea elegans* palms. (a,c) Variance in stem length at different ages under 5 scenarios of environmental variation: observed (A), stochastic (B), pH/light auto-correlated (C), PEx1.7 (D), SEx2.5/1.5 (E), and PEx1.7&SEx2.5/1.5 (F); in the last three scenarios the numbers indicate a factor of increase in PE, SE or both. (b-d) Explained variance in stem length for the complete range of PE and SE values. The gray scale indicates the fraction of the observed variation in stem length (at age of 20 years) explained by a model with associated values of PE and SE. Values larger than 1 indicate that the model with associated PE and SE values explained more than observed variance. Fraction of residual variance explained by pH/light indicates the fraction of residual variance that is being explained after accounting for stem length and light/pH. The locations of the scenarios in panels (a-c) are indicated in panels (b-d) by their corresponding letters.

## Discussion

This study shows that explaining long-term individual heterogeneity requires information on the temporal persistence of environmental factors affecting plant fitness. To our knowledge, this is the first study that has quantified the importance of temporal persistence in environmental variation for long-term performance differences.

*The effects of light and soil pH on short-term performance*

In our study, stem length growth, probability of reproduction and seed production of *C. elegans* plants were to a large extent determined by light availability, and to a lesser extent by soil characteristics (mostly pH). This result caused us to choose light availability and soil pH to model temporal persistence in environmental variation. Several studies have shown that light availability is one of the main drivers of performance in understorey palm species (Piñero & Sarukhán 1982; Chazdon 1986; Svenning 2002). Furthermore, the importance of soil characteristics for performance, and in particular of soil pH, has also been shown in other studies; for example, mineralisation of organic material and availability of cations are typically higher at the high pH values observed here (McLean 1982; Rousk, Brookes & Bååth 2009), both of which could have stimulated growth and reproduction. However, it is likely that there are other (unmeasured) environmental factors that influence individual performance. One unmeasured factor is soil microbial activity, which may persistently influence individual performance in the forest understorey, an effect that has been shown in other systems [*e.g.* in grasslands (e.g. de Kroon *et al.* 2012)]. Another critical factor not included in our analysis is genetic makeup. It is likely that some genotypes outperform others under certain environmental conditions, and that genotype-environment interactions partially explain the observed performance differences between individuals. We believe that even though we did not measure or model all factors that influence performance, light availability and soil pH represent two of the most important drivers of performance in this species, and were, therefore, suitable variables to explore the effect of temporal persistence of environmental heterogeneity on long-term inter-individual performance variation.

*The temporal dynamics of environmental variation*

Our studied palms experienced sudden changes in light availability between years, which we modeled separately. These sudden changes in local light environment were caused by forest gap dynamics. Transitions from low light to high light can represent the opening of gaps due to falling trees or branches (Van der Meer & Bongers 1996), a sudden, but relatively infrequent event (Martinez-Ramos *et al.* 1988; Van der Meer & Bongers 1996; Sterck *et al.* 1999). The fact that palms under high light levels had a high probability to experience a lower light level in the next year probably indicates that the small *C. elegans* plants are quickly overgrown by faster-growing neighbor plants after gap openings. This process has been documented for other understory plant species (van der Meer 1997) and tree seedlings also tend to experience relatively sudden reductions from high to low light (Sterck *et al.* 1999). We found soil pH to be autocorrelated over a two-year period but the relation was rather weak. Changes in soil pH can be induced by several factors; for example, soil pH can change

due to rainfall, changes in soil microbial composition or changes in plant species composition (Ulery, Graham & Amrhein 1993; Bååth *et al.* 1995; Finzi, Canham & Van Breemen 1998; Li *et al.* 2007).

We modeled the temporal persistence of the light levels and soil pH that individuals experience over longer time spans based on changes between two years. So, we used estimates of first order temporal auto-correlation in our simulations. This implies that temporal auto-correlation in light and pH persistently decreases (with decreasing speed) over time, and does not fluctuate. In the case of light availability, this decrease seems to resemble patterns that have been found in studies that measured changes in light over longer time spans. For example, (Sterck *et al.* 1999) found an auto-correlation pattern in crown exposure to direct light (Clark, Clark & Rich 1993) of tree seedlings over a period of five years, that resembled this pattern. Whether a persistent decrease realistically describes autocorrelation in soil pH over time is hard to tell, because of the scarcity of long-term soil pH studies in tropical forest. To detect fluctuations more years of data would be necessary, allowing higher order temporal auto-correlation to be included in our model, thereby increasing environmental realism in our simulations.

Also other aspects of the complexity of environmental dynamics could be included in models describing changes in spatial heterogeneity over time. In this study, we treated environmental factors as independent, but in reality, they might interact and have cascading effects that can be delayed for several years. For example, light changes may induce cascading effects on other environmental variables (humidity and temperature) which impacts microbial activity and thus ultimately soil pH and nutrient availability, especially when those changes are either strong or persistent (Denslow, Ellison & Sanford 1998). Including these aspects of environmental dynamics would require very detailed, longer-term data on a wide variety of environmental factors, which is so far hardly available.

The framework that we have presented in this study allows for including such relations; both the higher-order autocorrelation and the interacting effects of environmental variables can be taken into account when sufficient data is available.

*Explaining long-term performance differences*

Our analysis revealed that temporal persistence of heterogeneity in local environmental conditions strongly determines long-term inter-individual performance variation. Explained variance in stem length growth (over a period of 20 years) increased from 40 to 88% after including in our model the temporal autocorrelation in light availability and soil pH observed during the two years of our study. Furthermore, our simulations, in which we analysed a wide range of values of temporal persistence in environmental heterogeneity (PE), and effects of the environmental factor on short-term performance (SE), revealed a pattern showing that a large fraction of the observed long-term inter-individual performance variation is explained, as long as either SE or PE is high. This means that a factor that has a relatively small effect on short-term plant performance, and in a short-term term study may have been dismissed as

being unimportant, can actually have profound effects on differences in the long-term performance of individual plants if it is persistent over time and vice versa.

We expect that these type of effects are important to consider in any system that is characterized by strong spatial heterogeneity in environmental conditions, and in which environmental heterogeneity can strongly differ in temporal persistence. The forest understorey is particularly heterogeneous in this respect, but also other systems like grasslands and savannas are known to be spatially heterogeneous (Jaramillo & Detling 1992; Biggs 2003). Furthermore, beyond the realm of plants, coral reefs are, just like the forest understorey, known to be particularly heterogeneous (Connell 1978). For plants, likely candidates of environmental factors that in many short-term studies may have been dismissed as unimportant for long-term performance differences, but in reality contribute strongly due to their persistence, are soil texture, the presence of mycorrhiza, or relative water availability. All of these are known to persist over time but do not necessarily strongly influence short-term performance.

*Implications for research and management*

In this study, we used a simulation approach that allowed us to analyze the importance of temporal persistence of environmental variation in determining long-term performance differences, without the need to collect long-term data on both performance and environmental variation. We think that this approach has the potential to analyze the importance of environmental factors for differences in life performance in different systems, and we believe it can also be a useful tool in exploring the eco-evolutionary consequences of environmental variation.

Knowing the relative importance of different environmental factors for long-term variation in plant performance will provide better insights into plant environmental adaptations. Particularly the adaptive significance of relatively constitutive traits (*i.e.* attributes and responses that are not easily changed) in relation to a given environmental factor strongly depends on the persistence of that factor. The pattern in which environmental factors drive differences between individuals in lifetime fitness, and associated selective forces can only be adequately understood, when the persistence of environmental variation is explicitly considered.

Taking into account long-term performance differences and the drivers underlying these differences can also be important for the management of populations. Leaves of our study species are an important Non-Timber Forest Product (NTFP) and inter-individual variation in long-term performance could be considered in harvesting regimes by differentially harvesting super- and under-performers within populations (Jansen *et al.* (2012)). Furthermore, when NTFP harvesting is combined with selective logging (Guariguata, Sist & Nasi 2012), this may also affect the temporal persistence in environmental conditions and therefore the dynamics of managed populations. In general, when long-term inter-individual performance variation is strongly determined by spatial heterogeneity in certain environmental factors and these factors shift due to human disturbances, this may importantly drive population viability and

future harvest potential. We, therefore, suggest that persistence of local environmental variation is included in studies on the ecology and management of natural plant populations.

## Acknowledgements

## Supporting information

**Appendix S3.1** *R-script of simulations.*
**Appendix S3.2** *Methods used for the construction of Fig. 3.5.*
**Figure S3.1** A*uto-correlation in simulated and observed performance.*
**Table S3.1** *Environmental measurements: dates and sample sizes.*
**Table S3.2** *Results regression analysis relating palm performance to environmental variables (per vital rate per environmental variable per year).*
**Table S3.3** *Results regression analysis relating palm performance to environmental variables (environmental variables combined per vital rate per year).*
**Table S3.4** *Results mixed-effect multiple regression analyses relating palm performance to the combined effect of relative light level and soil pH.*
**Table S3.5** *Models relating environment at time t to environment at time t+1.*

**Appendix S3.1** *R-script of simulations.*

# This script contains the code that was used to simulate life growth and reproduction trajectories in four different scenarios with different levels of temporal autocorrelation in environmental variation. The script contains five parts. In the first parts coefficients from regression analyses are given, that form the input of the simulations. In part two these results/coefficients are transformed into probability density functions that are transformed into transition kernels in part 3. Simulations are run in part 4, and in part 5 quantiles, variances and auto-correlation are calculated, and results are plotted. Running this script produces a figure similar to figures 3.4 and S3.1, only the observed variation lines are not added.
# Note: the construction of the kernels and part of the simulations are adaptations from the R-script provided as supplementary material in Ellner and Rees (2006)

#### 1: Coefficients from regression analyses ####

## 1.1: Coefficients vital rate relations
gpi12= -4.134228; gpxsqrt12= 0.3131293; gpl12= 99.57267; gpp212=0.04677737; gpvi12= 0.6275276; gpy12= 0.850037; gply12= -41.60379 ;
si= 1.591392; sx= -0.03732842; sxsqrt= 0.3959128;
ri= -228.3372; rx=-3.438378; rxsqrt=57.51056; rl=0;
fi=  -149.7271;   fl=1570.833;   fp=12.15605;   fx=0;   fxsqrt=4.106728;   fv=4.156277;
fy=31.21249; fly= -918.5942;

## 1.2: Coefficients temporal relations light and pH
li= 0.009369386; ll= 0.7300795; lvi=  0.004683123; lic= 0.08736148; llc= -0.4277033; lvic=0.01726588 ; ci= -5.33601; cl=125.21484;
phi3= 2.847298; pp3=0.5749112; pv3=0.2788015;

#### 2: Construction probability density functions ####

# Growth function year 1
```
gxylp<-function(x,y,l,p) {
  sigmax<-gpvi12 ;
  sigmax2<-sigmax^2;
  mux<-gpi12+x+gpxsqrt12*sqrt(x)+gpl12*l+gpp212*p^2;
  fac1<-sqrt(2*pi)*sigmax;
  fac2<-((y-mux)^2)/(2*sigmax2);
  return(exp(-fac2/fac1));
}
```

# Growth function year 2
```
gxylp14<-function(x,y,l,p) {
  sigmax<-gpvi12 ;
```

```
  sigmax2<-sigmax^2;
  mux<-gpi12+gpy12+x+gpxsqrt12*sqrt(x)+(gpl12+gply12)*l+gpp212*p^2;
  fac1<-sqrt(2*pi)*sigmax;
  fac2<-((y-mux)^2)/(2*sigmax2);
  return(exp(-fac2)/fac1);
}

# Survival function
sxyl<-function(x,y,l){ef<-exp(si+sx*x+sxsqrt*sqrt(x));
                return((ef/(1+ef))^(1/2))}

# Reproduction chance function
frxl<-function(x,l) {
  fac<-exp(ri+rx*x+rxsqrt*sqrt(x)+rl*l)
  return(fac/(1+fac))
}

#seed production function year 1
fzl<-function(z,x,l,p) {
  sigma<-fv
  sigma2<-sigma^2
  mur<-(fi+fl*l+fp*p+fx*x+fxsqrt*sqrt(x));
  fac1<-sqrt(2*pi)*sigma;
  fac2<-((z-mur)^2)/(2*(sigma2));
  return(exp(-fac2)/fac1)
}

#seed production function year 2
fzl14<-function(z,x,l,p) {
  sigma<-fv
  sigma2<-sigma^2
  mur<-(fi+fy+(fl+fly)*l+fp*p+fx*x+fxsqrt*sqrt(x));
  fac1<-sqrt(2*pi)*sigma;
  fac2<-((z-mur)^2)/(2*(sigma2)); #still check if formula is correct (sig and var)
  return(exp(-fac2)/fac1)
}

# Light level transition function
lll2<-function(l,l2) {
  sigmal<-(lvi) ; #variance growth relation
  sigmal2<-(sigmal)^2
  mul<-li+ll*l; #mean
  fac1<-sqrt(2*pi)*sigmal;
```

```
  fac2<-((l2-mul)^2)/(2*sigmal2);
  return(exp(-fac2/fac1);
}
lll2c<-function(l,l2) {
  sigmal<-(lvic) ; #variance growth relation
  sigmal2<-(sigmal)^2
  mul<-l+lic+llc*sqrt(l); #mean
  fac1<-sqrt(2*pi)*sigmal;
  fac2<-((l2-mul)^2)/(2*sigmal2);
  return(exp(-fac2/fac1);
}
fs<-function(l){
  term<-exp(ci+cl*l)
  return(term/(1+term))}
lll2cp<-function(l,l2){return((1-fs(l))*lll2(l,l2)+fs(l)*lll2c(l,l2))}

# pH transition function
ppf3<-function(p,p2) {
  sigma<- pv3;
  sigma2<-(sigma)^2;
  mu<-phi3+pp3*p;
  fac1<-sqrt(2*pi)*sigma;
  fac2<-((p2-mu)^2)/(2*sigma2);
  return(exp(-fac2/fac1);
}

#### 3: Construction transition kernel from probability density functions ####

# Data limits
L= 5.8; U=189.5; Ll= 0.007093806; Ul=0.08850193; Lp= 4.88; Up=8.16; Lz=0; Uz=90;

# Step size, etc.
n=300; nl=50 ; np=50; nf=100; nz=90 # Number of mesh points
b = L+c(0:n)*(U-L)/n; y = 0.5*(b[1:n]+b[2:(n+1)]); # Boundary points b and mesh points y
for size
bl = Ll+c(0:nl)*(Ul-Ll)/nl; yl = 0.5*(bl[1:nl]+bl[2:(nl+1)]); # Boundary points b and mesh
points y for light level
bp = Lp+c(0:np)*(Up-Lp)/np; yp = 0.5*(bp[1:np]+bp[2:(np+1)]); # Boundary points b and
mesh points y for pH
bz = Lz+c(0:nz)*(Uz-Lz)/nz; yz = 0.5*(bz[1:nz]+bz[2:(nz+1)]); # Boundary points b and
mesh points y for number of produced seeds
h = y[2]-y[1]; hl = yl[2]-yl[1]; hp = yp[2]-yp[1]; hz = yz[2]-yz[1] # step sizes for midpoint
rule
```

## Create growth, survival, reproduction chance and seed production kernels

```
# Growth year 1
GLP<-array(NA,dim=c(n,n,nl,np))
for(p in 1:np){
  for(l in 1:nl){
    GLP[,,l,p]<-h*t(outer(y,y,gxylp,l=yl[l],p=yp[p]))
  }}

# Growth year 2
GLP14<-array(NA,dim=c(n,n,nl,np))
for(p in 1:np){
  for(l in 1:nl){
    GLP14[,,l,p]<-h*t(outer(y,y,gxylp14,l=yl[l],p=yp[p]))
  }}

# Survival
S<-array(NA,dim=c(n))
S<-sxyl(y,1,1)

# Reproduction chance
R<-array(NA,dim=c(n,nl))
for(x in 1:n){
  for(l in 1:nl){
    R[x,l]<-frxl(y[x],yl[l])
  }}

# Seed production year 1
FR<-array(NA,dim=c(nz,n,nl))
for(x in 1:n){
  for(l in 1:nl){
    for(p in 1:np){
      FR[,x,l]<-fzl(yz,y[x],yl[l],yp[p])
    }}}

# Seed production year 2
FR14<-array(NA,dim=c(nz,n,nl))
for(x in 1:n){
  for(l in 1:nl){
    for(p in 1:np){
      FR14[,x,l]<-fzl14(yz,y[x],yl[l],yp[p])
    }}}
```

## Create light and pH transition kernels

```
L2<-array(NA,dim=c(nl,nl)); P3<-array(NA,dim=c(np,np));
L2[,]<-hl*t(outer(yl,yl,lll2cp)); P3[,]<-hp*t(outer(yp,yp,ppf3))
```

## Estimate stable light and pH distributions (necessary for simulations)##
# (run light and pH kernels for many individuals and many years to determine stable light
distribution)

```
ltempstore=matrix(NA,200000,100)
for(j in 1:200000){
 lt=sample(yl,1)
 for (i in 1:100) {
  lv<-yl%in%lt;# determine matrix elements (TF vec)
  ls<-c(1:nl)[lv] # select matrix elements
  ltempstore[j,i]<-lt # save sampled value last round
  lt1<-sample(yl,1,prob=L2[,ls]) # sample from light probability
  lt=lt1;
 }}
help<-hist(ltempstore[10000:200000,90],breaks=bl)
rm(ltempstore)
d2<-help$counts #stable light distribution

ptempstore=matrix(NA,200000,100)
for(j in 1:200000){
 pt=sample(yp,1)
 for (i in 1:100) {
  pv<-yp%in%pt;
  ps<-c(1:np)[pv]
  ptempstore[j,i]<-pt
  pt1<-sample(yp,1,prob=P3[,ps])
  pt=pt1;
 }}
help<-hist(ptempstore[10000:200000,90],breaks=bp)
rm(ptempstore)
d3<-help$counts # stable pH distribution

#### 4: Run simulations for the four scenarios ####

m=46; # number of simulated time steps (maximum estimated age)
o=10000; # number of simulated individuals
```

```
GLPlist<-list(GLP,GLP14)
fzllist<-list(fzl,fzl14)

## Scenario 1: Completely stochastic simulations ##
xstorepnr=matrix(NA,o,m)
lstorepnr<-matrix(NA,o,m)
pstorepnr<-matrix(NA,o,m)
sstorepnr=matrix(NA,o,m)
rstorepnr=matrix(NA,o,m)
fstorepnr=matrix(NA,o,m)

for(j in 1:o){
 xt=y[10] # start at stem length closest to 10cm
 lt=sample(yl,1,prob=d2) # sample start light value from stable light distribution
 pt=sample(yp,1,prob=d3) # sample start pH value from stable pH distribution
 st=0; sty2=0 # state that at start individual is alive
 for (i in 1:m) {

  #growth transitions
  xstorepnr[j,i]<-xt; # store sampled size last round
  xv<-y%in%xt; lv<-yl%in%lt; pv<-yp%in%pt # determine matrix elements (TF vec)
  xs<-c(1:n)[xv];ls<-c(1:nl)[lv]; ps<-c(1:np)[pv] # select matrix elements
  glps<-sample(c(1,2),1,prob=c(0.5,0.5)) # determine which of 2 year kernels is used
  xt1=sample(y,1,prob=GLPlist[[glps]][,xs,ls,ps]) # sample from GLP

  #light and pH transitions
  lstorepnr[j,i]<-lt # save sampled value last round
  pstorepnr[j,i]<-pt # save sampled value last round
  lt1<-sample(yl,1,prob=d2)# sample from stable light distribution (so no dependence on
previous time steps)
  pt1<-sample(yp,1,prob=d3) # sample from stable pH distribution (so no dependence on
previous time steps)

  # survival next step
  st1<-ifelse(st==1,1,sample(c(0,1),1,prob=c(S[xs],1-S[xs]))) # sample if died
  sstorepnr[j,i]<-st #store sampled value last round

  #reproduction chance next step
  rt1<-sample(c(1,0),1,prob=c(R[xs,ls],1-R[xs,ls]))#sample if reproduced
  rstorepnr[j,i]<-rt1 #store sampled value

  #produced fruits next step
```

```
    ft1<-sample(yz,1,prob=fzllist[[glps]](yz,y[xs],yl[ls],yp[ps]))# sample number of produced
seeds
    fstorepnr[j,i]<-ft1 #store sampled value

    #reset everything
    xt=xt1;
    lt=lt1;
    pt=pt1;
    st=st1;
  }}

# create growth vector from created size vector
growthstorepnr<-xstorepnr
growthstorepnr[,m]<-NA
for(j in 1:o){for(i in 1:(m-1)){growthstorepnr[j,i]<-xstorepnr[j,i+1]-xstorepnr[j,i]}}

# create cumulative reproduction vector
rfstorepnr<-rstorepnr
for(j in 1:o){for(i in 1:m){rfstorepnr[j,i]<-ifelse(rstorepnr[j,i]<1,0,fstorepnr[j,i])}}
cumrfstorepnr<-rfstorepnr
for(j in 1:o){for(i in 2:m){cumrfstorepnr[j,i]<-cumrfstorepnr[j,i-1]+rfstorepnr[j,i]}}

## Scenario 2: pH auto-correlated ##

xstorepr=matrix(NA,o,m)
lstorepr=matrix(NA,o,m)
pstorepr=matrix(NA,o,m)
sstorepr=matrix(NA,o,m)
rstorepr=matrix(NA,o,m)
fstorepr=matrix(NA,o,m)

for(j in 1:o){
 xt=y[10]
 xty2=y[10]
 lt=sample(yl,1,prob=d2)
 pt=sample(yp,1,prob=d3)
 st=0
 sty2=0
 for (i in 1:m) {
  xstorepr[j,i]<-xt;
  xv<-y%in%xt; lv<-yl%in%lt; pv<-yp%in%pt;
  xs<-c(1:n)[xv]; ls<-c(1:nl)[lv]; ps<-c(1:np)[pv];
  glps<-sample(c(1,2),1,prob=c(0.5,0.5))
```

```
    xt1=sample(y,1,prob=GLPlist[[glps]][,xs,ls,ps])
    lstorepr[j,i]<-lt
    pstorepr[j,i]<-pt
    lt1<-sample(yl,1,prob=d2)
    pt1<-sample(yp,1,prob=P3[,ps]) # sample new pH from pH transition kernel (so depends
on pH in previous time step)
    st1<-ifelse(st==1,1,sample(c(0,1),1,prob=c(S[xs],1-S[xs])))
    sstorepr[j,i]<-st
    rt1<-sample(c(1,0),1,prob=c(R[xs,ls],1-R[xs,ls]))
    rstorepr[j,i]<-rt1
    ft1<-sample(yz,1,prob=fzllist[[glps]](yz,y[xs],yl[ls],yp[ps]))
    fstorepr[j,i]<-ft1
    xt=xt1;
    lt=lt1;
    pt=pt1;
    st=st1;
  }}

growthstorepr<-xstorepr
growthstorepr[,m]<-NA
for(j in 1:o){for(i in 1:(m-1)){growthstorepr[j,i]<-xstorepr[j,i+1]-xstorepr[j,i]}}

rfstorepr<-rstorepr
for(j in 1:o){for(i in 1:m){rfstorepr[j,i]<-ifelse(rstorepr[j,i]<1,0,fstorepr[j,i])}}
cumrfstorepr<-rfstorepr
for(j in 1:o){for(i in 2:m){cumrfstorepr[j,i]<-cumrfstorepr[j,i-1]+rfstorepr[j,i]}}

## Scenario 3: Light auto-correlated ##

xstorelr=matrix(NA,o,m)
lstorelr<-matrix(NA,o,m)
pstorelr<-matrix(NA,o,m)
sstorelr=matrix(NA,o,m)
rstorelr=matrix(NA,o,m)
fstorelr=matrix(NA,o,m)

for(j in 1:o){
  xt=y[10]
  lt=sample(yl,1,prob=d2)
  pt=sample(yp,1,prob=d3)
  st=0; sty2=0
  for (i in 1:m) {
    xstorelr[j,i]<-xt;
```

```
    xv<-y%in%xt; lv<-yl%in%lt; pv<-yp%in%pt;
    xs<-c(1:n)[xv]; ls<-c(1:nl)[lv]; ps<-c(1:np)[pv]
    glps<-sample(c(1,2),1,prob=c(0.5,0.5))
    xt1=sample(y,1,prob=GLPlist[[glps]][,xs,ls,ps])
    lstorelr[j,i]<-lt
    pstorelr[j,i]<-pt
    lt1<-sample(yl,1,prob=L2[,ls]) # sample new light level from light transition kernel (so
depends on light level in previous time step)
    pt1<-sample(yp,1,prob=d3) # back to sampling from stable pH distribution
    st1<-ifelse(st==1,1,sample(c(0,1),1,prob=c(S[xs],1-S[xs])))
    sstorelr[j,i]<-st
    rt1<-sample(c(1,0),1,prob=c(R[xs,ls],1-R[xs,ls]))
    rstorelr[j,i]<-rt1
    ft1<-sample(yz,1,prob=fzllist[[glps]](yz,y[xs],yl[ls],yp[ps]))
    fstorelr[j,i]<-ft1
    xt=xt1;
    lt=lt1;
    pt=pt1;
    st=st1;
}}

growthstorelr<-xstorelr
growthstorelr[,m]<-NA
for(j in 1:o){for(i in 1:(m-1)){growthstorelr[j,i]<-xstorelr[j,i+1]-xstorelr[j,i]}}

rfstorelr<-rstorelr
for(j in 1:o){for(i in 1:m){rfstorelr[j,i]<-ifelse(rstorelr[j,i]<1,0,fstorelr[j,i])}}
cumrfstorelr<-rfstorelr
for(j in 1:o){for(i in 2:m){cumrfstorelr[j,i]<-cumrfstorelr[j,i-1]+rfstorelr[j,i]}}

## Scenario 4: Light and pH auto-correlated

xstorelpr=matrix(NA,o,m)
lstorelpr<-matrix(NA,o,m)
pstorelpr<-matrix(NA,o,m)
sstorelpr=matrix(NA,o,m)
rstorelpr=matrix(NA,o,m)
fstorelpr=matrix(NA,o,m)

for(j in 1:o){
 xt=y[10]
 lt=sample(yl,1,prob=d2)
 pt=sample(yp,1,prob=d3)
```

```
 st=0; sty2=0
 for (i in 1:m) {
  xstorelpr[j,i]<-xt;
  xv<-y%in%xt; lv<-yl%in%lt; pv<-yp%in%pt;
  xs<-c(1:n)[xv]; ls<-c(1:nl)[lv]; ps<-c(1:np)[pv];
  glps<-sample(c(1,2),1,prob=c(0.5,0.5))
  xt1=sample(y,1,prob=GLPlist[[glps]][,xs,ls,ps])
  lstorelpr[j,i]<-lt
  pstorelpr[j,i]<-pt
  # sample both new light level and pH from light and pH transition kernels:
  lt1<-sample(yl,1,prob=L2[,ls])
  pt1<-sample(yp,1,prob=P3[,ps])
  st1<-ifelse(st==1,1,sample(c(0,1),1,prob=c(S[xs],1-S[xs])))
  sstorelpr[j,i]<-st
  rt1<-sample(c(1,0),1,prob=c(R[xs,ls],1-R[xs,ls]))
  rstorelpr[j,i]<-rt1
  ft1<-sample(yz,1,prob=fzllist[[glps]](yz,y[xs],yl[ls],yp[ps]))
  fstorelpr[j,i]<-ft1
  xt=xt1;
  lt=lt1;
  pt=pt1;
  st=st1;
 }}


growthstorelpr<-xstorelpr
growthstorelpr[,m]<-NA
for(j in 1:o){for(i in 1:(m-1)){growthstorelpr[j,i]<-xstorelpr[j,i+1]-xstorelpr[j,i]}}

rfstorelpr<-rstorelpr
for(j in 1:o){for(i in 1:m){rfstorelpr[j,i]<-ifelse(rstorelpr[j,i]<1,0,fstorelpr[j,i])}}
cumrfstorelpr<-rfstorelpr
for(j in 1:o){for(i in 2:m){cumrfstorelpr[j,i]<-cumrfstorelpr[j,i-1]+rfstorelpr[j,i]}}

#### 5: Quantify quantiles, variance and auto-correlation and create figure 3.4 ####

xarrayr<-array(NA,dim=c(o,m,4))
sarrayr<-array(NA,dim=c(o,m,4))
rarrayr<-array(NA,dim=c(o,m,4))
garrayr<-array(NA,dim=c(o,m,4))
rfarrayr<-array(NA,dim=c(o,m,4))

xarrayr[,,1]<-xstorepnr; xarrayr[,,2]<-xstorepr; xarrayr[,,3]<-xstorelr; xarrayr[,,4]<-xstorelpr;
sarrayr[,,1]<-sstorepnr; sarrayr[,,2]<-sstorepr; sarrayr[,,3]<-sstorelr; sarrayr[,,4]<-sstorelpr;
```

```
rarrayr[,,1]<-cumrfstorepnr;        rarrayr[,,2]<-cumrfstorepr;        rarrayr[,,3]<-cumrfstorelr;
rarrayr[,,4]<-cumrfstorelpr;
garrayr[,,1]<-growthstorepnr;      garrayr[,,2]<-growthstorepr;      garrayr[,,3]<-growthstorelr;
garrayr[,,4]<-growthstorelpr;
rfarrayr[,,1]<-rfstorepnr;   rfarrayr[,,2]<-rfstorepr;   rfarrayr[,,3]<-rfstorelr;   rfarrayr[,,4]<-
rfstorelpr;

# Calculate quantiles, means and variances

moms2r<-array(NA,dim=c(4,m,4))
for(k in 1:4){
 for(a in 1:m){
  moms2r[1,a,k]<-mean(xarrayr[,a,k][sarrayr[,a,k]<1],na.rm=T)
  moms2r[2,a,k]<-var(xarrayr[,a,k][sarrayr[,a,k]<1],na.rm=T)
  moms2r[3,a,k]<-quantile(xarrayr[,a,k][sarrayr[,a,k]<1],0.05)
  moms2r[4,a,k]<-quantile(xarrayr[,a,k][sarrayr[,a,k]<1],0.95)
 }}


rmoms2r<-array(NA,dim=c(4,m,4))
for(k in 1:4){
 for(a in 1:m){
  rmoms2r[1,a,k]<-mean(rarrayr[,a,k][sarrayr[,a,k]<1],na.rm=T)
  rmoms2r[2,a,k]<-var(rarrayr[,a,k][sarrayr[,a,k]<1],na.rm=T)
  rmoms2r[3,a,k]<-quantile(rarrayr[,a,k][sarrayr[,a,k]<1],0.05)
  rmoms2r[4,a,k]<-quantile(rarrayr[,a,k][sarrayr[,a,k]<1],0.95)
 }}

# calculate spearman rank correlation coefficients between years
tm=25
ccs2r<-array(NA,dim=c(tm,tm,2,4))
for(a in 1:tm){
 for(k in 1:4){
  for(i in 1:tm){
   ts<-cor.test(garrayr[,a,k],garrayr[,i,k],method="spearman")
   ccs2r[a,i,1,k]<-ts$estimate; ccs2r[a,i,2,k]<-ts$p.value;
   }}}

ccs2repro<-array(NA,dim=c(tm,tm,2,4))
for(a in 1:tm){
 for(k in 1:4){
  for(i in 1:tm){
   ts<-cor.test(rfarrayr[,a,k],rfarrayr[,i,k],method="spearman")
```

```
    ccs2repro[a,i,1,k]<-ts$estimate; ccs2repro[a,i,2,k]<-ts$p.value;
  }}}
```

# re-order rank correlation results per time-lag

```
timelagmatr<-array(NA,dim=c(tm,tm,2,4))
for(k in 1:4){
  for(t in 0:(tm-1)){
    for(i in 1:(tm-t)){timelagmatr[t+1,i,1,k]<-ccs2r[i,i+t,1,k]
                 timelagmatr[t+1,i,2,k]<-ccs2r[i,i+t,2,k]
  }}}
```

```
timelagmatrepro<-array(NA,dim=c(tm,tm,2,4))
for(k in 1:4){
  for(t in 0:(tm-1)){
    for(i in 1:(tm-t)){timelagmatrepro[t+1,i,1,k]<-ccs2repro[i,i+t,1,k]
                 timelagmatrepro[t+1,i,2,k]<-ccs2repro[i,i+t,2,k]
  }}}
```

# calculate mean rank-correlation coefficient per time-lag

```
meanmatr<-array(NA,dim=c(tm,4))
for(k in 1:4){
  for(t in 1:(tm-1)){
    sel<-timelagmatr[t,,2,k]<0.05
    meanmatr[t,k]<-mean(timelagmatr[t,,1,k],na.rm=T)
  }}
```

```
meanmatrepro<-array(NA,dim=c(tm,4))
for(k in 1:4){
  for(t in 1:(tm-1)){
    sel<-timelagmatrepro[t,,2,k]<0.05
    meanmatrepro[t,k]<-mean(timelagmatrepro[t,,1,k],na.rm=T)
  }}
```

## Plot similar to figure 3.4 (but without observed quantiles, variance, and autocorrelation) ##

```
par(mfrow=c(3,2),xpd=T,mar=c(5.1,4.1,2.1,2.1))
sel<-c(rep(T,20),rep(F,m-20))
tcks=0.1
```

# a&b: Quantiles

```
plot(moms2r[3,,1][sel]~c(1:m)[sel],axes=F,xlim=c(1,20),type="l",ylim=c(0,120),xlab="Age
(years)",ylab="Stem length (cm)")
lines(moms2r[4,,1][sel]~c(1:m)[sel],type="l")
for(i in 2:4){
  lines(moms2r[3,,i][sel]~c(1:m)[sel],type="l",lty=i+1)
  lines(moms2r[4,,i][sel]~c(1:m)[sel],type="l",lty=i+1)
}
axis(2,tck=tcks,at=c(0,40,80,120))
axis(1,tck=tcks,at=c(1,5,10,15,20))
text(1+19/50,120+120/50,label="(a)")
legend("topleft",c("Stochastic","pH  autocorrelated","Light autocorrelated","pH  and  light
autocorrelated"),lty=c(1:5),bty="n",cex=0.9)

plot(rmoms2r[3,,1][sel]~c(1:m)[sel],axes=F,lty=2,xlim=c(1,20),type="l",ylim=c(0,500),xlab=
"Age (years)",ylab="Cumulative reproduction (# seeds)")
for(i in 1:4){
  lines(rmoms2r[3,,i][sel]~c(1:m)[sel],type="l",lty=i+1)
  lines(rmoms2r[4,,i][sel]~c(1:m)[sel],type="l",lty=i+1)
}
axis(2,tck=tcks,at=c(0,250,500))
axis(1,tck=tcks,at=c(1,5,10,15,20))
text(1+19/50,500+500/50,label="(b)")

# c&d: Variances
plot(moms2r[2,,1][sel]~c(1:m)[sel],type="l",xlim=c(1,20),ylim=c(0,150),axes=F,lty=2,cex.la
b=1,cex.axis=1,xlab="Age (years)",ylab="Variance in stem length")
for(i in 2:4){lines(moms2r[2,,i][sel]~c(1:m)[sel],lty=i+1)}
text(1+19/50,150+150/50,label="(c)")
axis(2,tck=tcks,at=c(0,50,100,150))
axis(1,tck=tcks,at=c(1,5,10,15,20))

plot(rmoms2r[2,,1][sel]~c(1:46)[sel],axes=F,lty=2,type="l",xlim=c(1,20),ylim=c(0,10000),ce
x.lab=1,cex.axis=1,xlab="Age (years)",ylab="Variance in reproductive output")
for(i in 2:4){lines(rmoms2r[2,,i][sel]~c(1:46)[sel],lty=i+1)}
text(1+19/50,10000+10000/50,label="(d)")
axis(2,tck=tcks,labels=c("0","2500","5000","7500","10000"),at=c(0,2500,5000,7500,10000))
axis(1,tck=tcks,at=c(1,5,10,15,20))

# e&f: Auto correlation
plot(meanmatr[2:tm,1][sel]~c(1:(tm-
1))[sel],axes=F,lty=2,cex.axis=1,cex.lab=1,xlim=c(1,20),type="l",xlab="Time          lag
(years)",ylab=expression('Correlation coefficient ('*rho*')'),ylim=c(0,1))
for(k in 2:4){lines(meanmatr[2:tm,k][sel]~c(1:(tm-1))[sel],lty=k+1)}
```

```
text(1+19/50,1+1/50,label="(e)")
axis(2,tck=tcks,at=c(0,0.25,0.5,0.75,1))
axis(1,tck=tcks,at=c(1,5,10,15,20))

plot(meanmatrepro[2:tm,1][sel]~c(1:(tm-
1))[sel],axes=F,lty=2,cex.axis=1,cex.lab=1,xlim=c(1,20),type="l",xlab="Time      lag
(years)",ylab=expression('Correlation coefficient ('*rho*')'),ylim=c(0,1))
for(k in 2:4){lines(meanmatrepro[2:tm,k][sel]~c(1:(tm-1))[sel],lty=k+1)}
text(1+19/50,1+1/50,label="(f)")
axis(2,tck=tcks,labels=c("0","0.25","0.5","0.75","1"),at=c(0,0.25,0.5,0.75,1))
axis(1,tck=tcks,at=c(1,5,10,15,20))
```

**Appendix S3.2** *Methods used for the construction of figure 3.5.*

In the construction of figure 3.5, we used similar methods as those described in the methods section, but we virtually changed the slopes, intercepts and residual variances of the soil acidity (pH) and light level persistence, and stem length growth relations that we obtained with regression analysis. These changes simulate the effect of higher persistence in pH and light and a larger contribution of pH and light in explaining variation in growth rate.

To simulate different levels of persistence of soil pH and light level, we made the following adaptation to the models used in the simulations:

$$pH_{t+1} = \alpha + \beta * pH_t + \varepsilon + \alpha_{ext} + \beta_{ext} * pH_t + \varepsilon_{ext} \qquad\qquad \text{Eq. S3.2.1}$$

$$Light_{t+1} = \alpha + \beta * Light_t + \varepsilon + \alpha_{ext} + \beta_{ext} * Light_t + \varepsilon_{ext} \quad \textit{(for } \delta \textit{ light} < 0.015) \qquad \text{Eq. S3.2.2}$$

$$Light_{t+1} - Light_t = \alpha + \beta * \sqrt{(Light_t)} + \varepsilon + \alpha_{ext} + \beta_{ext} * Light_t + \varepsilon_{ext} \quad \textit{(for } \delta \textit{ light} > 0.015) \qquad \text{Eq. S3.2.3}$$

in these formulas $\alpha$ is the intercept, $\beta$ the slope, and $\varepsilon$ the error term. The terms provided with the subscript "ext" are the changes in $\alpha$, $\beta$, and $\varepsilon$. When variation in pH is completely persistent, $pH_{t+1}=pH_t$ ($\beta + \beta_{ext}=1$, $\varepsilon + \varepsilon_{ext}=0$, and $\alpha + \alpha_{ext}=0$). When there is no relation between $pH_{t+1}$ and $pH_t$, $\beta + \beta_{ext}=0$. Making the assumption that residual variance changes linearly with change in slope, $\alpha_{ext}$ and $\varepsilon_{ext}$ can easily be calculated for this situation. From these coefficients, making the same assumption, values for $\alpha_{ext}$, $\beta_{ext}$ and $\varepsilon_{ext}$ for intermediate levels of persistence were also calculated. These procedures were slightly adjusted for light because we modelled small and large changes in light availability separately (Table S3.5). Coefficients in Equation S3.2.2 were determined in the same way as for pH. Coefficients in equation S3.2.3 were determined two times, two allow for both positive and negative changes in light availability at low persistence.

To simulate larger and smaller contributions of pH and light in explaining variation in growth rate, we also artificially adjusted the relations used in previous analysis:

Eq. S3.2.4:

Stem length growth1 = a1 + b1*light + c*pH$^2$ + d*sqrt(stem length) + *er* + $a_{ext}$ + $c_{ext}$*pH$^2$ + $b1_{ext}$*light+ $er_{ext}$

Eq. S3.2.5:

Stem length growth2 = a2 + b2*light + c*pH$^2$ + d*sqrt(stem length) + *er* + $a_{ext}$ + $c_{ext}$*pH$^2$ + $b2_{ext}$*light + $er_{ext}$

In this formula a is the intercept, b the slope, and er the error term. The additions 1 and 2 indicate different years because we found a significant effect of year and of the interaction between year and light (Table S3.4). For simplicity, we changed only the effect and persistence in one environmental factor per simulation and thus did not analyze changes in the persistence and the effect of light and pH at the same time. When the extra pH and light terms would explain all residual variance of this model, maximum measured pH$^2$ or light value would explain the largest residual term, and the minimum measured pH$^2$ or light value the smallest residual term. From this, we determined the maximum value of $c_{ext}$. For the rest, to

determine the maximum, minimum, and intermediate values of $a_{ext}$, $c_{ext}$, and $er_{ext}$ similar methods were used as described above.

For the three new lines in figure 3.5c and the grey scaled areas in figure 3.5d the following values were used:

| | | Figure 3.5a | Figure 3.5b | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Persistence pH | $\alpha+\alpha_{ext}$ | 0.15 | 6.70 | 6.03 | 5.36 | 4.69 | 4.02 | 3.35 | 2.68 | 2.01 | 1.34 | 0.67 | 0.00 |
| | $\beta+\beta_{ext}$ | 0.98 | 0.00 | 0.10 | 0.20 | 0.30 | 0.40 | 0.50 | 0.60 | 0.70 | 0.80 | 0.90 | 1.00 |
| | $\varepsilon+\varepsilon_{ext}$ | 0.00 | 0.18 | 0.16 | 0.15 | 0.13 | 0.11 | 0.09 | 0.07 | 0.06 | 0.04 | 0.02 | 0.00 |
| Explained residual variance by pH | $a+a_{ext}$ | -6.94 | -2.27 | - 3.01 | - 3.76 | - 4.50 | - 5.25 | - 6.00 | - 6.74 | - 7.49 | - 8.23 | - 8.98 | - 9.73 |
| | $c+c_{ext}$ | 0.12 | 0.00 | 0.02 | 0.04 | 0.06 | 0.07 | 0.09 | 0.11 | 0.13 | 0.15 | 0.17 | 0.19 |
| | $er+er_{ext}$ | 0.20 | 0.57 | 0.51 | 0.46 | 0.41 | 0.36 | 0.30 | 0.25 | 0.20 | 0.15 | 0.09 | 0.04 |

For the three new lines in figure 3.5a and the grey scaled areas in figure 3.5b the following values were used:

| | | Figure 3.5a | Figure 3.5b | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Persistence light (for δ light < 0.015) | $\alpha+\alpha_{ext}$ | 0.00157 | 0.03 | 0.02 | 0.02 | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 | 0.00 | 0.00 | 0.00 |
| | $\beta+\beta_{ext}$ | 0.954758 | 0.00 | 0.14 | 0.28 | 0.42 | 0.56 | 0.70 | 0.77 | 0.83 | 0.89 | 0.94 | 1.00 |
| | $\varepsilon+\varepsilon_{ext}$ | 3.84E-06 | 5.09E-05 | 4.54E-05 | 3.99E-05 | 3.44E-05 | 2.89E-05 | 2.34E-05 | 1.86E-05 | 1.40E-05 | 9.39E-06 | 4.80E-06 | 0.00E+00 |
| Persistence light positive (for δ light < 0.015) | $\alpha+\alpha_{ext}$ | 0.014643 | 0.03 | 0.04 | 0.05 | 0.06 | 0.07 | 0.09 | 0.07 | 0.05 | 0.04 | 0.02 | 0.00 |
| | $\beta+\beta_{ext}$ | -0.071689 | 0.00 | -0.08 | -0.16 | -0.25 | -0.33 | -0.41 | -0.36 | -0.27 | -0.18 | -0.09 | 0.00 |
| | $\varepsilon+\varepsilon_{ext}$ | 5.01E-05 | 0.000233 | 0.000245 | 0.000258 | 0.00027 | 0.000283 | 0.000295 | 0.00025 | 0.000188 | 0.000125 | 6.27E-05 | 0.00E+00 |
| Persistence light negative (for δ light < 0.015) | $\alpha+\alpha_{ext}$ | 0.014643 | -0.03 | -0.01 | 0.02 | 0.04 | 0.06 | 0.08 | 0.07 | 0.05 | 0.04 | 0.02 | 0.00 |
| | $\beta+\beta_{ext}$ | -0.071689 | 0.00 | -0.08 | -0.16 | -0.25 | -0.33 | -0.41 | -0.36 | -0.27 | -0.18 | -0.09 | 0.00 |
| | $\varepsilon+\varepsilon_{ext}$ | 5.01E-05 | 0.000164 | 0.000189 | 0.000215 | 0.000241 | 0.000267 | 0.000292 | 0.00025 | 0.000188 | 0.000125 | 6.27E-05 | 0.00E+00 |
| Explained residual variance by light year 1 | $a+a_{ext}$ | -6.444777 | -0.64 | -1.24 | -1.83 | -2.42 | -3.02 | -3.61 | -4.21 | -4.80 | -5.40 | -5.99 | -6.58 |
| | $c+c_{ext}$ | 165.4422 | 0.00 | 16.94 | 33.88 | 50.82 | 67.76 | 84.70 | 101.64 | 118.58 | 135.53 | 152.47 | 169.41 |
| | $er+er_{ext}$ | 0.022554 | 0.96 | 0.86 | 0.76 | 0.67 | 0.57 | 0.48 | 0.38 | 0.29 | 0.19 | 0.10 | 0.00 |
| Explained residual variance by light year 2 | $a+a_{ext}$ | -5.607381 | -1.25 | -1.57 | -1.88 | -2.19 | -2.51 | -2.82 | -3.57 | -4.11 | -4.65 | -5.19 | -5.73 |
| | $c+c_{ext}$ | 124.1988 | 0.00 | 8.97 | 17.93 | 26.90 | 35.86 | 44.83 | 66.20 | 81.60 | 97.00 | 112.40 | 127.80 |
| | $er+er_{ext}$ | 0.020421 | 0.72 | 0.67 | 0.62 | 0.57 | 0.52 | 0.47 | 0.35 | 0.26 | 0.17 | 0.09 | 0.00 |

**Figure S3.1** *Auto-correlation in simulated and observed performance.*
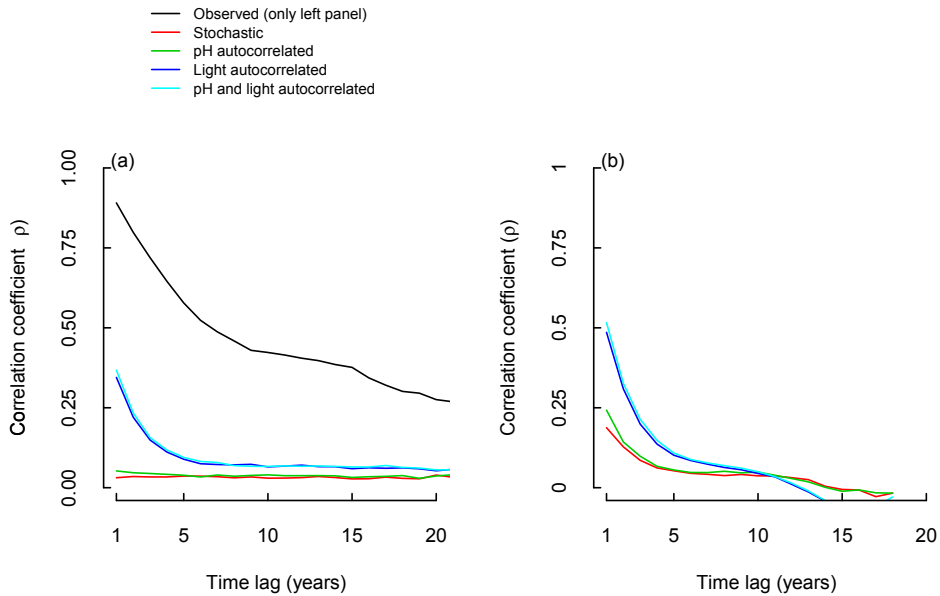


Temporal autocorrelation (Spearman rank correlation coefficient, $\rho$) in observed and simulated lifetime trajectories for stem growth rate (a) and reproductive output (b) of *Chamaedorea elegans* palms under four different environmental scenarios. Displayed $\rho$-values are the average of all possible combinations for a given time lag. The large distance between the "observed" and the "simulated" lines in panel (a) indicates that the auto-correlation of growth rate over time was strongly underestimated by all four simulated scenarios, especially in the stochastic scenario and the scenario where only pH was temporally autocorrelated.

**Table S3.1** *Environmental measurements: dates and sample sizes.*

Numbers indicate the number of individuals that were measured for that environmental factor in the indicated period.

| Environmental factor | Oct-Nov 2013 | Mar 2014 | Nov '14 - Jan '15 | January 2015 |
|---|---|---|---|---|
| *Relative light level* | 101 | | 255 | |
| *Leaf Damage* | 599 | | | |
| *Soil:* | | | | |
| *pH* | 370 | | | 101 |
| *Depth* | 784 | | | |
| *Water content* | 780 | 735 | | |
| *Texture* | | | | 101 |
| *N&P availability* | | | | 101 |

**Table S3.2** *Results of all sub-set multiple regression analysis per vital rate per environmental variable per year with size dependence, defoliation treatment and interactions included.*

Only models where the environmental variable appeared in the best model based on AIC are shown. Soil depth, sand content, and silt content did not appear in any of the best models and are therefore not present in this table. The $R^2$ of the survival chance and reproduction chance models are Nagelkerke $R^2$ (Nagelkerke 1991).

| | | | Estimate | SE | t-value | p-value | Total model $R^2$ | δ $R^2$ | N |
|---|---|---|---|---|---|---|---|---|---|
| ***Stem length growth (year 1)*** | Relative light availability | Intercept | -1.914 | 1.064 | -1.799 | 0.076 | 0.595 | 0.352 | 86 |
| | | Light | -0.052 | 0.02 | -2.548 | 0.013 | | | |
| | | Stem length | 20.475 | 17.062 | 1.2 | 0.234 | | | |
| | | Sqrt(stem length) | 0.821 | 0.281 | 2.923 | 0.004 | | | |
| | | Light*Stem length | 0.866 | 0.304 | 2.85 | 0.006 | | | |
| | Soil pH | Intercept | 31.335 | 15.525 | 2.018 | 0.044 | 0.298 | 0.02 | 298 |
| | | pH | -9.891 | 4.428 | -2.234 | 0.026 | | | |
| | | Stem length | -0.063 | 0.013 | -4.957 | 0 | | | |
| | | Sqrt(stem length) | 1.171 | 0.186 | 6.311 | 0 | | | |
| | | $pH^2$ | 0.728 | 0.315 | 2.308 | 0.022 | | | |
| | | Defoliation | -0.645 | 0.264 | -2.448 | 0.015 | | | |
| | | Defoliation treatment *Stem length | 0.01 | 0.005 | 2.234 | 0.026 | | | |
| | Soil moisture in wet season | Intercept | 0.3 | 0.572 | 0.525 | 0.6 | 0.218 | 0.008 | 623 |
| | | moisture wet | -0.002 | 0.001 | -2.465 | 0.014 | | | |
| | | Stem length | -0.031 | 0.01 | -3.209 | 0.001 | | | |
| | | Sqrt(stem length) | 0.682 | 0.138 | 4.946 | 0 | | | |
| | | Defoliation treatment | -0.549 | 0.184 | -2.991 | 0.003 | | | |
| | | def*Stem length | 0.009 | 0.003 | 2.699 | 0.007 | | | |
| | Leaf damage | Intercept | 0.407 | 0.579 | 0.703 | 0.482 | 0.215 | 0.017 | 523 |
| | | leaf damage | -0.017 | 0.007 | -2.597 | 0.01 | | | |
| | | leaf damage$^2$ | 0 | 0 | 1.669 | 0.096 | | | |
| | | Stem length | -0.023 | 0.01 | -2.236 | 0.026 | | | |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Sqrt(stem length) | 0.543 | 0.153 | 3.546 | 0 | | | |
| | | Defoliation treatment | -0.592 | 0.201 | -2.942 | 0.003 | | | |
| | | Defoliation treatment *Stem length | 0.009 | 0.004 | 2.524 | 0.012 | | | |
| *Stem length growth (year 2)* | Relative light availability | Intercept | -0.591 | 0.395 | -1.493 | 0.137 | 0.253 | 0.076 | 210 |
| | | Light | 33.082 | 7.188 | 4.603 | 0.000 | | | |
| | | Sqrt(stem length) | 0.299 | 0.042 | 7.065 | 0.000 | | | |
| | Soil pH | Intercept | -2.671 | 1.403 | -1.903 | 0.060 | 0.186 | 0.058 | 93 |
| | | Sqrt(stem length) | 0.304 | 0.080 | 3.814 | 0.000 | | | |
| | | $pH^2$ | 0.063 | 0.025 | 2.532 | 0.013 | | | |
| | Soil moisture in dry season | Intercept | -0.293 | 0.537 | -0.545 | 0.586 | 0.178 | 0.009 | 553 |
| | | moisture dry | -0.002 | 0.001 | -2.438 | 0.015 | | | |
| | | Stem length | -0.034 | 0.010 | -3.291 | 0.001 | | | |
| | | Sqrt(stem length) | 0.733 | 0.151 | 4.867 | 0.000 | | | |
| | | Defoliation treatment | -0.243 | 0.096 | -2.527 | 0.012 | | | |
| | Available PO4 | Intercept | 0.004 | 0.740 | 0.006 | 0.995 | 0.155 | 0.051 | 93 |
| | | sqrt(PO4) | 0.261 | 0.153 | 1.711 | 0.091 | | | |
| | | Sqrt(stem length) | 0.293 | 0.081 | 3.605 | 0.001 | | | |
| | Available NH4 | Intercept | -0.985 | 0.895 | -1.101 | 0.274 | 0.183 | 0.079 | 93 |
| | | $sqrt(NH_4)$ | 0.181 | 0.074 | 2.462 | 0.016 | | | |
| | | sqrt(stem length) | 0.325 | 0.080 | 4.045 | 0.000 | | | |
| *Survival (over 2 years)* | Leaf damage | Intercept | 6.721 | 0.946 | 7.105 | 0 | 0.163 | 0.036 | 599 |
| | | leaf damage | -0.038 | 0.013 | -2.837 | 0.005 | | | |
| | | Stem length | -0.039 | 0.011 | -3.573 | 0 | | | |
| | | Leaf damage * Stem length | 0 | 0 | 1.803 | 0.071 | | | |
| | | Defoliation treatment | -3.124 | 0.893 | -3.499 | 0 | | | |
| | | Defoliation treatment * Stem length | 0.02 | 0.011 | 1.842 | 0.066 | | | |
| *Reproduction chance (year 1)* | Relative light availability | Intercept | -5.559 | 1.638 | -3.394 | 0.001 | 0.259 | 0.127 | 101 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Sqrt(light) | 21.514 | 7.508 | 2.865 | 0.004 | | | |
| | | Sqrt(stem length) | 0.179 | 0.144 | 1.240 | 0.215 | | | |
| | | Defoliation | -1.988 | 0.768 | -2.588 | 0.010 | | | |
| | Soil pH | Intercept | -11.618 | 3.390 | -3.428 | 0.001 | 0.290 | 0.013 | 208 |
| | | pH$^2$ | 0.056 | 0.038 | 1.492 | 0.136 | | | |
| | | Stem length | -0.155 | 0.053 | -2.935 | 0.003 | | | |
| | | Sqrt(stem length) | 2.383 | 0.761 | 3.132 | 0.002 | | | |
| | | Def | -1.995 | 0.402 | -4.965 | 0.000 | | | |
| | Leaf damage | Intercept | -3.910 | 1.896 | -2.062 | 0.039 | 0.299 | 0.025 | 326 |
| | | leaf damage | -0.019 | 0.007 | -2.582 | 0.010 | | | |
| | | Stem length | -0.081 | 0.036 | -2.271 | 0.023 | | | |
| | | Sqrt(stem length) | 1.248 | 0.528 | 2.365 | 0.018 | | | |
| | | Def | -2.197 | 0.307 | -7.157 | 0.000 | | | |
| *Reproduction chance (year 2)* | Light availability | Intercept | -25.807 | 8.368 | -3.084 | 0.002 | 0.502 | 0.058 | 125 |
| | | Sqrt(Light) | 23.768 | 9.419 | 2.523 | 0.012 | | | |
| | | Stem length | -0.353 | 0.134 | -2.635 | 0.008 | | | |
| | | Sqrt(stem length) | 5.629 | 2.083 | 2.703 | 0.007 | | | |
| | | Defoliation | -3.118 | 0.713 | -4.370 | 0.000 | | | |
| | Available NO3 | Intercept | -126.808 | 53.956 | -2.350 | 0.019 | 0.651 | 0.165 | 53 |
| | | NO3 | -1.330 | 0.660 | -2.016 | 0.044 | | | |
| | | sqrt(NO3) | 15.475 | 7.801 | 1.984 | 0.047 | | | |
| | | Stem length | -1.195 | 0.575 | -2.078 | 0.038 | | | |
| | | Sqrt(stem length) | 20.230 | 9.557 | 2.117 | 0.034 | | | |
| | | Def | -4.381 | 1.468 | -2.985 | 0.003 | | | |
| | Available NH4 | Intercept | -139.446 | 68.207 | -2.044 | 0.041 | 0.723 | 0.236 | 53 |
| | | NH4 | -1.997 | 1.097 | -1.820 | 0.069 | | | |
| | | sqrt(NH4) | 22.303 | 12.323 | 1.810 | 0.070 | | | |
| | | Stem length | -1.067 | 0.649 | -1.644 | 0.100 | | | |
| | | Sqrt(stem length) | 18.709 | 11.116 | 1.683 | 0.092 | | | |
| | | Def | -4.923 | 1.744 | -2.822 | 0.005 | | | |
| | Soil clay content | Intercept | -83.321 | 39.420 | -2.114 | 0.035 | 0.630 | 0.143 | 53 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Clay | 0.069 | 0.050 | 1.387 | 0.165 | | | |
| | | Stem length | -1.094 | 0.540 | -2.025 | 0.043 | | | |
| | | Sqrt(stem length) | 18.864 | 9.176 | 2.056 | 0.040 | | | |
| | | Def | -13.104 | 8.300 | -1.579 | 0.114 | | | |
| | | Clay*def | 0.176 | 0.137 | 1.279 | 0.201 | | | |
| *Seed production (year 1)* | Relative light availability | Intercept | -7.895 | 6.273 | -1.259 | 0.24 | 0.863 | 0.759 | 14 |
| | | Light | 646.853 | 91.569 | 7.064 | 0 | | | |
| | | Stem length | 0.066 | 0.1 | 0.652 | 0.53 | | | |
| | | Defoliation treatment | -59.039 | 13.412 | -4.402 | 0.002 | | | |
| | | Defoliation treatment *Stem length | 0.556 | 0.193 | 2.875 | 0.018 | | | |
| | Soil pH | Intercept | 238.974 | 99.127 | 2.411 | 0.02 | 0.218 | 0.147 | 48 |
| | | pH | -32.657 | 13.941 | -2.343 | 0.024 | | | |
| | | Stem length | -4.101 | 1.53 | -2.681 | 0.01 | | | |
| | | pH*Stem length | 0.608 | 0.216 | 2.818 | 0.007 | | | |
| | Soil moisture in dry season | Intercept | -14.561 | 13.031 | -1.117 | 0.267 | 0.152 | 0.047 | 89 |
| | | moisture dry | 0.137 | 0.077 | 1.777 | 0.079 | | | |
| | | Stem length | 0.664 | 0.228 | 2.908 | 0.005 | | | |
| | | Defoliation treatment | -6.918 | 4.606 | -1.502 | 0.137 | | | |
| | | moisture dry*Stem length | -0.003 | 0.001 | -2.124 | 0.037 | | | |
| | Leaf damage | Intercept | 17.83 | 5.798 | 3.075 | 0.003 | 0.199 | 0.065 | 84 |
| | | leaf damage | -0.491 | 0.199 | -2.467 | 0.016 | | | |
| | | Stem length | 0.021 | 0.102 | 0.211 | 0.834 | | | |
| | | Defoliation treatment | -7 | 3.949 | -1.773 | 0.08 | | | |
| | | leaf damage*Stem length | 0.008 | 0.004 | 2.046 | 0.044 | | | |
| *Seed production (year 2)* | Soil pH | Intercept | -124.600 | 46.539 | -2.677 | 0.025 | 0.628 | 0.383 | 12 |
| | | pH | 21.019 | 6.727 | 3.125 | 0.012 | | | |
| | | Defoliation treatment | -20.948 | 6.569 | -3.189 | 0.011 | | | |

**Table S3.3** *Results of all subset regression analyses in which the vital rates growth, reproduction, and survival were related to a combination of environmental factors.*

Only environmental factors that individually significantly influenced performance (Table S3.1) were included in the analyses. A correction for stem length, defoliation treatment and interactions were applied. Model selection was based on AIC. The $R^2$ of the survival chance and reproduction chance models are Nagelkerke $R^2$ (Nagelkerke 1991). Note that the models for survival chance and seed production in year 2 are the same as the models shown in table S3.2, as for these vital rates there was only one environmental factor that had a significant influence.

| | | Estimate | SE | t-value | p-value | Total model $R^2$ | δ $R^2$ | N |
|---|---|---|---|---|---|---|---|---|
| *Growth year 1* | Intercept | 51.079 | 25.537 | 2 | 0.051 | 0.718 | 0.546 | 60 |
| | Light | 28.688 | 18.476 | 1.553 | 0.127 | | | |
| | pH | -16.431 | 7.193 | -2.284 | 0.027 | | | |
| | pH^2 | 1.302 | 0.508 | 2.564 | 0.013 | | | |
| | Soil moisture in wet season | -0.004 | 0.002 | -1.829 | 0.073 | | | |
| | Leaf damage | 0.381 | 0.111 | 3.433 | 0.001 | | | |
| | pH * Leaf damage | -0.053 | 0.016 | -3.424 | 0.001 | | | |
| | Light * Stem length | 0.882 | 0.318 | 2.773 | 0.008 | | | |
| | Stem length | -0.049 | 0.022 | -2.242 | 0.029 | | | |
| | sqrt(stem length) | 0.712 | 0.323 | 2.202 | 0.032 | | | |
| *Growth year 2* | Intercept | 1.48 | 6.049 | 0.245 | 0.807 | 0.451 | 0.251 | 82 |
| | Light | 184.574 | 63.02 | 2.929 | 0.005 | | | |
| | pH | -1.077 | 0.813 | -1.325 | 0.189 | | | |
| | Soil moisture in dry season | 0.017 | 0.01 | 1.721 | 0.09 | | | |
| | availability NH4 | -0.266 | 0.11 | -2.422 | 0.018 | | | |
| | availability PO4 | -0.003 | 0.161 | -0.016 | 0.987 | | | |
| | sqrt(availability PO4) | 0.886 | 0.47 | 1.884 | 0.064 | | | |
| | sqrt(stem length) | 0.381 | 0.085 | 4.461 | 0 | | | |
| | light * soil moisture in dry season | -0.738 | 0.349 | -2.115 | 0.038 | | | |
| | Light * PO4 | -10.081 | 3.306 | -3.049 | 0.003 | | | |
| | pH * NH4 | 0.04 | 0.016 | 2.541 | 0.013 | | | |
| *Survival (over 2 years)* | Intercept | 6.721 | 0.946 | 7.105 | 0 | 0.163 | 0.036 | 599 |
| | leaf damage | -0.038 | 0.013 | -2.837 | 0.005 | | | |
| | Stem length | -0.039 | 0.011 | -3.573 | 0 | | | |
| | Leaf damage * Stem length | 0 | 0 | 1.803 | 0.071 | | | |
| | Defoliation treatment | -3.124 | 0.893 | -3.499 | 0 | | | |
| | Defoliation treatment * Stem length | 0.02 | 0.011 | 1.842 | 0.066 | | | |
| *Reproduction chance year 1* | Intercept | -64.264 | 41.408 | -1.552 | 0.121 | 0.401 | 0.309 | 69 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Light | 3323.289 | 2021.660 | 1.644 | 0.100 | | | |
| | pH | 8.926 | 5.948 | 1.501 | 0.133 | | | |
| | Light*pH | -468.652 | 289.888 | -1.617 | 0.106 | | | |
| | Defoliation treatment | -2.343 | 1.064 | -2.202 | 0.028 | | | |
| *Reproduction chance year 2* | Intercept | -50.432 | 28.913 | -1.744 | 0.081 | 0.416 | 0.164 | 97 |
| | Sqrt(Light) | 22.210 | 10.655 | 2.084 | 0.037 | | | |
| | Soil clay content | 0.104 | 0.049 | 2.137 | 0.033 | | | |
| | Stem length | -0.587 | 0.405 | -1.450 | 0.147 | | | |
| | Sqrt(Stem length) | 9.786 | 6.758 | 1.448 | 0.148 | | | |
| | Defoliation treatment | -2.362 | 0.882 | -2.678 | 0.007 | | | |
| *Seed production year 1* | Intercept | 28.518 | 6.63 | 4.302 | 0.004 | 0.920 | 0.904 | 11 |
| | Light | 501.421 | 77.302 | 6.487 | 0 | | | |
| | Soil moisture in dry season | -0.158 | 0.032 | -5.013 | 0.002 | | | |
| | defoliation treatment | -19.488 | 4.654 | -4.188 | 0.004 | | | |
| *Seed production year 2* | Intercept | -124.600 | 46.539 | -2.677 | 0.025 | 0.628 | 0.383 | 12 |
| | Soil pH | 21.019 | 6.727 | 3.125 | 0.012 | | | |

**Table S3.4.** *Results of all subset mixed-effect multiple regression analyses of the relation between performance (stem length growth rate, reproduction chance and number of produced seeds) and the combined effect of relative light level and soil pH.*

Defoliation treatment, stem length, year and interactions were included to account for treatment, ontogenetic and year effects respectively. The $R^2$ of the survival chance model is Nagelkerke $R^2$ (Nagelkerke 1991).

|  |  | Estimate | AIC | N |
|---|---|---|---|---|
| ***Stem length growth*** | Intercept | -4.13423 | 514.2625 | 328 |
|  | Light | 99.57267 |  |  |
|  | $pH^2$ | 0.046777 |  |  |
|  | sqrt(stem length) | 0.313129 |  |  |
|  | Year | 0.850037 |  |  |
|  | Light*Year | -41.6038 |  |  |
| ***Reproduction chance*** | Intercept | -228.337 | 54.5 | 95 |
|  | Stem length | -3.43838 |  |  |
|  | Sqrt(Stem Length) | 57.51056 |  |  |
|  | defoliation | -22.5023 |  |  |
| ***Seed production*** | Intercept | -149.727 | 129.0783 | 25 |
|  | Light | 1570.833 |  |  |
|  | pH | 12.15605 |  |  |
|  | sqrt(Stem length) | 4.106728 |  |  |
|  | Year | 31.21249 |  |  |
|  | defoliation | -23.2504 |  |  |
|  | Light*year | -918.594 |  |  |

**Table S3.3.** *Models relating environment at time t to environment at time t+1.*

| Model | Intercept | Slope | p-value | $R^2$ |
|---|---|---|---|---|
| $Light_{t+1} \sim Light_t$ (δ light < 0.015) | 0.009 | 0.730 | <2.2e-16 | 0.563 |
| $Light_{t+1}-Light_t \sim \sqrt{(Light_t)}$ (δ light > 0.015) | 0.087 | -0.42 | <0.001 | 0.717 |
| Relative contribution light models | -5.336 | 125.215 | 0.022 | δAIC=19.667 |
| $pH_{t+1} \sim pH_t$ | 2.849 | 0.562 | 0.033 | 0.303 |

Note: δAIC is given for the relative contribution light model, as general non-linear regression does not provide $R^2$ values.

# Chapter 4

Strong genetic variation in growth parameters, but not for tolerance to leaf loss and underlying responses within a population of an understorey palm

Merel Jansen, Aad van Ast, Frans Bongers, Marcos Malosetti, Miguel Martínez-Ramos, Juan Núñez-Farfán, Pieter A. Zuidema, Niels P.R. Anten

## Abstract

Leaf loss (*e.g.* through disturbances such as herbivory, physical damage or harvesting) is an ubiquitous stressor that can strongly limit individual plant performance. Defoliation tolerance, the ability of plants to maintain performance while suffering leaf loss, is often associated with compensatory growth. Genetic variation in tolerance and compensatory growth responses, in turn, play an important role in the evolutionary adaptation of populations to changing disturbance regimes but has been poorly investigated for long-lived woody species. Generally, tolerance to leaf damage is expected to trade-off against plant performance (growth, reproduction), but depending on the compensatory mechanism tolerance and growth could also be positively related.

We address the extent to which genetic variation in plant growth, tolerance (in terms of growth rate), and compensatory responses to leaf damage (*i.e.*, increases in specific leaf area, allocation of biomass to new leaf growth and growth per unit leaf area) is present in a population, and evaluate if a genetic correlation exists between growth and tolerance. We performed a greenhouse experiment with 1440 seedlings from 202 half-sib families of the understorey palm *Chamaedorea elegans*. Seeds were collected from a small (0.7ha) natural population in Mexico. A two-third defoliation treatment was applied to half of the individuals to simulate leaf loss. We found that growth rate was strongly heritable and that plants compensated strongly for leaf loss. Genetic variation in tolerance, compensation, and the individual compensatory responses were however estimated to be low. Correlations between family mean growth parameters in the two treatments were high. We did not find a relation between tolerance and growth rate, *i.e.*, there being no evidence for growth-tolerance trade off. The low genetic variation in tolerance and compensatory responses that we found, suggests that the potential for evolutionary adaptation of populations to a changing disturbance regime might be limited.

### Keywords

## Introduction

Leaf loss (*e.g.* through herbivory, physical damage or harvesting) is an ubiquitous stressor that can strongly limit individual plant performance as it entails a reduction in photosynthesis and thus future growth as well as a direct loss of resources. Performance reductions due to leaf loss are often proportionately smaller than expected based on the fraction of leaf that is being removed (Strauss & Agrawal 1999; Núñez-Farfán, Fornoni & Valverde 2007) and in some cases plants even increase their performance under leaf loss (Belsky *et al.* 1993; Agrawal 2000). In that sense plants can be tolerant to leaf loss, and this tolerance is often associated with compensatory growth because of which negative effects of leaf loss are mitigated (Stowe *et al.* 2000). There are basically three compensatory growth responses; plants can compensate for growth by allocating more new assimilates to leaves, by allocating new assimilates more efficiently to leaf area (*i.e.* by increasing specific leaf area), or by growing faster with existing leaf area (*i.e.* by increasing net assimilation rate, Anten, Martínez-Ramos & Ackerly 2003).

Many plant species have evolved tolerance to leaf loss (*e.g.* Stowe *et al.* 2000; Tiffin 2000; Anten & Pierik 2010; Fornoni 2011), which indicates that plants have evolved compensatory growth responses. However, relatively little work has been done to study these compensatory growth responses and genetic variation therein (Anten & Pierik 2010). Furthermore, tolerance can only evolve when there is heritable variation for it present in populations (Strauss & Agrawal 1999), and thus for the underlying compensatory growth responses. Therefore, in order to be able to estimate how fast populations will adapt to changes in disturbance, estimations of genetic variation in compensatory growth responses and associated leaf-loss tolerance are important (Lande & Shannon 1996).

Plants have to balance between investing in tolerance mechanisms that have an energy cost [*e.g.* storage of carbohydrate reserves (Tiffin 2000)] versus growth and reproductive capacity under no disturbance. Therefore there might be a trade-off between tolerance and performance under no disturbance (Stowe *et al.* 2000). However, there are other mechanisms by which plants can tolerate leaf loss, for example by increased photosynthetic activity due to less self-shading, or because of a underbalanced root-shoot ratio which allows high stomatal conductance (Tiffin 2000; Anten & Pierik 2010). If this is the case, fast-growing plants could potentially keep up their growth rate when losing leaf area. The trade-off between growth and tolerance is believed to be a significant factor in determining species habitat adaptation (Kobe 1997). If tolerance and performance under unstressed conditions are negatively correlated, this could explain the maintenance of genetic diversity in populations with varying levels of disturbance, while a positive genetic relation would allow for superior genotypes that can lead to large variation in life histories. However, so far very little is known about the level of within-population genetic correlations between tolerance and performance under unstressed conditions.

Many studies have evaluated genetic variation in short-lived species like annuals and biannuals in performance under undisturbed conditions, for leaf-loss tolerance, and some for genetic correlations between the two (Geber & Griffen 2003). However, for long-lived woody

plant species much less is known about this (Stevens, Waller & Lindroth 2007). Haukioja & Koricheva (2000) argue that tolerance to leaf loss might be just as important for long-lived species as it is for short-lived species. Tolerance might be especially relevant for understorey species because shade tolerance is often associated with storage of reserves that allow recovery after damage (Kobe 1997). More information on the existence of genetic variation in performance, tolerance and genetic correlations between the two, would increase our understanding of the adaptive ability of long-lived plant populations to environmental changes.

In this study we analyzed the extent to which growth and tolerance to leaf loss are heritable and if the two are related. We did this for the shade tolerant understorey palm *Chamaedorea elegans*. Leaf loss due to herbivory and physical damage is high and an important factor limiting the performance of this species (Valverde, Hernandez-Apolinar & Mendoza-Amarom 2006; Martínez-Ramos, Anten & Ackerly 2009). *C. elegans* has been shown to compensate for leaf loss, by changing net assimilation rate (NAR) and allocation of biomass to leaf mass (Anten, Martínez-Ramos & Ackerly 2003). Furthermore, the leaves of this species are a non-timber forest product, and populations of this species are under pressure due to increased harvesting activities (Reining *et al.* 1992).

Specifically, we aimed to answer the following questions:

1. Is there evidence for genetic variation in growth parameters within a population?
2. Is there evidence in this population for genetic variation in tolerance to leaf loss (in terms of growth rate), compensatory growth, and compensatory growth responses (*i.e.* changes in net assimilation rate (NAR), specific leaf area (SLA) and biomass allocation to leaves)?
3. Are growth rate and tolerance to leaf loss genetically correlated in this population?

To answer these questions, we performed a greenhouse experiment in which a defoliation treatment was applied. We estimated genetic variation in growth parameters, tolerance (in terms of growth), compensatory growth and compensatory growth responses. We used an iterative growth model (Anten, Martínez-Ramos & Ackerly 2003) to estimate NAR, SLA changes, and biomass allocation, which we used to calculate compensation. Furthermore, we analyzed the extent to which tolerance to leaf loss and growth rate were related.

## Methods

*Species and site of seed collection*

The experiment was performed with the forest understorey palm species *Chamaedorea elegans* Mart, which naturally occurs in rainforest in Mexico, Guatemala, and Belize (Hodel 1992). It is single stemmed, produces a single cluster of leaves and is dioecious. It naturally occurs on karstic outcrops. Herbivory and falling canopy debris are both major causes of leaf loss in this species (Anten, Martínez-Ramos & Ackerly 2003; Martínez-Ramos, Anten &

Ackerly 2009). Furthermore, leaves are harvested as a Non-Timber Forest Product (NTFP), causing many populations to be under pressure (Reining *et al.* 1992).

Seeds of *Chamaedorea elegans* were collected from a natural population in south-eastern Mexico in the state of Chiapas. In October 2012, close to the Chajul biological station (16˚06' N, 90˚56' W), we set up a 0.7 ha plot, where 830 individuals with a stem length of >10cm were mapped and tagged (see Chapter 3 for details). From all female fruiting individuals (175 individuals in Nov-Dec 2012) within this plot seeds were collected. In addition to that, seeds were collected from 32 individuals in an adjacent study area (Martínez-Ramos, Anten & Ackerly 2009) to assure a sufficiently large sample size. In total 3009 seeds from 207 different mother plants were collected, with number of seeds per mother plant ranging from one to 95 seeds. Seeds were cleaned (mesocarp was removed), air dried and weighed, and they were kept in zip-lock bags that allowed some gas exchange.

*Germination and greenhouse conditions*

The experiment was conducted at the Unifarm greenhouse and growth chamber facilities of Wageningen University, the Netherlands. Seeds were planted at approximately 0.5 cm depth in large trays filled with potting soil. The tray was placed in a growth chamber, where the temperature was being kept constant at 30°C day and night, air humidity at 90%, light levels were kept low and soil was being kept moist but not wet (with water at room temperature). Germination of individual seeds was recorded two times a week.

One and a half weeks after emergence, seedlings were transplanted into small pots of 8.5 x 8.5 x 9.5 cm (l x w x h), filled with low nutrient soil (40% peat moss peat, 20% Nordic fraction 2, 20% Baltic peat agent, 20% normal garden peat, 1% pg mix, 0.2% Micromax) and moved to a greenhouse where they were placed in a cage covered with 75% shade cloth to allow for adjustment to changed climatic conditions. After one week, they were moved to a table with flood system allowing water to be absorbed from below into the pots. The experiment was laid out as a randomized block design with six blocks. To this end, the table was divided into six equal parts lengthwise to create the blocks. Individuals within plant families were randomly distributed over the blocks and over position within the block. Because families differed in number of seedlings, sometimes a family was only present in one block (this was the case for families with only one seedling), and sometimes in all six (which was the case for families with at least six seedlings).

The pots were watered with the flood system when necessary with a nutrient solution (pH 5.0, EC 0.8, NPK ratio 12-14-24). To simulate forest conditions, temperature in the greenhouse was kept at a minimum day/night temperature of 24/22°C, air humidity at 80%, day length was reduced to a maximum of twelve hours using automatically closing black screens. Light levels were in summer months reduced using (depending on the month) either 25% or 50% shade cloth, such that plants received approximately 2mol per day, which is the average light intensity in the forest understorey at the site where seeds were collected. Necessary shading levels were per month determined based on the 10 year (2004 – 2013)

monthly average light intensities recorded for that month on the location where the experiment was conducted, measured by Unifarm.

*Experimental setup*

Six months after germination seedling stem length and diameter, of all leaves leaf width, lamina length, rachis length, rachis diameter, leaflet width, number of leaflets, and length of unopened leaf were measured. From this, seedling biomass (per plant part) and leaf area were estimated using an allometric model, that we constructed based on data of a destructive harvest of extra seedlings of six months of age from the same experimental conditions (see Appendix S4.1 of the Supporting Information for details).

Half of the individuals from each family were then subjected to a two-third defoliation treatment in which two out of every three leaflets were cut off. This treatment was repeated (for newly produced leaves) every eight weeks. The other half of the plants of each family was not defoliated (*i.e.*, the control group). To assign plants to control or defoliation treatments, we ranked all plants in a family according to age (*i.e.* date of emergence). We then randomly assigned a defoliation treatment to the oldest one, giving the other treatment to the second oldest plant and alternating in this way across the age hierarchy.

After 28 weeks surviving seedlings were destructively harvested (1387 in total). Roots were carefully washed to remove all soil particles. Leaf area was measured of the second fully developed leaf (counting from the apex), using a leaf area meter (LiCor LI3100 Lincoln NE, USA.). Roots, stem, rachis, undeveloped leaves, lamina of non-defoliated leaves and lamina of defoliated leaves were separated, and dried in a stove at 70°C for at least 72 hours, after which dry mass per plant part was determined.

*Data curation*

Measured weights and leaf area were checked for mistakes. Mistakes included incomplete defoliation treatment, no separation of undefoliated leaf mass at harvest, no defoliation of new leaves at harvest, and unrealistic values. Unrealistic values were defined as deviations of more than a factor ten from the mean observed relative value compared to other plant parts (*e.g.* from the leaf mass / stem mass ratio). A total of 88 plants were excluded from further analysis. From the included individuals, we selected only those that belonged to families (*i.e.* were obtained from a mother palm) that contained at least 12 individuals. The selection reduced the initial number of 207 families sampled in the field to 47 families included in the analyses. Analyses were conducted on a total of 731 seedlings.

*Estimation NAR, biomass allocation to leaves, changes in SLA and RGR*

To estimate growth and several growth-related parameters [net assimilation rate (NAR), fraction of newly assimilated mass that is allocated to lamina growth ($f_{lam}$), fraction in daily change in mean specific leaf area ($\gamma$) and relative growth rate (RGR)], we used an iterative growth model following the method of Anten & Ackerly (2001). This method of growth analysis allows more exact estimations of growth parameters than either the classic or

functional approaches of growth analysis (Poorter 1989) when a plant experiences repeated leaf loss because it includes timing of leaf loss (Anten & Ackerly 2001). Input for this model is biomass, leaf mass, and leaf area at the beginning and end of the experiment, and leaf loss (mass and area, and time of removal) during the experiment. We, however, did not measure leaf loss directly but assumed this to be two third of existing leaf mass. To allow for this, we adjusted the Anten & Ackerly (2001) model. A more detailed description of these methods is provided in Appendix S4.2.

*Estimation of tolerance and compensatory responses*

Tolerance and compensatory growth are both measures of performance under leaf loss, compared to a control situation without leaf loss. To be able to estimate genetic variation in these measures, information on differences in tolerance within families, and therefore per individual is necessary. In order to be able to calculate tolerance and compensation per individual, each individual in the defoliation treatment was paired with a family member from the control treatment, based on rank order of estimated biomass at six months of age (the beginning of the experiment). Using the values of the coupled control individual, tolerance in growth rate was calculated as:

Tolerance = (Growth$_{Defol}$-Growth$_{Control}$)/Growth$_{Defol}$

Where the subscript Defol and Control indicate the defoliation- and control treatment respectively. For tolerance in RGR, RGR values were obtained with the iterative growth model. For tolerance in biomass growth, we calculated biomass change between 6 months and 12 months of age, for which the values were obtained from direct measurements. We excluded leaf mass in this calculation.

We estimated compensatory growth per individual using the approach of Anten, Martínez-Ramos and Ackerly (2003). Compensation is the fraction of the potential loss in growth due to leaf loss that is mitigated through compensatory mechanisms. We used the coupled control family members as a null-model to be able to estimate growth rate in a hypothetical, non-compensating individual. Using the start-biomass of the defoliated individual, but the growth parameters (NAR, f$_{lam}$, γ) of the control individual, we calculated biomass growth rate and RGR based on the iterative growth model, for both the control and defoliation treatment. Compensation was then calculated as:

$$Compensation = \frac{L_{pot} - L_{real}}{L_{pot}}$$  eqn 4.1a

in which

L$_{pot}$=C0-D0 and L$_{real}$=C0-D  eqn 4.1b

L$_{pot}$ (the potential reduction in growth) is therefore calculated as the growth of a control individual with the null-model growth parameters (C0), minus growth of a defoliated individual with the same null-model growth parameters (D0). L$_{real}$ (the realized reduction in

growth) is calculated as C0 minus the actually realized growth of the defoliated individual (D).

*Statistical analysis*

To estimate genetic variation in growth parameters (NAR, $f_{lam}$ and $\gamma$), variables biomass growth (without leaf mass) and RGR, and for tolerance and compensation, we constructed mixed effect models, in which (half-sib) family (F) was included as random factor. Seed weight (s) was included as fixed effect when its effect was significant, to correct for potential maternal effects. The resulting models were:

$$y_{ij} = \mu + s_j + F_i + e_{ij} \qquad\qquad \text{eqn 4.2a}$$

and

$$y_{ij} = \mu + F_i + e_{ij} \qquad\qquad \text{eqn 4.2b}$$

with

$$F_i \sim N(0,\sigma_F^2) \text{ and } e_{ij} \sim N(0,\sigma^2) \qquad\qquad \text{eqn 4.2c}$$

From the between variance component ($\sigma_F^2$) and the residual variance component ($\sigma^2$) narrow sense heritability was estimated as:

$$h^2 = \frac{4\sigma_F^2}{\sigma_F^2 + \sigma^2} \qquad\qquad \text{eqn 4.3}$$

Estimates for plants that were part of the defoliation treatment were calculated separately.

To analyze genetic variation in response to defoliation, we constructed mixed effect models for all estimated growth parameters in which treatment (T) was included as a fixed effect, family as a random effect, as was the interaction term between treatment and family. A relatively large interaction term between defoliation treatment and family in the models of biomass growth or RGR, is an indication of genetic variation in tolerance (*e.g.* Agrawal, Strauss & Stout 1999). Likewise, a relatively large interaction term between treatment and family in the mixed models for the growth parameters NAR, $f_{lam}$ and $\gamma$, are indications of genetic variation in compensatory traits. When visual inspection of the data suggested more complex variance structures, these were modeled as well, and the best model was selected based on AIC. The best model was for all tested variables the model in which separate within group variance components were estimated per treatment, which is:
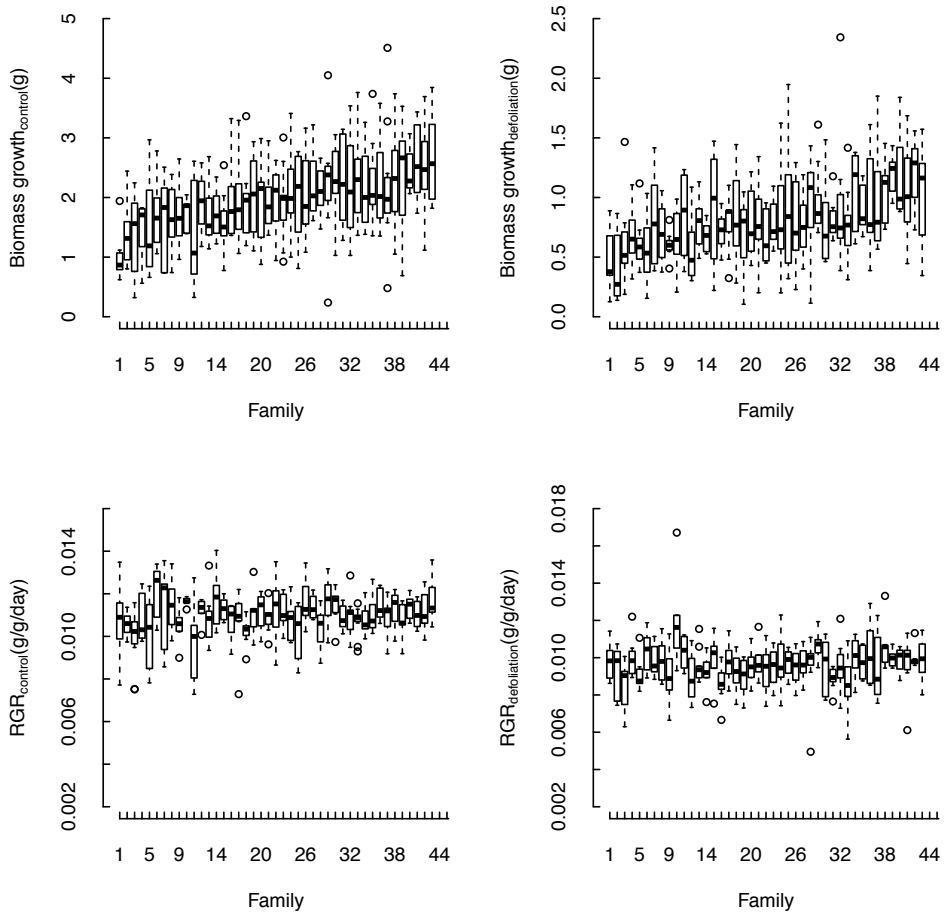
$$y_{ijk} = \mu + T_j + s_k + F_i + F \times T_{ij} + e_{ijk} \qquad\qquad \text{eqn 4.4a}$$

with

$$F_i \sim N(0,\sigma_F^2), \; FxT_{ij} \sim N(0,\sigma_{FxT}^2) \text{ and } e_{ijk} \sim N(0,\sigma_j^2) \qquad\qquad \text{eqn 4.4b}$$

Mixed effect models were analyzed in Genstat (VSN International 2011), all other analyses were performed in R (R Development Core Team 2014).

# Results



**Figure 4.1**. Boxplots of biomass growth and RGR for control and defoliated seedlings of 47 families of *Chamaedorea elegans* from a Mexican forest. Families are ordered based on mean biomass growth. The changing rank of families between treatments is a first indication that families that grow relatively fast without the stress of leaf loss, do not necessarily grow relatively fast when they suffer leaf loss. The changes in rank between biomass growth rate and RGR indicate that families that grew fast in absolute terms, didn't necessarily grew fast in relative terms.

*Genetic variation in  growth parameters*

We found large variation between different families in biomass growth and RGR (Fig. 4.1). We determined within and between family variance components for biomass growth rate, RGR, and the growth parameters NAR, biomass allocation ($f_{lam}$), and SLA change ($\gamma$) that were estimated by the iterative growth model (Table 4.1). Based on the estimated variance components, we estimated narrow-sense heritability of growth rate to be relatively large for non-defoliated plants, and only slightly lower for plants that were subjected to the defoliation treatment ($h^2$ values for biomass growth and RGR ranged from 0.41 to 0.46 for control plants and from 0.32 to 0.35 for defoliated plants, Table 4.1). Surprisingly, estimations of heritability of the growth parameters NAR, $f_{lam}$, and $\gamma$, were much lower, especially for the control individuals (Table 4.1).

**Table 4.1**. Estimated within- and between-family variance components and narrow-sense heritability ($h^2$) for several growth parameters for a small (0.7ha) population of the understorey palm *Chamaedorea elegans*, for which seedlings were grown in a greenhouse and subjected to a defoliation treatment. Biomass growth (excluding leaf mass) was determined from direct measurements. The growth parameters RGR, NAR, $f_{lam}$ and $\gamma$ were estimated using an iterative growth model. All growth parameters were estimated for seedling growth between six and twelve months of age. Variance components were estimated from mixed-effect models with REML estimation.

| | **Control** | | | **Defoliation** | | |
|---|---|---|---|---|---|---|
| | $\sigma^2_{Family}$ | $\sigma^2$ | $h^2$ | $\sigma^2_{Family}$ | $\sigma^2$ | $h^2$ |
| *Biomass growth (g/6months)* | 0.0574 | 0.502 | 0.410 | 0.0103 | 0.109 | 0.347 |
| *RGR (g/g/day)* | 1.65E-07 | 1.26E-06 | 0.463 | 1.39E-07 | 1.58E-06 | 0.324 |
| *NAR* | 6.30E-18 | 5.49E-10 | 4.66E-08 | 5.45E-11 | 9.37E-10 | 0.220 |
| *$f_{lam}$* | 3.80E-12 | 3.77E-03 | 4.04E-09 | 2.92E-10 | 8.03E-03 | 1.44E-07 |
| *$\gamma$* | 0.000220 | 0.00618 | 0.138 | 0.000547 | 0.0127 | 0.165 |

Note: RGR = Relative growth rate; $f_{lam}$ = fraction of newly assimilated mass that is allocated to lamina growth; $\gamma$ = fraction in daily change in mean specific leaf area

*Genetic variation in tolerance, compensation, and compensatory traits*

We compared family mean control and defoliation treatment values of all growth parameters (Fig. 4.2). Family mean biomass growth rate was as expected, lower in the defoliation treatment for all families and for RGR in almost all families. However, all family mean values of NAR and biomass allocation, and almost all family mean values of SLA change, were higher in the defoliation treatment than in the control treatment. Therefore, all families clearly showed compensatory responses to leaf loss by increasing their NAR and SLA, and changing their biomass allocation.

We tested if families responded differently to defoliation, and therefore if there is genetic variation in  response to defoliation, with a mixed effect model in which we included the

random interaction between treatment and family. This model yielded only relatively small variance components for the interaction between treatment and family for all evaluated parameters (Table 4.2). This suggests that families do not respond differently to leaf loss in terms of biomass growth, RGR, NAR, allocation to leaf mass nor SLA changes. Therefore, even though families compensate strongly for leaf loss, we did not find evidence for strong within-population genetic variation in this response.

To estimate genetic variation in tolerance and compensation itself, we paired defoliation treatment individuals with control individuals from within the same family. By doing this, we were able to estimate tolerance and compensation per individual and could, therefore, estimate the heritability of these parameters. Even though we found large variation between family mean values of tolerance and compensation (*e.g.* family mean compensation in biomass growth ranged from 0.16 to 1.03, *i.e.*, 16 - ~100% of potential loss being mitigated), within-family variance was much larger, because of which estimations of heritability of tolerance and compensation were low (the highest estimated heritability was for compensation in biomass growth, which was only 0.01, Table 4.3).

**Table 4.2**. Estimated family, family*treatment and residual variance components for several growth parameters, estimated from a greenhouse experiment that was performed with seedlings for which the seeds came from a small (0.7ha) Mexican population of the understorey palm *Chamaedorea elegans*. Biomass growth was determined from direct measurements, the other parameters with an iterative growth model that takes into account the timing of leaf removal. Variance components were estimated using mixed effects models with REML estimation.

| | $\sigma^2_{Family}$ | $\sigma^2_{Family*Treatment}$ | $\sigma^2_{Control}$ | $\sigma^2_{Defoliation}$ |
|---|---|---|---|---|
| *Biomass growth (g/6months)* | 2.53 | -1.44 | 53.91 | 10.69 |
| *RGR (g/g/day)* | 0.00129 | 0.0002 | 0.0127 | 0.0159 |
| *NAR* | 0.00242 | -0.00199 | 0.0545 | 0.0983 |
| *$f_{lam}$* | 0.000168 | -0.00018 | 0.00378 | 0.00803 |
| *$\Gamma$* | 0.00043 | -0.00013 | 0.00613 | 0.0129 |

Note: RGR = Relative growth rate; $f_{lam}$ = fraction of newly assimilated mass that is allocated to lamina growth; $\gamma$ = fraction in daily change in mean specific leaf area ($\gamma$)
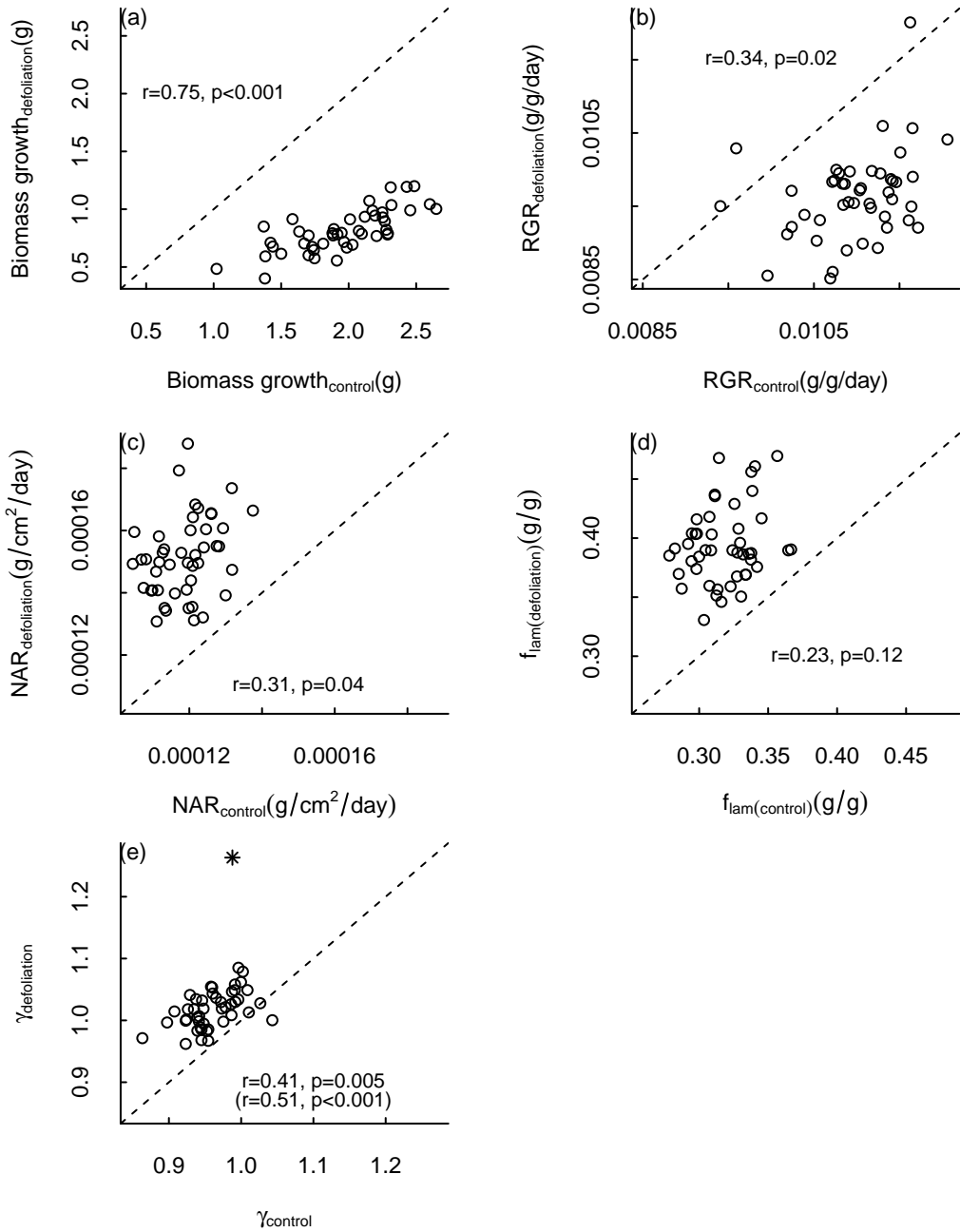
**Figure 4.2**. Comparison of control and defoliation treatment family means of several growth parameters for the understorey palm *Chamaedorea elegans*, determined from a greenhouse experiment with 731 seedlings of 42 half-sib families, for which the seeds were collected in a small population in Chiapas, Mexico. Biomass growth (above and below ground, without leaf mass) was determined from direct measurements. RGR, NAR, allocation of biomass to leaf tissue ($f_{lam}$) and changes in SLA ($\gamma$), were all estimated using an iterative growth model that takes time of leaf removal into account. The dashed line indicates the 1-to-1 line. Pearson correlation coefficients and associated p-values are shown. The asterisk in panel (e) is an outlying data point, correlation coefficient and p-value without this data point are shown in between brackets.

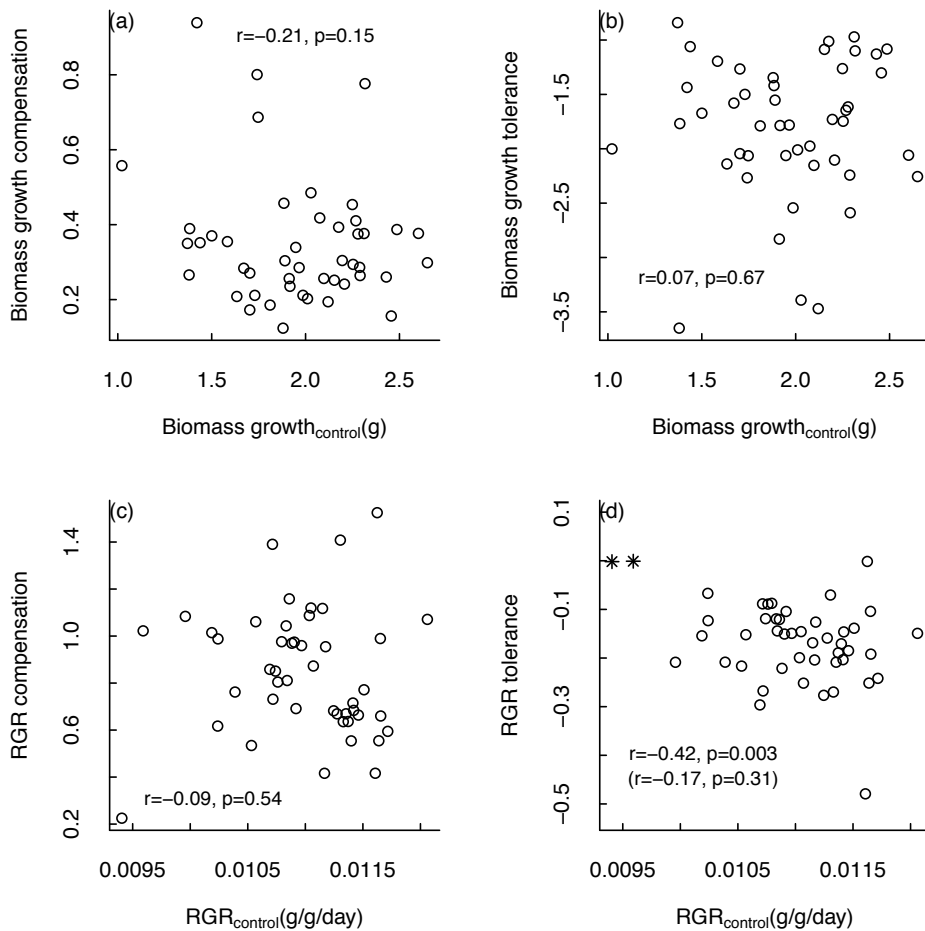*Relation between growth and tolerance*

Comparison of family mean values showed positive correlations between family mean control values and family mean defoliation treatment values for all growth parameters, indicating that growth performance is positively genetically correlated between treatments (Fig. 4.2). The correlation coefficient for biomass growth was highest (r=0.75), those of RGR, NAR and $\gamma$, lower but still significant (r=0.34, r=0.31, and r=0.41 respectively). Only the estimated positive correlation coefficient of $f_{lam}$ (r=0.23) was not significant. This suggests the existence of superior genotypes that grow fast while still being able to tolerate leaf loss.

Furthermore, it is possible that even though (to some extent) the same families grew fastest in both treatments, the relative reduction in growth rate might still have been larger for families that grew fast in the control treatment. If this was the case there would be a negative relation between tolerance or compensation (both relative measures) and growth rate in the control treatment. To test this we compared family mean values for tolerance and compensation, to family mean values of biomass growth rate and RGR in the control treatment (Fig. 4.3). This did not yield clear evidence for any positive or negative relation between tolerance/compensation and biomass growth/RGR. The only significant correlation that we found was between tolerance and RGR, but this relation was heavily pulled by two outlying data points, without these two points there was no longer a significant correlation. Therefore we did not find evidence that would suggest costs to tolerance in terms of growth.

**Table 4.3.** Estimated within and between family variance components and heritability of tolerance to, and compensation after repeated defoliation events in a greenhouse experiment, performed with 731 seedlings of 42 half-sib families for the understorey palm *Chamaedorea elegans*. To be able to estimate tolerance and compensation, individuals from the defoliation treatment were coupled to individuals from the control treatment based on their estimated biomass at the start of the experiment. Compensation was calculated by using an iterative growth model that allowed estimation of a hypothetical non-compensating individual.

| | Tolerance | | | Compensation | | |
|---|---|---|---|---|---|---|
| | $\sigma^2_{Family}$ | $\sigma^2$ | $h^2$ | $\sigma^2_{Family}$ | $\sigma^2$ | $h^2$ |
| *Biomass growth (g/6months)* | 0.00636 | 2.796 | 0.00908 | 0.000559 | 0.1820 | 0.0122 |
| *RGR (g/g/day)* | 1.53E-10 | 6.18E-02 | 9.90E-09 | 1.76E-09 | 5.23E-01 | 1.35E-08 |

Note: RGR = Relative growth rate

**Figure 4.3**. Comparison between family mean compensation (a,c), tolerance (b,d) and family mean growth rate. Data were obtained in a greenhouse experiment with 731 seedlings from 47 half-sib families of the understorey palm *Chamaedorea elegans,* in which a defoliation treatment was applied. Seeds for this experiment were collected in a small natural Mexican population. Compensation, RGR tolerance and RGR were estimated with an iterative growth model that takes into account timing of leaf removal. This model was also used to estimate RGR and biomass growth of a hypothetical non-compensating plant. This measure was used to calculate compensation. For the calculation of compensation and tolerance, defoliation treatment individuals were paired with control individuals from within the same family based on size at the start of the experiment. Pearson correlation coefficients and associated p-values are provided. The asterisks in panel d are two outlying data points; Pearson correlation coefficient and p-value without these data points are shown in between brackets.

## Discussion

This study showed that genetic variation in tolerance and compensatory responses to leaf loss is limited within a population of a long-lived tropical forest species. We also showed that genetic variation in growth potential was much larger than values usually detected for small populations. These results suggest that this population might have limited ability to adapt in terms of tolerance to environmental changes that entail leaf loss but does have the ability to adapt to environments that require different growth rates. Furthermore, this is one of the first studies that has analyzed genetic variation in compensatory growth responses to leaf loss.

*Heritability of growth potential*

We found large within-population genetic variation in growth rate, with estimations of narrow-sense heritability ranging from 0.32 to 0.46. These estimations are higher than the estimations from the few other studies that have been performed with long-lived plant species. For example, (Bonal *et al.* 2010) estimated for the shade tolerant rainforest tree *Sextonia rubra* heritability for several growth-related traits ranging from 0.23 to 0.28, and (Stevens, Waller & Lindroth 2007) estimated values between 0.20 and 0.37 for *Populus tremuloides*. The values that we found are especially high considering that the seeds used in this experiment were collected in a very small area (0.7 ha). Furthermore, the high genetic variation that we found is somewhat surprising because inbreeding in C*hamaedorea* species has been estimated to be high in several other Mexican *C. elegans* populations (Cibrián-Jaramillo, Hahn & Desalle 2008). This suggests that genetic variation in growth might be higher in understorey palms than in trees, but further research on multiple populations and species is necessary to determine this.

*Compensatory responses and heritability of tolerance*

We found individuals to compensate strongly for leaf loss, by increasing NAR, allocating more biomass to leaf mass, and by increasing SLA, which are similar responses that have been found in other studies (*e.g.* Anten, Martínez-Ramos & Ackerly 2003; Camargo, Tapia-López & Núñez-Farfán 2015)), including one that was also performed with *C. elegans* (albeit with adults, Anten, Martínez-Ramos & Ackerly 2003). Mean families values of compensation varied strongly (*e.g.* for biomass growth between 0.16 to 1.03, *i.e.*, the extent of compensation from about 1/8 to full compensation). However, we found only very limited evidence for genetic variation in compensatory responses and tolerance. Genetic variation in tolerance has been found for many different species (see *e.g.* Strauss & Agrawal 1999 for a review on this), but as Stevens, Waller & Lindroth (2007) point out, much less is known about the level of genetic variation in tolerance in long-lived species. A reason for this is that resistance (*e.g.* chemical defenses) rather than tolerance has long been seen as a more effective measure for long-lived species to persist under the pressure of herbivory, due to their different life-histories (Haukioja & Koricheva 2000). However, as explained in (Haukioja & Koricheva 2000), tolerance could be just as important for long-lived species, partly because herbivore attacks can never be completely avoided, and often leaf loss is due to physical damage and not herbivory. Tolerance could be particularly well developed in understorey species because

shade tolerance is often associated with storage of reserves that allow recovery after damage (Kobe 1997) and because understory plants are subjected to falling canopy elements like branches. Studies that have been performed were all on tree species (in which part of the studies detected genetic variation in tolerance, *e.g.* Stevens, Waller & Lindroth 2007, while others did not, *e.g.* Axelsson & Hjältén 2012). To our knowledge, genetic variation in tolerance and compensatory responses have not been studied in natural populations of other types of long-lived plant species like lianas, ferns or palms.

*Relation between growth and tolerance*

We did not detect a genetic correlation between growth and tolerance or compensation, even though it has been shown that a negative relation exists at least on the between ecotype level (Camargo, Tapia-López & Núñez-Farfán 2015). Therefore the strong differences in growth that we detected between families cannot be explained by a trade-off with compensatory growth capacity. We thus found that 'super-performing' families that grew relatively fast under undisturbed conditions also grew fast when exposed to leaf loss. These type of superior genotypes could play a key role in population resistance (in terms of growth rate) when the population is being disturbed by for example a storm (and associated increase in trees and debris) or a herbivore attack. Fast growers have been shown to be disproportionately important for population growth (Zuidema, Brienen & During 2009; Jansen *et al.* 2012), our results suggest that this ranking is maintained under disturbance. However, this is not only influenced by response to disturbance in terms of growth but is also influenced by the ability to maintain seed production under stress. Therefore it would be very interesting to test if fast growing adult plants are better able to maintain seed production when they suffer leaf loss, especially because *C. elegans* individuals have been shown to be relatively intolerant to leaf loss in terms of reproduction (Anten, Martínez-Ramos & Ackerly 2003).

A trade-off with tolerance did not explain why genetic diversity for growth potential was high within the population that we studied. However, it is possible that there are other trade-offs with growth than the one with tolerance, for example, genotype x environment trade-offs (*i.e.* GxE interactions). Possibly, genotypes that grew fast in the environment of the greenhouse in this experiment are not the ones that would grow fast in other environments, that are for example nutrient poor. However, it is hard to estimate how likely this is, as GxE interactions have hardly been studied in long-lived plant species, in particular, those that occur in tropical forests.

*Implications*

The low genetic variation in compensatory responses and tolerance that we found, could have consequences for the adaptive potential of populations to environmental changes (Lande & Shannon 1996). If leaf loss in a population persistently increases due to *e.g.* an increase of disturbance frequencies (which is predicted in several climate change scenarios, Dale *et al.* 2001) or introduction of an invasive herbivore (Vitousek *et al.* 1996), populations with limited genetic variation in tolerance might not be able to adapt to this increased pressure on performance due to leaf loss. On the contrary, the high genetic variation that we estimated for

growth potential, might increase the adaptability of populations if pressure for light competition changes. This could, for example, happen if canopy dynamics change due to differences in storm frequencies, or because of the introduction of a new faster-growing understorey species. In this case, genotypes that allow high growth might be selected for.

This suggests that it is critical to obtain accurate information on genetic variation in quantitative traits present in populations in order to be able to evaluate what the effect of environmental change will be on populations (Lande & Shannon 1996). Especially information on genetic variation in traits that are directly linked to individual vital rates is essential to be able to link evolutionary and demographic processes (Vindenes & Langangen 2015). However, at this point, surprisingly little is known about this for tropical forest species. Therefore we strongly recommend more studies that evaluate the amount of within population genetic variation causing differences in vital rates, and what the consequences of this are for the adaptive potential of populations to changing environments.

Strong genetic variation in growth rate as we found in this study, can also have implications for management practices. The existence of superior individuals that grow faster while still being able to strongly compensate for leaf loss offers opportunities for *e.g.* selection. These individuals can be used when a species is commercialized, especially when this is for its leaves. In the case of *C. elegans,* leaves are harvested as a NTFP, and are increasingly being planted in secondary forests for enrichment or in intercropping systems with species that provide shade (Trauernicht & Ticktin 2005). This study shows that it might be beneficial to select seeds from individuals that have high growth rates, which can be easily identified for this species (Jansen *et al.* 2012). We believe that there are many more long-lived tropical forest species for which it could be valuable to explore this potential.

## Acknowledgements

## Supporting information

**Appendix S4.1** *Allometric model*
**Appendix S4.2** *Methods iterative growth model.*

**Appendix S4.1** *Allometric model*

To be able to relate non-destructive measurements of seedlings at six months of age to seedling biomass (per plant part) and leaf area, we constructed an allometric model based on regression results.

We destructively harvested 61 extra seedlings of six months of age from the same experimental conditions as the main experiment. We measured seedling stem length and diameter, of all leaves leaf width, lamina length, rachis length, rachis diameter, leaflet width, number of leaflets, and length of the unopened leaf. We also determined biomass per plant part, and leaf area, where we followed the same procedures as in the main experiment.

For each response variable, we analyzed a full model where all relevant explanatory variables and likely non-linear terms were included and selected from this the best using the dredge function of the MuMIn package in R (Barton 2015). We constructed separate models for leaf area, leaf mass, rachis mass, the mass of the unopened leaf, stem mass and root mass. The resulting statistical models are shown in the table below.

|  |  | Estimate | P | $R^2$ |
|---|---|---|---|---|
| *Leaf area* | Intercept | 0.491 | 0.663 | 0.957 |
|  | Leaf length$^2$ | 0.00748 | <0.001 |  |
|  | Rachis diameter$^2$ | 2.16 | <0.001 |  |
|  | Leaf width$^2$ | 6.66E-04 | <0.001 |  |
| *Leaf mass* | Intercept | 6.11E-03 | 0.0541 | 0.961 |
|  | Leaf length$^2$ | 2.83E-05 | <0.001 |  |
|  | Leaf width$^2$ | 3.23E-06 | <0.001 |  |
| *Rachis mass* | Intercept | 7.04E-03 | 0.11 | 0.914 |
|  | Rachis length | 3.73E-04 | <0.001 |  |
|  | Leaf length | -6.11E-04 | <0.001 |  |
|  | Leaf length$^2$ | 6.54E-06 | 0.00982 |  |
|  | Rachis diameter$^2$ | 2.88E-03 | <0.001 |  |
|  | Leaf width | -3.01E-04 | 0.0204 |  |
|  | Leaf width$^2$ | 2.21E-06 | 0.0238 |  |
| *Unopened leaf mass* | Intercept | 1.93E-03 | 0.406 | 0.922 |
|  | Unopened leaf length$^2$ | 1.03E-05 | <0.001 |  |
| *Stem mass* | Intercept | 5.33E-02 | 0.00622 | 0.973 |
|  | Stem diameter | -4.70E-02 | <0.001 |  |
|  | Stem length$^2$ | 2.61E-05 | <0.001 |  |
|  | Stem diameter$^2$ | 1.21E-02 | <0.001 |  |
| *Root mass* | Intercept | 7.70E-02 | 0.00109 | 0.972 |
|  | Stem length | -9.03E-03 | <0.001 |  |
|  | Stem length$^2$ | 1.88E-04 | <0.001 |  |
|  | Stem diamter$^2$ | 7.04E-03 | <0.001 |  |

**Appendix S4.2** *Methods iterative growth model.*

The input of the iterative growth model presented by (Anten & Ackerly 2001) is biomass, leaf mass, and leaf area at the beginning and end of the experiment, and leaf loss (mass and area, and time of removal) during the experiment. We, however, did not measure leaf loss directly but assumed this to be two third of existing leaf mass. To allow for this, we adjusted the (Anten & Ackerly 2001) model. Mathematically this model can be described in the following way. As in (Anten & Ackerly 2001), daily changes in total plant mass (W), leaf mass (L) and leaf area (A), from time=t to time=t+1 are:

$$W_{t+1} = W_t + G_t - W_{loss,t}$$ <div style="float:right">eqn S4.1a</div>

$$L_{t+1} = L_t + f_{lam} * G_t - L_{loss,t}$$ <div style="float:right">eqn S4.1b</div>

$$A_{t+1} = A_t + \gamma * SLA_t * f * G_t - A_{loss,t}$$ <div style="float:right">eqn S4.1c</div>

In which

$$G_t = A_t \times NAR$$ <div style="float:right">eqn S4.1d</div>

and $\gamma$ is the proportional difference between the specific leaf area (SLA) of newly produced leaves and the current mean SLA of the plant. We extended this model by describing the changes in plant weight and leaf area on days that defoliation occurs as:

$$W_{loss,t} = L_{loss,t} = \frac{2}{3}\left(L_t - \frac{1}{2}\sum_{i=0}^{t-1} L_{loss,i}\right)$$ <div style="float:right">eqn S4.2a</div>

$$A_{loss,t} = \frac{2}{3}\left(A_t - \frac{1}{2}\sum_{i=0}^{t-1} A_{loss,i}\right)$$ <div style="float:right">eqn S4.2b</div>

where i indicates the different days. The total loss up to time t-1 multiplied by ½ is remaining leaf area at time t-1. $L_t$ – remaining leaf area is newly produced leaf area. In this way we estimated daily NAR, $f_{lam}$ and $\gamma$ for each individual, using the R function nls, using the port algorithm and with realistic start values and boundaries provided (estimated from data and literature). We applied the extra restriction that the total leaf loss must equal estimated leaf loss from direct biomass measurements. Using the estimated values of NAR, f and $\gamma$, RGR was calculated per iteration step, and then averaged. NAR, f and $\gamma$ estimations were also averaged.

# Chapter 5

Towards smarter harvesting from natural populations by sparing the most important individuals in an exploited palm species

Merel Jansen, Niels P.R. Anten, Frans Bongers, Miguel Martínez-Ramos, Pieter A. Zuidema

## Abstract

1. Natural populations provide a wide range of products that are the main source of income for millions of people, making proper management essential. Within these populations, large individual differences in performance may exist, which can strongly shape population dynamics. This knowledge provides a large so far untouched potential for improved management practices.

2. We explored the potential of using individual heterogeneity to design smarter harvest schemes, by sparing individuals that contribute most to future productivity, using the understorey palm *Chamaedorea elegans. C. elegans* leaves are an important non-timber forest product, and long-term growth variability between individuals is apparent from differences in mean internode length.

3. We studied a population of 830 individuals, half of which was subjected to a 67% defoliation treatment for three years. We measured effects of defoliation on vital rates and leaf size – a trait that has direct commercial relevance. We constructed integral projection models in which vital rates depended on stem length, past growth rate, and defoliation. We evaluated transient population dynamics to quantify the development of the population and leaf harvest. We then virtually spared that part of the individuals that are most important for population growth or are not yielding leaves of marketable size.

4. Individuals varying in size or past growth rate responded similarly to leaf harvesting in terms of growth and reproduction. Defoliation-induced reduction in survival chance was smaller in large individuals compared to small ones. Harvest simulations showed that reductions in population size can be largely prevented by sparing the individuals that contribute most to population growth. This was however at the cost of a small reduction in cumulative leaf harvest over 20 years but ensures production in the period after that. Furthermore, we found that harvest of leaves of commercial size can increase by three-fold when sparing individuals with small leaves and therefore allowing these individuals to recover.

5. This study shows that there is a potential to create smarter harvesting systems for palm leaves by incorporating differences between individuals within exploited populations. Sparing those individuals that contribute most to future leaf production ensures the sustainability of harvesting practices while leaf yield can in some cases be increased. The methods presented are applicable to a wide variety of species, and could, therefore, contribute to improved management practices in general.

**Keywords**

*Chamaedorea*, forest management, harvest simulations, individual heterogeneity, Integral Projection Model, leaf harvesting, NTFP, sustainability

## Introduction

Natural systems provide a wide range of products and are the main source of income for many millions of people worldwide (Iqbal 1993). Examples of some of the most widely exploited products are fish and timber, but also other products like leaves (*e.g.* palm leaves for the construction of roofs) or fruits (*e.g.* açai berries) are exploited in many areas, and are being used as a source of food, construction material or for decoration. Ideally, harvesting is being controlled sustainably, *i.e.* the supply of the harvestable product is sustained over time. When exploitation is at a small scale or low intensity, extraction of the product does not necessarily have a large impact on the harvested population. However, in many cases products are being harvested at high intensities, which can negatively impact populations and even provoke (regional) species extinction, as has occurred with overexploitation of many fish species, large mammals for bush-meat, tropical hardwoods for timber, and understory palms for leaves of ornamental value (Hutchings & Reynolds 2004; Bridgewater *et al.* 2006; Morris 2010). Therefore responsible management of the populations is essential. Responsible management requires clear guidelines that can be used by managers and policy makers, on which levels of exploitation are sustainable (*i.e.* do not lead to a decline of the population and/or the harvestable product). To determine these levels, population models are often used. With these models, the effect of different management options is evaluated. These are for example harvest frequency and intensity (Ticktin 2004).

A common characteristic of most populations (including the managed ones), is that individuals within a population are not ecologically equivalent, some will persistently grow, or reproduce faster than others (Zuidema, Brienen & During 2009). Ecologists increasingly recognize that this individual heterogeneity strongly influences several population processes (*e.g.* Tuljapurkar, Steiner & Orzack 2009; Vindenes & Langangen 2015; Snyder *et al.* 2016), including population growth rate (Pfister & Stevens 2003), and mortality (Vaupel, Manton & Stallard 1979). However, studies that evaluate the effect of harvesting, which are the basis of management recommendations, are usually based on mean population attributes, ignoring the large inter-individual variation in performance within populations. Brienen & Zuidema (2007) showed that timber yield estimations can increase strongly when this individual heterogeneity is taken into account. By doing so, there is a great potential for improving harvest practices. Taking into account ecological differences among individuals, and the role this variation plays in population processes can be used to create smarter harvesting systems.

An option to create smarter harvest systems based on individual heterogeneity is to spare certain individuals. Which individuals to spare will depend on the different roles individuals play in population processes. There are three factors to be considered in this regard. First, some individuals are more important for population growth than others (Zuidema, Brienen & During 2009; Jansen *et al.* 2012). Therefore, it might be beneficial for future production to spare those individuals that grow fast and/or produce more offspring.

Second, individuals could also differ in the way they respond to harvesting. This is relevant in cases where not the whole individual is harvested, but only part of the individual (for example bark, leaf or resin harvesting). Harvesting from individuals that experience only small

reductions in their vital rates due to harvesting (*e.g.* because of a higher stock of reserves), will impair future yield less, than harvesting from individuals that respond strongly to this. However, when tolerance to harvesting is related to performance in undisturbed conditions (*e.g.*, a trade-off between fast growth and tolerance if tolerance is governed by investment in reserves, Kobe 1997; Myers & Kitajima 2007), both performance in undisturbed conditions and response to harvesting should be considered when deciding which individuals to spare.

A third factor that needs to be considered when sparing certain individuals are signs of stress that influence the production or quality of the harvestable product. For example, in *Chamaedorea ernesti-augustii*, an understorey palm of which the leaves are harvested, leaf size can be strongly influenced by the stress of leaf harvesting, making the new leaves so small that they are unmarketable (Hernández-Barrios, Anten & Martínez-Ramos 2015). In such cases, it might be beneficial to spare those individuals that show the clearest signs of stress and let them recover until their harvestable product has reached higher productivity or marketable quality again.

Here, we analyzed the potential of sparing certain individuals to promote population recovery and increase future yields. We did this for *Chamaedorea elegans*, a tropical rainforest understorey palm species. The leaves of *C. elegans* are an economically important NTFP, that are used in the floral industry in flower arrangements, and provide income to many people (Hodel 1992). Individuals within *C. elegans* populations have been shown to differ strongly in their contribution to population growth rate (Jansen *et al.* 2012), leaf size is strongly affected by leaf harvesting (Lopez-Toledo *et al.* 2012), which has negative economic consequences as small leaves have less or none commercial value (Sol-Sánchez *et al.* 2007).

Specifically, we answer the following questions:

- To what extent do small and large individuals, and fast- and slow-growing individuals differ in their response to leaf loss?
- What is the effect of sparing the most important individuals from harvesting on (1) population recovery and (2) future leaf yield?

We answered these questions by performing harvest simulations using integral projection modeling and transient population dynamics. This is one of the first studies to evaluate the effect of sparing individuals to increase yield and improve population recovery after harvesting.

## Methods

*Site and species*

Data were collected in the Montes Azules Biosphere Reserve in Chiapas, Mexico, close to the Chajul Biological Station (16˚06' N, 90˚56' W). The main vegetation type in this area is lowland tropical rainforest. Annual rainfall of about 3000 mm, with a distinctive dry season

(<100mm) from January to April and an average temperature of 25 $^{O}$C, characterize the climate in this locality (Martínez-Ramos et al. 2009).

*Chamaedorea elegans* is a dioecious understorey palm that naturally occurs in Mexico, Guatemala, and Belize. It is single stemmed, produces a single cluster of leaves and produces clear internodes. The leaves (also known as *Xate*) are extracted commercially from natural populations for use in the floral industry (mostly in the U.S. and Europe, Hodel 1992). Leaf collection is usually performed by local people (*xateros*) who sell the leaves to middlemen. *Xateros* may return once or twice a year to the same palm to harvest 30–100% of all standing leaves (Reining *et al.* 1992). Generally, larger leaves are more valuable and leaves smaller than 25cm are unmarketable (Sol-Sánchez *et al.* 2007).

*Plot setup and data collection*

A 0.7 ha plot was set up in October-November 2012 on a karstic range site, in an area with no history of leaf harvesting. All individuals within the plot with a stem length >10cm (830 individuals in total) were mapped and tagged, and their stem length, size (*i.e.* lamina length) of the newest fully opened leaf, length of new unopened leaf (when present), number of leaves, and the lengths of all internodes were measured. In consecutive censuses in November 2013, November 2014 and November 2015 the number of newly produced leaves, length of new unopened leaves and leaf size were again measured, and we also counted the number of fruits and number of scars present on infructescences for all individuals. In November 2014 the length of all newly produced internodes was measured.

To simulate leaf harvesting, we applied a two-third defoliation treatment in November 2012 to half of the (randomly selected) individuals in which two of every three leaves were removed (counting from below). When only two leaves were present, only the lower leaf was removed. The defoliation treatment was repeated two times per year during the three years of the study where each time two of every three newly produced leaves were removed.

*Statistical analysis*

All statistical relations described in this section were analyzed following the approach described in Zuur (2009, p90-92). First, a full regression model was constructed which included all possible explanatory variables and non-linear terms, if visual inspection of the data suggested non-linearity. Residual variance structure of the model (that was fitted using REML estimation) was inspected visually and heteroscedasticity was modeled if necessary. Then we refitted the model using ML estimation and used all-subset regression to select the best model based on lowest AIC, using the dredge function from the MuMIn package (Barton 2015). The selected model was refitted using REML. All analysis were performed in R (R Development Core Team 2014). For normally distributed response variables fixed effect models were fitted using the gls function from the nlme package (Pinheiro *et al.* 2014), and mixed-effect models using the lmer function from the lme4 package (Bates *et al.* 2014). For response variables with a binomial distribution, fixed-effect models were fitted using the glm function, and mixed-effect models with the glmer function of the lme4 package.

Quantifying past growth rate

Past growth rate was quantified for all individuals based on mean internode length. We corrected this measure for stem length effects by performing a regression analysis in which the relation between mean internode length and stem length and the square root of stem length was analyzed. The standardized residuals of this model were used in further analysis as a measure of past growth rate. Note that this measure does not reflect exact annual growth rate, because the annual production of leaves varied between individuals, and within individuals between years. However, because we do not know the complete annual leaf production history of the individuals, we chose not to take differences in leaf production into account.

We also analyzed the relation between annual changes in past growth rate, and stem length and past growth rate (where past growth rate was calculated as defined above). Change in past growth rate was quantified as the difference in past growth rate up to 2012 and up to 2014. We divided this by two, to estimate annual change, which we then related to stem length and past growth rate. The statistical results of the relation between mean internode length and stem length, and the relation between changes in past growth rate, and past growth and stem length, are provided in Table S5.1 of the supporting information.

Performance indicators & response to harvesting

Stem length growth was calculated by multiplying leaf production by the mean length of internodes that became visible between November 2012 and November 2014. In determining leaf production, we took the contribution of any unopened leaves into account. Leaf production was therefore calculated as the number of newly produced, fully opened leaves, plus the length of the unopened leaf divided by the length of the newest fully opened leaf, minus the length of leaf that was still unopened the year before divided by the length of fully opened leaf that was the newest the year before. To calculate the probability of reproduction, the presence of infructescences was used. Half of the individuals that were not reproductive in any of the census years (and for which we, therefore, could not determine the gender) were included in the analysis. Thus, we assumed an equal sex ratio among the non-reproductive individuals. Seed production was quantified as the number of fruits and fruit scars present (each fruit contains only one seed).

We analyzed the relations between all performance indicators (stem length growth, leaf production, leaf size, survival, probability of reproduction, seed production), and stem length, past growth rate, and defoliation effect. We included interactions between stem length and past growth rate, and defoliation treatment to test for a relation between these two parameters and response to defoliation treatment. Year and individual were included as random effects in these analyses. Defoliation treatment was included as a random slope to test for differences in response to defoliation between years, but only if it improved the full model (before selection of fixed effects) with δAIC >2.

The resulting function for probability of reproduction, however, predicted an unrealistically low probability of reproduction for the range of stem lengths and past growth rates in our study population. For this reason, we decided to use the mean of the three functions of

separate analysis per census year. The relation that resulted from this did predict the observed probability of reproduction with the observed stem lengths and past growth rates relatively well (fractions of female palms that were reproductive, for control and defoliation treatment palms, predicted by the statistical model, were 0.38 and 0.07 respectively, observed values were 0.34 and 0.04).

*Model construction*

Seedlings

To construct the model that we used to perform harvest simulations, information on seedling recruitment and growth was necessary. Our field study did not include seedling dynamics (*i.e.* individuals <10cm stem length). To parameterize the number of new seedlings per produced seed, and seedling start stem length distribution, we, therefore, obtained seedling dynamics data from a similar demographic study on *C. elegans* , performed in the same area, at <1 km distance (see Martínez-Ramos, Anten & Ackerly 2009 for details).

The size distribution of new seedlings was determined from the stem lengths of seedlings at the time they reached 10 cm stem length in the Martinez-Ramos study. We fitted an exponential distribution (using the fitdistr function in R) on the (seedling stem length [cm] – 10 [cm])  to determine the probability density function of stem lengths of new seedlings larger than 10cm. To determine the probability density function of past growth rates of new seedlings, we used the observed normal distribution and standard deviation of past growth rate (*i.e.* residual mean internode length) in our own study. Thus, we assumed no relation between stem length and past growth rate for new seedlings.

To determine how many new individuals would enter each year in our model per produced seed, we first calculated the average time it takes seedlings to reach the size of 10cm stem length, by dividing 10cm by the mean seedling growth rate of seedlings smaller than 10cm (using the Martinez-Ramos data). We then multiplied this by the average annual seedling survival probability (same data). This number represents the proportion of new seedlings that actually reach the size of 10cm. This number was multiplied by the available data of probability of a seed becoming a seedling, to determine the number of new seedlings (per seed) of 10cm stem length.

Recovery

Our simulations also included recovery of individuals after leaf harvesting. To this end, we estimated vital rates during recovery, where we gradually let vital rates return to control values. Recovery time was estimated based on results from Lopez-Toledo *et al.* (2012). In that study, *C. elegans* palms were allowed to recover after a two years of bi-annual defoliation; the same treatment as applied here. That study included one harvesting intensity corresponding to ours (two-third of the leaves). Lopez-Toledo *et al.* (2012) report recovery times per vital rate per gender, but here we used the average of male and female recovery time because we pooled male and female individuals in the analyses of vital rates . For vital rates that had not fully recovered after three years, we estimated additional recovery time based on

the visual trends reported by Lopez-Toledo *et al.* (2012). The recovery times that we estimated from the results reported by Lopez-Toledo *et al.* (2012) were two years for stem length growth, survival, and leaf production rate, three years for leaf length, and five years (estimated) for probability of reproduction.

Kernel construction

Based on the regression results, we constructed an Integral Projection Model (IPM), which are a kind of transition matrix model commonly used to simulate the dynamics of populations based on continuous functions of size-dependent survival, growth and fecundity rates (Easterling, Ellner & Dixon 2000; Ellner, Childs & Rees 2016). We based our model not on one state variable, as is commonly done, but on both size and past growth rate, and included both size and past growth rate transitions. By including past growth rate as a second state variable, performance differences between individuals persisted throughout the model. In the construction of this model, we followed methods described in (Ellner & Rees 2006). We also constructed separate matrices describing the probability density functions of leaf size, and leaf size * leaf production, per stem length x past growth rate category.

We used 200 stem length classes, 50 past growth rate classes, and 100 leaf size classes. Boundaries of the model were taken as maximum observed past growth rate, stem length, and leaf size, and minimum observed past growth rate and leaf size, and 10cm stem length (which was the criteria of minimum size with sampling). Probability of reproduction estimated by the statistical model was divided by two because we assume that half of our individuals are males.

We constructed separate transition kernels for control plants, defoliation treatment plants, and plants that were in recovery. In total we constructed four recovery matrices (because all vital rates were estimated to be fully recovered after five years).

*Harvest simulations*

Scenario selection

We analyzed several hypothetical scenarios involving different decisions that managers and harvesters can take about sparing individuals that are most important for future production. These decisions necessarily need to be based on palm characteristics that can be easily verified in the field. The visual indicators used here are internode length, stem length and leaf size. Choice of scenarios was based on two of the three factors that determine the importance of individuals for future yield: contribution to population growth, and signs of stress that lead to the production of unmarketable product. We did not include a scenario that was based on differences in response to harvesting because we found the differences in response to be only minimal (Fig. 5.2-5.4).

The first scenario we simulated was a business as usual scenario (BAU from now on), in which leaves were harvested from all individuals (no plants were spared). This is common

practice in *Xate* leaf harvesting (Reining *et al.* 1992; Sol-Sánchez *et al.* 2007), and served as a reference scenario for the simulations.

In the next scenarios, we spared those individuals that contribute most to population growth rate, based on stem length and past growth rate. To identify such individuals, we calculated the elasticity values of each stem length x past growth rate category in the control matrix. We calculated stable state distributions and elasticity values (following methods described in Ellner & Rees 2006), and we divided the elasticity values of each stem length x past growth rate category by their value in the stable state distribution. We thus obtained a per-capita estimate of the importance for population growth of each category of stem length x past growth rate. Based on this we ranked categories on individual importance for population growth, and decided to spare the top categories based on this rank. The top was taken to be a given percentage of the total individuals, based on the stable state distribution values. We analyzed a wide range of percentages (10, 20, 30, 40, 50, 60, 70, 80 and 90%), therefore sparing the top 10-90% of individuals, based on their elasticity values. To check if any effects were really due to selection based on importance for population growth rate, we also simulated scenarios where the same percentages of individuals were spared, but where the size and past growth rate categories were randomly sorted (*i.e.* not based on elasticity values).

In the last scenario we analyzed, all individuals with leaves smaller than 25cm were spared. Therefore, as soon as an individual is stressed and because of this produces small leaves, it is allowed to recover until it returns to producing leaves >25cm.

Simulations

Using the constructed IPM we performed harvest simulations in which we projected the yield of harvestable leaves over a period of 20 years. Twenty years was chosen as a time frame as *C. elegans* is a long-lived species, so a long period is necessary for demographic effects to take place, while 20 years is in our opinion an acceptable and realistic period to simulate implications for management. Simulation output are population size (number of individuals per hectare), number of harvested leaves, and the sizes of the harvested leaves. The model that we used for the simulations, is graphically explained in Fig. 5.1.

Because we simulated over a period of 20 years, we analyzed the transient dynamics of the population. Transient analyses were started with the observed counts of individuals per size and past growth rate category. We added an extra dimension to the state vector to be able to determine if categories were either spared (not harvested from at all), harvested from, or recovering from a previous harvest. In each time step individuals in categories that met the spare criteria either stayed in the control category (*i.e.* no leaf harvest), or moved to the (next) recovery category. Individuals in categories that did not meet the spare criteria, either stayed in or moved to the harvest category. We only had one harvest category because we did not find any significant differences in harvest effects between years (Fig. 5.2-5.5). To be able to analyze the scenario in which individuals are spared based on leaf size, we added an extra dimension to the state vector for leaf size. Leaf size distribution in each time step was based on stem length and past growth rate. From the simulated states in each time step, leaf

production and the sizes of produced leaves were determined, using the constructed matrices for leaf size and leaf production. R script of all simulations is available upon request.
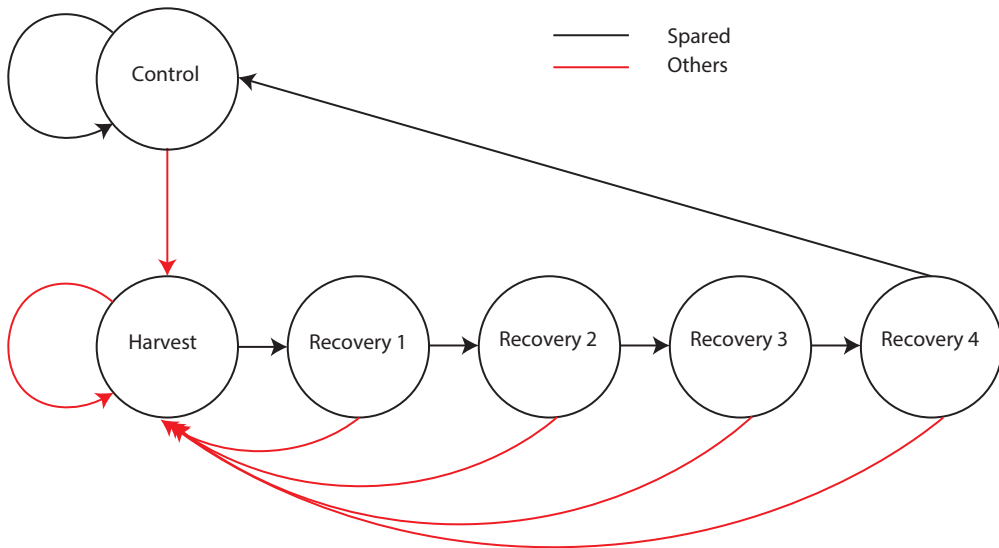


**Figure 5.1**. Schematic overview of the model structure used to simulate the effect of sparing certain individuals in harvesting practices. This model is based on six "status" classes (*i.e.* Control, Harvest, Recovery 1,2,3,4), and the states stem length, past growth rate and leaf size. States that meet the "spare" criteria, *i.e.* categories of not to harvest from, either recover (go to Recovery 1,2,3, or 4), or are already completely recovered and go to or stay in the Control status. States that do not meet the spare criteria either go to or stay in the Harvest status. Note that leaf harvest is based on the state that individuals that go to the harvest state move *from*. With this model it is possible to simulate if smarter harvesting by sparing certain individuals, can lead to higher yield and more sustainability in harvest practices.

## Results

*Vital rates and response to defoliation*

We related performance indicators (stem length growth, survival chance, probability of reproduction, seed production, leaf production and leaf size), to stem length, past growth, and defoliation treatment. Stem length appeared in the regression model with the lowest AIC for all tested response variables (Table S5.2 of the supporting information). Residual past growth rate appeared in these best models for all response variables except seed production and leaf production (Table S5.2). This indicates that both stem length and past growth rate are good indicators of individual performance.

We also tested if small and large, and fast and slow growing individuals responded differently to defoliation, because response to leaf harvesting is relevant for the contribution to future leaf production. We did this by including interaction terms between stem length and defoliation treatment, and past growth and defoliation treatment. The interaction between

defoliation treatment, and residual past growth rate, was not included in any of the best models (Table S5.2). This means that we found no evidence for differences in response to defoliation between fast and slow growing individuals. The interaction between defoliation treatment and stem length was only included in the best model of survival chance (Table S5.2). Therefore we found only very limited evidence for differences in response to defoliation between small and large individuals.

To test if the effects of leaf loss differed between years, we included a random interaction between year and defoliation treatment in the statistical models. The random interaction between year and defoliation was not significant for any of the vital rates, therefore, the effect of leaf harvesting did not increase significantly with repeated harvest (Table S5.2). All vital rate relations are shown in Fig. 5.2 (stem length growth, survival, probability of reproduction and seed production), and Fig. 5.3 (leaf production and leaf size).

In the harvest simulations where we spared individuals with leaves smaller than 25cm, about 80% of the individuals fell into this category and were thus spared. In Fig. 5.4 we compare results of these simulations to those of simulations of scenarios where a similar proportion of the population was spared, but then either based on their contribution to population growth (elasticity) or randomly selected. In Fig. 5.4, we also compare all three scenarios to a business as usual (BAU) scenario in which no individuals were spared.

Projected population growth rates and population sizes (Fig. 5.4a,b), were much higher than the BAU scenario in all three scenarios in which individuals were spared. The increase in population growth rate was clearly highest in the scenario in which the most important individuals were spared: after 20 years, projected population size was more than 11 times higher than the BAU scenario, compared to six times higher and five times higher in the scenarios where individuals were randomly spared, and individuals with leaves <25cm were spared respectively. The scenario in which the most important individuals were spared, was also the only scenario in which population growth rate was projected to be positive. This indicates that sparing the most important individuals could be a means to prevent large reductions in population size due to harvesting.

*Sparing a fixed proportion of individuals*

Compared to the BAU scenario, annual leaf harvest was slightly higher at the end of the simulation period for those scenarios in which individuals were spared randomly, or those with leaves < 25 cm were spared, and even 82% higher for the scenario in which the most important individuals were spared (Fig. 5.4c). However, in terms of cumulative leaf harvest over 20 years, harvest was much lower in all scenarios than in the BAU scenario (between 55 and 57 % lower, Fig. 5.4d). Therefore, the increase in population growth in the three scenarios in which individuals were spared, came at the cost of a smaller total leaf harvest over 20 years.
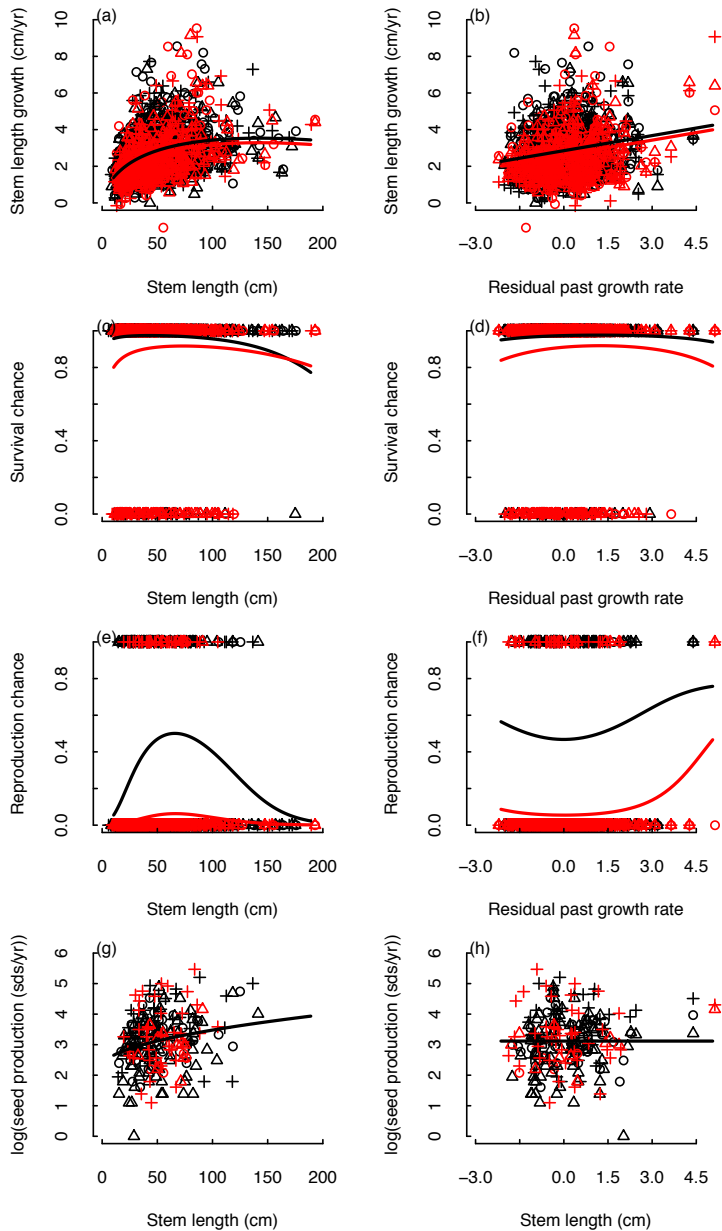
**Figure 5.2**. Relationships between the vital rates growth rate (a,b), survivorship probability (c,d), probability of reproduction (e,f) and seed production (g,h) with palm performance indicators (stem length and residual past growth rate) under non-defoliated (black lines and symbols) and defoliation (red lines and symbols) treatments. Lines are modeled relationships, of which the statistical results are provided in Table S2 of the supporting information. The different symbols represent different census years (plusses represent year 1, triangles year 2, and circles year 3). Absence of red lines in a panels g and h indicates that we did not detect a significant effect of the defoliation treatment on seed production of reproductive female palms.
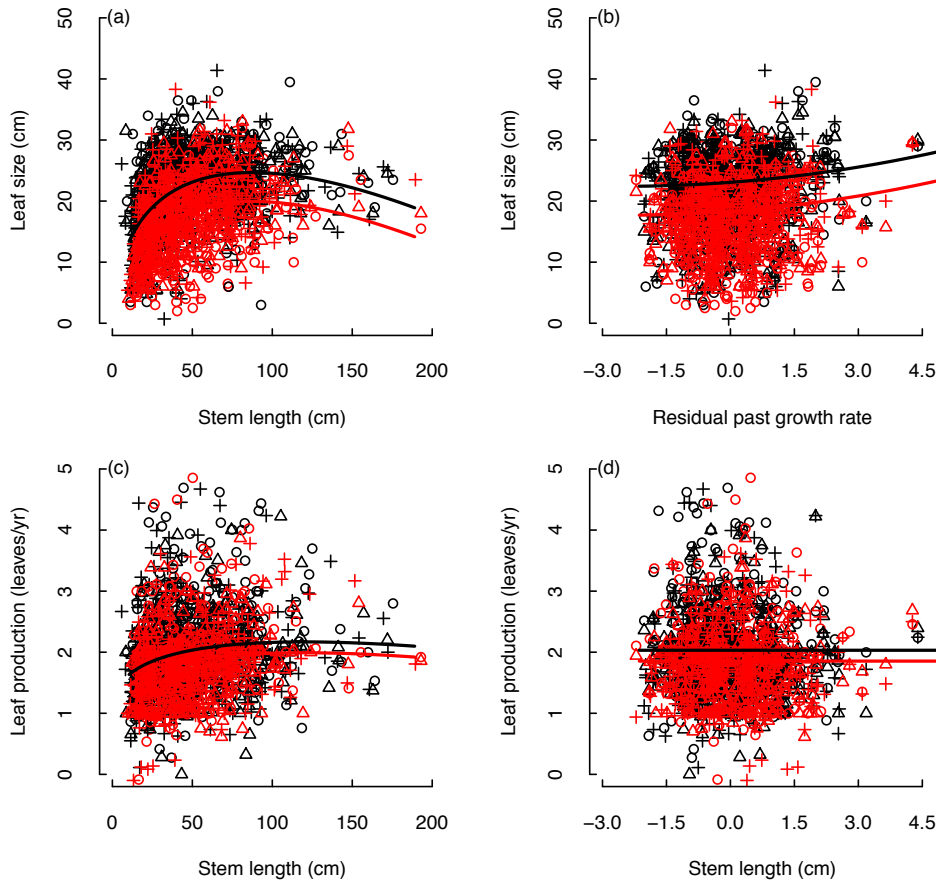
**Figure 5.3**. Relations between leaf size (a,b) and leaf production rate (c,d) with palm performance indicators (stem length and residual past growth rate), under non-defoliated (black lines and symbols) and defoliation (red lines and symbols) treatments. Lines are modeled relationships, of which the statistical results are provided in Table S5.2 of the supporting information. The different symbols represent different census years (plusses represent year 1, triangles year 2, and circles year 3).

When only considering the amount of leaves of commercial size (>25cm) that can be harvested, results changed importantly (Fig. 5.4e,f). In the scenarios where individuals were spared either based on their importance, or randomly, total leaf harvest after 20 years is still lower than in the BAU scenario (69 % and 35 % respectively). However, in the scenario where individuals with small leaves were spared (and were therefore allowed to recover), total leaf harvest increased by three-fold. This shows that sparing individuals with small leaves might be a very interesting scenario for managers and *xateros* as long as larger leaves have more value than smaller ones.

*Varying the proportions of spared individuals*

For the scenarios where either the most important individuals were spared, or individuals were randomly spared, we analyzed the full range of percentages of individuals to spare. In Fig. 5.5, we show the number of individuals, total leaf harvest over 20 years, and total leaf harvest of commercial leaves over 20 years. Values for the scenario where individuals were spared based on leaf size, are also shown in this figure.

Our simulations showed that one needs to spare at least 65% of the individuals that most strongly contribute to population growth in order for the population size to remain stable. When sparing a random sample of individuals, a much higher percentage of individuals (of 85%) needed to be spared for population size to remain stable.

Total number of harvested leaves over a period of 20 years, decreased when a percentage of individuals was spared, but this decrease was much slower than one would expect based on the percentage of individuals that was spared, and slowest when individuals were spared based on contribution to population growth. For example, when sparing 40% of the top contributing individuals, total leaf harvest over 20 years was only 8% lower than in the BAU scenario, while this reduction was 22% when sparing 40 % of the individuals randomly. This suggests that the reduction in leaf harvest due to sparing some individuals, is partly compensated by the higher growth, reproduction and survival chance of the spared individuals, and that this compensation is much stronger, when the most important individuals are spared.

When considering only leaves of commercial size, total leaf harvest over 20 years also decreased with an increasing part of the individuals being spared, but in this case the decrease was slower when individuals were randomly spared, then when the most important individuals were spared. For example, when 40 % of the individuals were spared, total leaf harvest of leaves of commercial size decreased with only 3 % compared to the BAU scenario when individuals were spared randomly, while sparing the 40 % most important individuals reduced harvest with 17 % compared to the BAU scenario. The larger reduction in the scenario where the most important individuals were spared is probably because the most important individuals are the ones that have the largest leaves. The position of the scenario in which individuals with leaves of non-commercial size are spared shows that, it is the only scenario that actually increases yield of leaves larger than 25 cm over a period of 20 years.
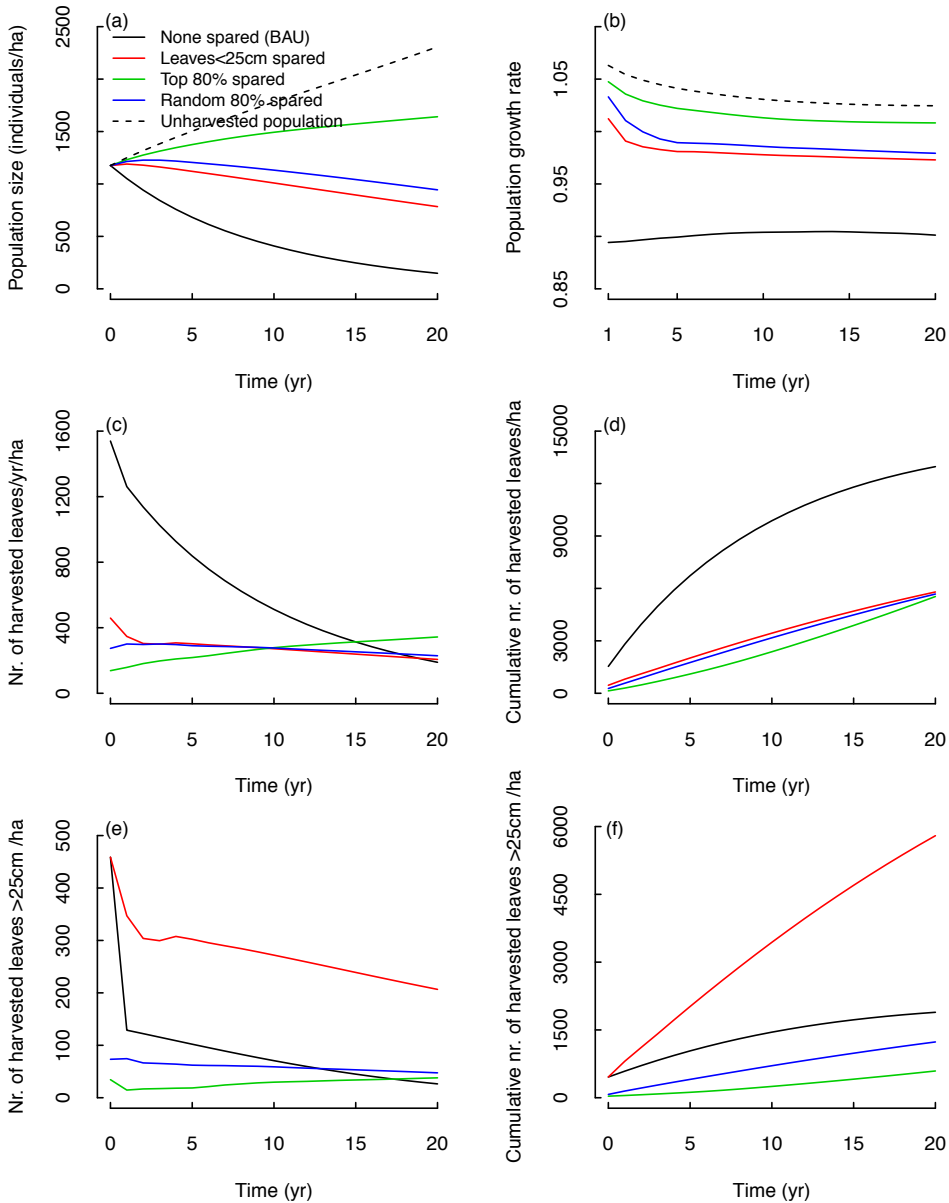
**Figure 5.4**. Simulated population size (a), transient population growth rate (b), number of harvested leaves (c), cumulative number of harvested leaves (d), number of harvested commercial leaves (e), and cumulative number of harvested commercial leaves (f) over time, for five harvest scenarios in which a proportion of individuals is spared from exploitation. The dashed line in panels a and b indicates the projected population growth rate and number of individuals for a control population where no leaf harvest takes place.

## Discussion

In this study, we showed that sustainability of palm leaf harvesting from a natural population can be improved by making use of inter-individual differences in demographic performance. We did this by performing harvest simulations in which we spared individuals that either were most important for population growth or that produced leaves of non-commercial size.

Although our study was performed for an understorey palm, the analytical and modeling methods here developed can be applied to any natural system from which either whole individuals, or parts of individuals, are harvested.

*Individual differences in response to leaf harvesting*

We hypothesized that fast growing individuals would respond differently to leaf harvesting than slow growing ones, because fast growth could come at the cost of lower investment in carbohydrate reserves. Our results, however, did not show any relationship between past growth rate and response to defoliation. Trade-offs between growth and storage of carbohydrates have been shown to exist at the inter-specific level (Kobe 1997), including species that grow in the forest understorey (Myers & Kitajima 2007). Furthermore, a growth-tolerance (to defoliation) trade-off has been found between ecotypes of the annual herb *Datura stramonium* (Camargo, Tapia-López & Núñez-Farfán 2015). However, we are not aware of studies that have documented this trade-off within populations, and this is a research area that demands further exploration. Because fast growing individuals of *Chamedorea elegans* responded similarly to defoliation compared to slow growers, these super-performing palms kept on performing well also under the stress of defoliation, which indicates no cost (*i.e.*, in terms of defoliation tolerance) of fast growth in our study system. Possibly, fast growers were even more tolerant than slow growers, as an equal absolute reduction means a relatively smaller reduction for fast-growing and more-reproducing individuals. Whether or not fast-growers are indeed more tolerant to leaf loss than slow growers, however, requires further study.
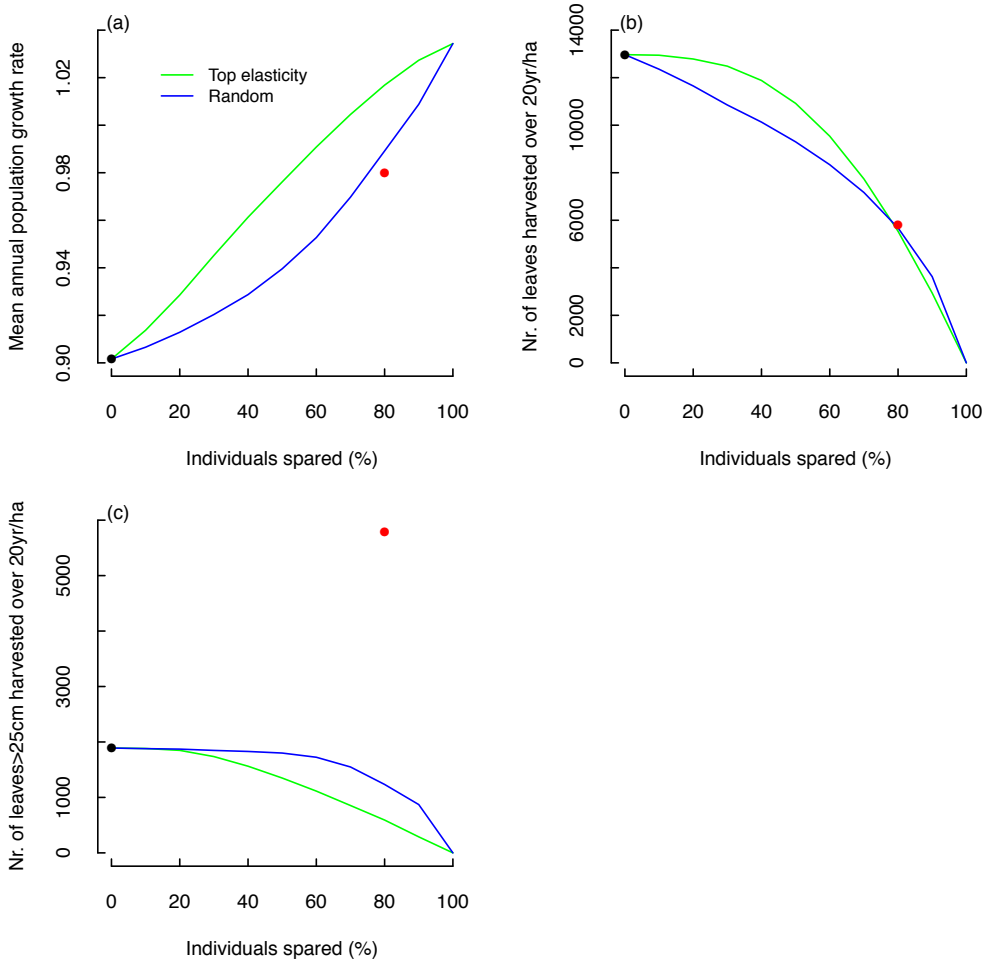
**Figure 5.5**. Simulated transient mean population growth rate (a) total number of harvested leaves (b) and total number of harvested leaves larger than 25cm (c) over a period of 20 years, for scenarios where the most important individuals (*i.e.* top elasticity) were spared, and scenarios where the characteristics of individuals to spare were determined randomly. The scenario where individuals with leaves smaller than 25cm were spared is indicated by the red point (red lines in Fig. 5.4). The black points indicate the position of a business as usual scenario in which no individuals were spared (black lines in Fig. 5.4).

*The potential of sparing the most important individuals in harvesting practices*

Several studies have shown that some individuals have greater importance than others for population dynamics. For example, Jansen *et al.* (2012, Chapter 2 of this thesis) found the 50% fastest growers to be almost two times as important for population growth as the 50% slowest growers, and similar differences in importance between fast and slow growers were found by (Zuidema, Brienen & During 2009). The current study shows that these differences can actually be used to develop smarter management practices when harvesting from natural

populations. Our simulated scenarios showed that sparing high-performing individuals might reduce the risk of extinction of populations under high levels of harvesting, without causing an important reduction in total amount of leaf harvest. Recognizing and making smart use of the extent of demographic differences among individuals can lead to such results. Condition is that the most important individuals are easily recognizable. In our system this is obviously the case because fast growers can be recognized by the length of their internodes.

It is well established that different life cycle stages contribute differently to population growth (de Kroon *et al.* 1986) and that this fact might be used to design sustainable management of biotic resources and conservation initiatives (Schemske *et al.* 1994; Silvertown, Franco & Menges 1996). However, there is an important difference between a life cycle stage and individual heterogeneity. Individual heterogeneity is about differences among individuals of the same life stage or even of the same size (*e.g.* two individuals of the same size can have very different growth rates). We show here that recognizing this individual heterogeneity within life stages (in this study by taking past growth rate into account) can also be beneficial in the management of populations.

When applying the methods presented in this paper to other populations, possibly other choices have to be made in how to select top contributors to population growth. In this study, we chose to determine such individuals based on elasticity values, because these can be fully used when only demographic data of an undisturbed population is available. Alternatively, individuals could be spared from the categories that most strongly influencing the decrease in population growth rate due to harvesting. This procedure is possible with LTRE analysis (Caswell 1989; Caswell 2001). An advantage of this approach is that individual differences in response to defoliation can be included in estimating which individuals best to spare.

*Sparing individuals with small leaves*

Sparing individuals with leaves of non-commercial size (leaves smaller than 25 cm,(Sol-Sánchez *et al.* 2007)) substantially increased the total harvest of leaves of commercial size, while only slightly reducing population growth rate. Over 20 years the total amount of harvested leaves of > 25 cm increased more than three-fold compared to standard (business as usual) harvesting practices, and total population size five-fold. Hernández-Barrios, Anten & Martínez-Ramos (2015) also showed that in *Chamaedorea ernesti-augustii,* it is more profitable to harvest less in order to have bigger, more valuable leaves, in the future.

For sustainability of *Chamaedorea* leaf harvesting practices, it is best to leave individuals with small leaves untouched. A clear market incentive that discourages harvest of small leaves (like a strong leaf size-price relation) could motivate harvesters to change their behavior. Although in some areas the price of *Chamaedorea* leaves is indeed determined by their size, this is not always the case (Sol-Sánchez *et al.* 2007). However, in some cases leaf harvesters are being paid per bunch of leaves, regardless of leaf size or other quality characteristics like damage. Leaf selection is then not made until late in the supply chain, leading to up to 70% of the harvested leaves being wasted (Sol-Sánchez *et al.* 2007). In such circumstances certification based on leaf size might be an option to discourage the harvest and

trade (at every part of the supply chain) of small leaves, which could increase the sustainability of *Chamaedorea* leaf harvesting practices.

*Towards smarter harvesting*

We explored the potential of sparing certain individuals in leaf harvesting practices in the understorey palm *C. elegans*, but the methods that we present here can be applied to a wide variety of other species subject to harvesting practices. The most obvious example is leaf harvesting in general. Many species are being exploited for their leaves of which many are palms [for example *Sabal yapa* (Martínez-Ballesté *et al.* 2005) and *Brahea aculeata* (Lopez-Toledo, Horn & Endress 2011)]. Sparing those individuals that are clearly stressed (individuals with small leaves in this study) will only be applicable to species where part of the individual is harvested and where this part-harvesting has a negative impact on vital rates. This could, for example, be the case in harvesting of resin or bark [for example the resin of *Boswellia papyrifera*, that is used for the production of perfumes and incenses (Groenendijk *et al.* 2012)]. Differentially harvesting based on elasticity analysis, however, can be applied to almost any natural population that is being exploited, although effects may take long to become visible in very-long-lived species like canopy trees. In animals, a similar procedure is already used in the management of game populations, where individuals are hunted based on their contribution to population dynamics (Milner, Nilsen & Andreassen 2007). However, to our knowledge this approach has not been applied to the management of plant populations. We therefore highly recommend further exploration of the potential of sparing certain individuals in the exploitation of natural plant populations.

In this study we explored the potential of differentially harvesting among individuals, but there are other measures that managers can take, which are currently more commonly considered. These are for example harvesting intensity, harvest frequency and seasonal timing (Ticktin 2004). For *Chamaedorea* species, the potential of a variety of these measured has been explored. For example, Hernández-Barrios *et al.* (2012) evaluated the effect of different leaf harvest intensities on vital rates of the three *Chamaedorea* species that are mainly used for leaf harvesting, Oyama & Mendoza (1990) in *Chamaedorea tepejilote*. Valverde, Hernandez-Apolinar & Mendoza-Amarom (2006) evaluated the effect of different annual frequencies of harvesting for *Chamaedorea elegans*, and Endress, Gorchov & Noble (2004) evaluated both intensity and frequency for *Chamaedorea radicalis*. Also in a variety other species the potential of these types of measures has been explored (Ticktin 2004).

So which of these management options is best? This will vary from product to product, and from case to case. Probably various management scenarios should be considered to come to optimal profit while ensuring sustained productivity. The contribution of this study is, that one more option *can* be considered. Using population models, the potential of the different types of management options can be explored. With these tools we can work towards smarter harvest systems, for *Chamaedorea* leaves and other products.

## Acknowledgements

## Supporting information

**Table S5.1** *Statistical results relations mean internode length and stem length, and changes in past growth rate.*

**Table S5.2** *Results regression analysis relating palm performance to stem length, past growth rate and defoliation treatment*

**Table S5.1** *Statistical results relations mean internode length and stem length, and changes in past growth rate.*

The standardized residuals of the upper model in the table below, are what is referred to as "past growth". Past growth change is the change and past growth between 2012 and 2014. Therefore between the standardized residuals of the first model in the table below, and the second model in this table. The heteroscedasticity of the residuals of the past growth change model was modeled as a power function (indicated in italic in the table below).

| | | Estimate | SE | P | $R^2$ |
|---|---|---|---|---|---|
| *Mean internode length (internodes up to 2012)* | Intercept | -1.52215 | 0.93561 | 0.104 | 0.506 |
| | Stem length | -0.11513 | 0.01924 | 3.22E-09 | |
| | √(Stem length) | 2.97524 | 0.27526 | < 2e-16 | |
| *Mean internode length (internodes up to 2014)* | Intercept | -1.9541 | 1.0675 | 0.0676 | 0.513 |
| | Stem length | -0.1215 | 0.0204 | 4.23E-09 | |
| | √(Stem length) | 3.0782 | 0.3019 | < 2e-16 | |
| *Past growth change* | Intercept | -0.1014987 | 0.0362873 | 0.0054 | AIC=-319.55 |
| | exp(Past growth) | -0.0046203 | 0.0015142 | 0.0024 | |
| | √(Past growth + 2.5) | 0.0504849 | 0.0241576 | 0.0373 | |
| | *Power of variance covariate. Stem length* | *-0.68268* | | | |

**Table S5.2** *Results regression analysis relating palm performance to stem length, past growth rate, and defoliation treatment*

| | Fixed effects | | | | Random effects | | |
|---|---|---|---|---|---|---|---|
| | | Estimate | SE | t-value | Variable | Variance | SD |
| Stem length growth (cm/yr) | Intercept | -0.537768 | 0.405818 | -1.325 | Individual | 0.72658 | 0.8524 |
| | Past growth | 0.274377 | 0.037067 | 7.402 | Year | 0.01538 | 0.124 |
| | Stem length | -0.028628 | 0.007761 | -3.689 | Residual | 0.48665 | 0.6976 |
| | Sqrt stem length | 0.682792 | 0.113988 | 5.99 | | | |
| | Defoliation | -0.24887 | 0.075092 | -3.314 | | | |
| Seed production (seeds/yr) | Intercept | 2.2595 | 0.3169 | 7.129 | Individual | 0.36787 | 0.6065 |
| | sqrt(Stem length) | 0.1218 | 0.0405 | 3.008 | Year | 0.04272 | 0.2067 |
| Leaf production (leaves/yr) | Intercept | 1.093954 | 0.206971 | 5.286 | Individual | 0.15082 | 0.3884 |
| | Stem length | -0.008965 | 0.003829 | -2.342 | Year | 0.01403 | 0.1184 |
| | sqrt(Stem length) | 0.19633 | 0.056036 | 3.504 | Residual | 0.24881 | 0.4988 |
| | Defoliation | -0.177865 | 0.037339 | -4.764 | | | |
| Leaf size (cm) | Intercept | -2.265 | 1.9437 | -1.165 | Individual | 21.449 | 4.6313 |
| | (Past growth + 2.5)^2 | 0.10411 | 0.03049 | 3.414 | Year | 0.447 | 0.6686 |
| | Stem length | -0.30011 | 0.03727 | -8.053 | Residual | 9.052 | 3.0087 |
| | sqrt(Stem length) | 5.61834 | 0.54377 | 10.332 | | | |
| | Defoliation | -4.73536 | 0.3697 | -12.809 | | | |

Logistic regression models

| | | Estimate | SE | p-value | Variable | Variance | SD |
|---|---|---|---|---|---|---|---|
| Survival probability | Intercept | 2.053991 | 0.894139 | 0.02161 | individual | 1.81E-09 | 4.25E-05 |
| | Past growth | 0.508146 | 0.253216 | 0.04477 | year | 1.13E-01 | 3.36E-01 |
| | (past growth + 2.5)^2 | -0.067981 | 0.040594 | 0.094 | | | |
| | Stem length | -0.046571 | 0.014457 | 0.00128 | | | |
| | sqrt(stemlength) | 0.610885 | 0.220573 | 0.00561 | | | |
| | Defoliation | -1.84015 | 0.334338 | 3.72E-08 | | | |
| | Stem length*Defoliation | 0.010871 | 0.005518 | 0.04882 | | | |
| Reproduction probability year 1 | Intercept | -8.77703 | 1.9227 | 5.00E-06 | | | |
| | Past growth | -0.66852 | 0.44692 | 0.134696 | | | |
| | (Past growth + 2.5)^2 | 0.13315 | 0.0712 | 0.061485 | | | |
| | Stem length | -0.12895 | 0.03669 | 0.000441 | | | |
| | sqrt(Stem length) | 2.05333 | 0.53137 | 0.000111 | | | |

| | | | | |
|---|---|---|---|---|
| | Defoliation | -2.92855 | 0.36496 | 1.02E-15 |
| *Reproduction probability year 2* | Intercept | -9.51172 | 2.12445 | 7.56E-06 |
| | stanres | -0.68413 | 0.47054 | 0.145967 |
| | (Past growth + 2.5)^2 | 0.13771 | 0.07546 | 0.068008 |
| | Stem length | -0.13123 | 0.03881 | 0.000721 |
| | sqrt(Stem length) | 2.17959 | 0.5743 | 0.000148 |
| | Defoliation | -2.79971 | 0.3724 | 5.56E-14 |
| *Reproduction chance year 3* | Intercept | -7.02196 | 2.44882 | 0.00414 |
| | Stem length | -0.09808 | 0.0465 | 0.03494 |
| | sqrt(Stem length) | 1.58444 | 0.68716 | 0.02112 |
| | Defoliation | -2.483 | 0.49038 | 4.12E-07 |
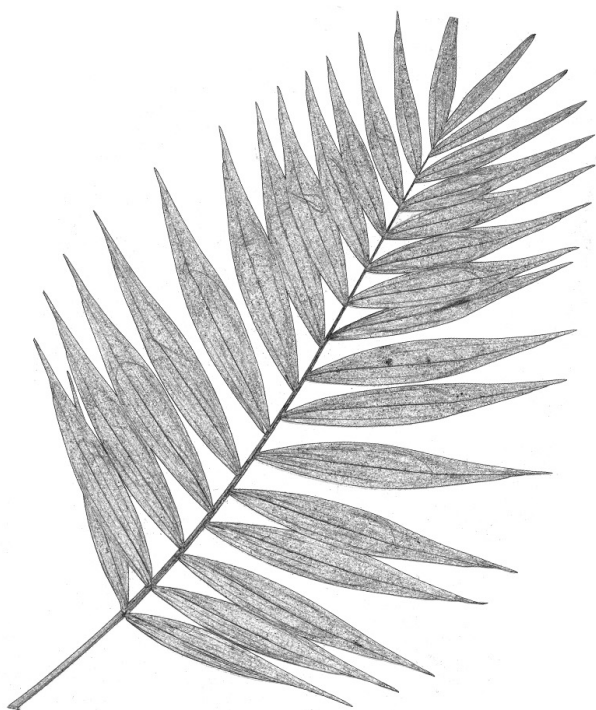
# Chapter 6

Synthesis and discussion

Merel Jansen

## Introduction

Do individuals belonging to the same species perform similarly? For many animal species (including humans) the answer to this question is clearly no. For example, an alpha male primate will almost certainly produce more offspring than an individual with a lower social status (*e.g.* Berard *et al.* 1993; Pusey, Williams & Goodall 1997; Jack & Fedigan 2006), and also in birds differences in reproduction can be large (*e.g.* Annett & Pierotti 1999; Steiner, Tuljapurkar & Orzack 2010). In general, such heterogeneity between individuals is well recognized and documented for animals (Clutton-Brock 1988). Also for plants, we know that individuals vary in their performance. For example, when measuring the growth rate of two individuals (either in a field or greenhouse experiment), it is highly unlikely that the two individuals will have the exact same growth rate.

Even though it has long been recognized that individuals clearly differ within plant species (Harper 1967), the ecological consequences of this are not always as well recognized as they are for animal species (*e.g.* who has ever heard of an alpha plant?). Possibly, individual heterogeneity is more persistent (*i.e.* the same individuals keep on performing better than others throughout time) in plants than in animals due to phenotypic plasticity and due to the sessile nature of plants (unlike most animals plants cannot move, entailing that their growth conditions can be more fixed).

Individual heterogeneity (both in animals and plants), likely influences demographic and evolutionary processes. For example, if individual heterogeneity is reflected in differential responses to stress, then it can contribute to the resilience of populations. Even though the importance of individual heterogeneity is increasingly recognized by ecologists (*e.g.* Zuidema, Brienen & During 2009; Steiner & Tuljapurkar 2012; Vindenes & Langangen 2015; Snyder *et al.* 2016), many of the consequences are still unclear, in particular in relation to the different aspects of individual heterogeneity.

In order to be able to properly quantify the demographic and evolutionary consequences of individual heterogeneity, it is important to know (i) the factors that drive these difference and (ii) the temporal and spatial pattern in which these factors take effect. In principle, these causes are either genetic (G), environmental (E) or a combination of the two (*i.e,* responses to environmental variation being genetically different, G*E interaction). Evidently, genetic differences tend to be permanent (save epigenetic effects) but can differ in their strength. Effects of different environmental factors (*e.g.* light, nutrients) differ in strength, space and in the degree to which they persist over time.

Individual heterogeneity is not just of interest in ecology and evolution; it may have important implications for the management and conservation of populations and species. Very fundamentally, in agriculture, the differences between individuals form the basis of plant and animal breeding. But in natural populations that are under exploitation (timber, fruits, leaves, meat), individual differences can also be used to increase harvest potential. Yet, in such systems, differences between individuals are usually not taken into account. Thus, the

potential of individual heterogeneity for ecologically sustainable exploitation has largely remained unexplored (Brienen & Zuidema 2007a).

In short, the most pressing issues with respect to individual heterogeneity are the persistence and long-term patterns of performance differences in long-lived species, the underlying causes of individual heterogeneity and its ecological, demographic and evolutionary consequences, and the potential to use individual heterogeneity to improve management practices of natural plant populations. In this thesis I addressed these issues, where the main questions were:

1. To what extent do individuals differ in performance? (Chapter 2,4)
2. What causes individual heterogeneity in performance? (Chapter 3,4)
3. What are the demographic and evolutionary consequences of individual heterogeneity? (Chapter 2,3)
4. Can individual heterogeneity be used to improve the management of populations? (Chapter 3,4,5)

To this end, I used the tropical forest understory palm *Chamaedorea elegans* as a model system. *C. elegans* naturally occurs on karstic outcrops in tropical rain forest in Mexico, Guatemala, and Belize. It is single-stemmed, produces a single cluster of leaves, grows up to a height of 1.5m and can live for several decades (*i.e.*, several plants > 40 years old were found in our area). *C. elegans* produces (like most other palm species) clear leaf scars on its trunk, from which growth histories can be reconstructed. This, and its small size make *C. elegans* an ideal system to study individual heterogeneity. Furthermore, the leaves of this species are an important Non-Timber Forest Product (NTFP), which are being used in the floral industry worldwide (Hodel 1992; Reining *et al.* 1992).

In this final chapter, I will synthesize the results of my thesis, and place these in a broader scientific framework. In so doing I will follow the structure of the four questions mentioned above and conclude with some methodological notes.

## 1. To what extent do individuals differ in their performance?

Throughout the chapters of this thesis, I have analyzed several aspects of individual heterogeneity in *C. elegans*. First of all, I have analyzed individual heterogeneity on different temporal scales. This scale ranges from short-term differences (*e.g.* in a given year some individuals grew faster than others) to differences over very long time spans close to the complete lifetime (*e.g.* individuals of 20 years old varied strongly in size). I have also analyzed the degree to which individual differences persist over time. So, do faster-growing individuals maintain their faster growth year after year? Short-term differences, long-term differences, and persistence are all strongly interrelated, and which measure is the best indicator of individual heterogeneity depends on the process of interest that it influences. For example, when considering the effect of individual heterogeneity on selection and evolution, life-long differences may be more relevant than short term differences. On the contrary, when

analyzing an ecological process like the establishment of an individual, short-term performance differences are more important.

In this section of this discussion, I give an overview of two different aspects of individual heterogeneity. The first relates to the time scale at which heterogeneity occurs and the second to the degree to which heterogeneity is persistent over time (Fig. 6.1). For each of these aspects I discuss the findings of this thesis, and how this relates to other studies.

*Short-term performance differences*

Individuals can differ in their current, short-term performance. Short-term is relative to the expected lifespan of a species. For example, short-term performance differences for long-lived species can be that in a given year some individuals grow faster, and/or reproduce more than others. This type of short-term variation in vital rates between individuals is present in almost all studies of natural systems (it is the cloud of points in a scatter plot of for example growth rates compared to a state variable like size or age, as in Fig. 2.2 in Chapter 2). In *C. elegans* we found short-term differences between individuals in growth rate (Chapter 2,3,4,5) and reproduction (Chapter 2,4,5) to be large. For example, in the first census year in chapter 3 and 5, the lowest measured growth rate was 0.08cm/yr, while the highest one was 7.29 cm/yr, an almost 100-fold difference.

Short-term differences between individuals are widespread among both plants and animals. For example, Greenberg (2000) found the annual production of acorns (averaged over a period of five years) to be zero for many individuals, while some produced almost 15000 acorns. Likewise, Broderick *et al.* (2003) documented up to a four-fold difference in number of eggs per clutch in green turtles. The existence if this type of individual heterogeneity has long been recognized (Harper 1967; Piñero, Martínez-Ramos & Sarukhan 1984; Sarukhán *et al.* 1984; Clutton-Brock 1988).

*Long-term performance differences*

Individual heterogeneity can also be measured over much longer time spans. So, a substantial part of the lifespan of an individual. Long-term differences between individuals will in many cases be a more relevant measure when considering for example fitness of an individual: which individuals contribute most to the future generation? In Chapters 2 and 3, we reconstructed lifetime growth histories from internodes (see the methodological note of this discussion for more details), and we found long-term difference in growth to be very large. For example, at age 20, there was a more than three-fold difference in plant size between the slowest and fastest growing individual (Fig. 3.1 in Chapter 3).

These findings are similar to those of studies on trees, where long-term growth differences were also large. For example, using tree ring analysis, Brienen & Zuidema (2006) found individuals of the same age to strongly vary in size, a result that was also suggested by modeling studies (*e.g.* Lieberman & Lieberman 1985; Martinez-Ramos & Alvarez-Buylla 1998). Long-term growth differences have also been documented for animal species (*e.g.*

Plard *et al.* 2015). Therefore it seems that long-term growth differences are wide-spread among both plants and animals.

In Chapter 3, we also estimated long-term differences in reproductive output based on short-term demographic data. Using regression analysis, I estimated annual probabilities of growth, survival, and reproduction based on stem length and environmental conditions. Based on these relations, I simulated possible individual reproduction trajectories over longer time spans. Using this approach I estimated long-term variance in reproductive output to be very large (at age 20 there was a more than ten-fold difference in cumulative reproductive output).

Long-term differences in reproductive output have been documented for several animal species [*e.g.* roe deer (Plard *et al.* 2012), fulmar (Orzack *et al.* 2011) and kittiwake (Steiner, Tuljapurkar & Orzack 2010)]. However, for long-lived plant species, there is surprisingly little information about long-term differences in reproductive output. I am not aware of any study up to now that documented long-term variation in reproductive output between individuals for long-lived plant species.

As short-term differences in reproduction in many long-lived plants are large, it is likely that, as I estimated in Chapter 3, this would result in at least some degree of long-term reproduction differences. More studies on the magnitude of long-term reproduction differences between individuals of long-lived plants would tell if this could be a general pattern.

*Persistence of performance differences*

An important aspect of individual heterogeneity is the extent to which short-term differences persist over time. In some cases, differences between individuals vary randomly over time. For example performance differences caused by genetic variation between individuals can be quite persistent, while the influence of something like falling branches on forest understory plants potentially only lasts for a very short time (*i.e*, it inflicts an instantaneous physical impact and causes a relatively short-lived increase in light). The causes of individual heterogeneity are discussed in more detail in section 2 of this discussion. In Chapter 3 I showed that random variation in short-term performance can already lead to large differences in long-term performance just by chance. In our study, this was slightly influenced by size dependence, but this process is still somewhat comparable to throwing a dice many times. Even though not large, there is a chance of many sixes occurring in a row. Likewise, it is possible to throw many ones just by chance. However, based on the growth histories that we reconstructed from internodes (Chapter 2 and 3), we know that growth differences in our study system are auto-correlated throughout most of the lifetime of individuals, and therefore very persistent. When we included persistence of short-term performance differences in the simulation of growth and reproduction trajectories, long-term performance differences became much larger, and simulations much better resembled the variance determined from the growth history reconstructions (Fig. 5.4 in Chapter 3).

Several other studies evaluated the effect of random variation in short-term performance on long-term performance differences. For example, Tuljapurkar, Steiner & Orzack (2009) could

explain observed variation in lifetime reproduction in mute swans with a completely neutral model. Plard *et al.* (2012) could explain long-term differences in several reproductive characteristics with a stochastic model, but not all, suggesting that more persistent differences play a role here as well. Furthermore, Pfister & Stevens (2002) showed that autocorrelation in performance can greatly increase long-term variation in growth rate between individuals. Together these results show that although some of the long-term individual heterogeneity that we observe may be due to random variation, at least some of it is due to more persistent differences between individuals.

The degree of persistence of performance differences can be influenced by size dependence. When performance is strongly size-dependent, a short-term advantage can lead to a large advantage over longer time spans (Pfister & Stevens 2002). Also, dependence on other states, like age or, in animals, social status, can have such effects (Vindenes & Langangen 2015). Size dependence may to some extent explain the large persistence of growth differences that I found from the growth history reconstruction from internodes (Chapter 2,3). However, in the simulations of growth histories, the persistence of growth differences was low with size dependence (Chapter 3), suggesting that the effect of size dependence on persistence and long-term individual heterogeneity was only small in my study system.

*Concluding remarks*

In many of the studies on individual heterogeneity, performance differences are considered to be either random or fixed. Not many studies specifically analyzed what the role of persistence in short-term performance is for long-term performance differences. Some studies implicitly include it as dynamic variation (*e.g.* through size or age dependence, Vindenes & Langangen 2015), but it is rarely included as an aspect on its own. However, as we argue in Chapter 3, in order to fully understand the origin and consequences of individual heterogeneity, one aspect of individual heterogeneity cannot be seen without the other. Short-term differences are necessary to generate long-term differences, but the extent to which short-term differences will lead to long-term differences will depend on the persistence of the short–term differences (see scheme Fig. 6.1). In the next sections of this discussion, I will explain in which way these different aspects are related to the causes and consequences of individual heterogeneity.

## 2. Causes of individual heterogeneity

To understand the evolutionary and demographic consequences of individual heterogeneity, it is important to know the causes of these differences. It is like the classic nature-nurture debate: do individuals differ because of differences in genotype, because of the environment that they experienced, or because of the interaction between the two? In this section, I will discuss the contribution of this thesis to this debate, where I will pay particular attention to the different forms of individual heterogeneity that are discussed in section 1 of this discussion. In Fig. 5.1 can be seen how this section relates to the previous section.
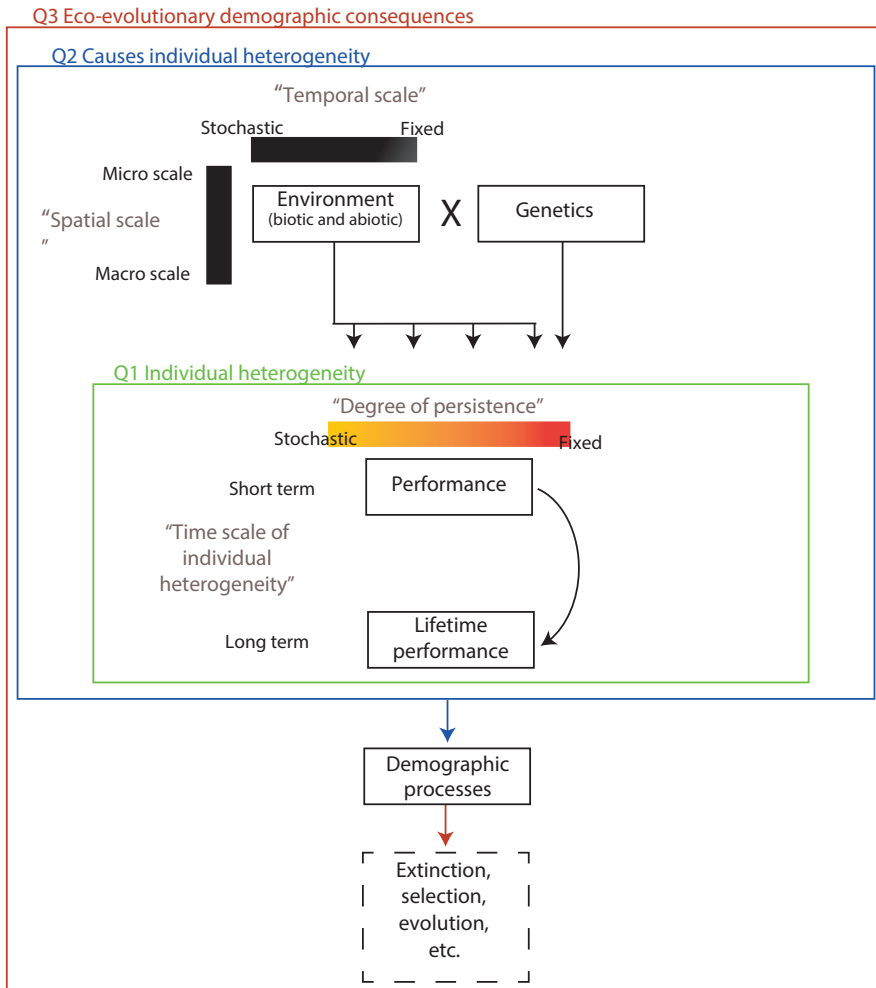
**Figure 6.1.** A schematic overview of the different aspects of individual heterogeneity as were dealt with in this thesis. Individual heterogeneity can vary on a temporal scale ranging from short-term performance differences to lifetime performance differences. The extent to which short-term performance differences lead to lifetime performance differences depends on the persistence of the short-term differences (Question 1). Question 2 addresses the causes of short-term performance differences, which are environmental variation, genetics, and the interaction between the two. The temporal heterogeneity in spatial environmental variation will determine the persistence of the performance differences, and therefore indirectly differences in lifetime performance. All these aspects together influence processes at the population level (*e.g.* extinction, selection, and evolution). Therefore, to understand such processes, individual heterogeneity, and the underlying causes have to be considered (Question 3). Management implications of individual heterogeneity (Question 4), are not included in this overview.

*Environment*

A large body of ecological research has been devoted to showing how environmental variation can cause short-term performance differences between individuals (*e.g.* Page, Bingham & Nelson 1972; Maschinski & Whitham 1989; Keeler & Holt 1990; Sydeman *et al.* 1991; Cahill & Casper 1999), and Chapter 3 fits this category. In Chapter 3, we related spatial variation in a wide range of environmental variables (light, leaf damage, and several soil characteristics) to short-term (*i.e.*, annual) differences in vital rates (growth, survival, reproduction) of *C. elegans*. We found light availability to be the main driver for most of these vital rates. This strong positive effect of light is not surprising for a species growing in the light limited understorey (Chazdon & Fetcher 1984; Chazdon 1986; Coomes & Grubb 1998). In any system that is characterized by strong spatial heterogeneity in environmental conditions [like the forest understorey, but also for example coral reefs (Connell 1978)], it can be expected that environmental variation importantly contributes to short-term performance differences.

But are the environmental factors that cause short-term variation the same factors that cause long-term variation between individuals? This is a question that most studies fail to address. In Chapter 3 we simulated the extent to which the observed relations between environment and short-term performance can lead to long-term performance differences. In these simulations, we specifically incorporated the effect of temporal persistence of environmental variation, for which we analyzed year-to-year changes in light and soil pH conditions. We showed that the contribution of an environmental factor to long-term performance differences is not only dependent on its contribution to short-term performance, but that this contribution strongly depends on the temporal persistence of the environmental factor in question. This means that an environmental factor that only has a weak effect on short-term performance, can still cause large long-term differences between individuals if the factor is very persistent over time. This could, for example, be the case for variation in soil texture, which is generally very persistent over time but may not always have a strong effect on short-term performance (see *e.g.* Russo *et al.* 2005 and Chapter 3), though of course in many environments it does have a strong effect. Likewise, a factor that causes strong short-term variation between individuals, but is highly variable over time [like light availability in the forest understorey, (Smith, Hogan & Idol 1992; Chazdon *et al.* 1996), or soil nutrient availability, which can in contrast to soil type be highly variable (Farley & Fitter 1999)], doesn't necessarily cause long-term differences between individuals. This result has important consequences for adaptation and selection, which will be dealt with further in section 3 of this discussion.

When studying the effect of environmental variation on individual performance, it is important to specify the spatial scale of this variation. In most of the literature on individual heterogeneity, environment is considered to vary over time but to be uniform across space [*i.e.* all individuals in a population are assumed to experience the same environment at the same time (Vindenes & Langangen 2015)]. However, Chapter 3 of this thesis shows that apart from the large-scale temporal fluctuation in environment (like temporal variation in rainfall, temperature, etc.), small-scale spatial variation in local environmental conditions, in combination with the temporal persistence of this variation, is a critical driver of both short-

and long-term individual heterogeneity. Spatial variation in light availability was an important driver of long-term performance differences, which was to a large extent due to the persistence of spatial differences in light levels over time. I, therefore, concluded that temporal persistence of spatial variation should not be excluded from studies on individual heterogeneity. Thus, the framework presented by Vindenes & Langangen (2015) needs to be expanded to include both the spatial and the temporal scale of environmental variation. This can relatively easily be done by including local environment as a dynamic trait . Transition probabilities of local environment can be included in the same manner as for other state variables like size. This is the framework that we used in Chapter 3, and a similar approach has been applied on canopy trees by Metcalf *et al.* (2009).

Of course, it is impossible to quantify the effect of all possible environmental factors that determine plant performance. However, in many cases, there are one or two environmental factors that are known to be the main drivers of performance differences [like light for canopy trees as in Metcalf *et al.* (2009), and light and soil pH in our system]. When this is the case, including these factors in population models could provide important insights into the origin of individual heterogeneity and lead to more realistic simulations of population dynamics.

There is one aspect of the relation between environmental variation and performance differences that I did not consider in this thesis: carry-over effects. Possibly, the effect of certain conditions on vital rates continues even though the condition that originally caused the effect already changed. For example, Lopez-Toledo *et al.* (2012) showed that leaf loss can cause reductions in vital rates until several years after the last defoliation event. Furthermore, Harrison *et al.* (2011) argue that in animals, carry-over effects between seasons of both macro and micro nutrient availability could be major determinants of observed variation in performance among individuals. Also from tree ring analysis, it is known that dry years can cause reduced growth rate in the subsequent year (Rozendaal & Zuidema 2011). It would be interesting to analyze if such carry-over effects (of for example light availability) also contributed to observed individual heterogeneity in our study system.

*Genetics*

To what extent can individual heterogeneity be explained by inherited characteristics of individuals? To determine this information is necessary about the extent of genetic variation in performance -related traits within populations. In Chapter 4 we analyzed within-population genetic variation for several growth parameters of young *C. elegans* seedlings. We collected seeds from all reproductive females in a small natural population in Mexico and analyzed within and between family variation in a greenhouse experiment. We found genetic variation of growth parameters to be high, and estimated narrow-sense heritability to be between 0.35 and 0.46 (depending on the growth parameter, and on the treatment, control or defoliation). This number is quite high considering that seeds were collected in an area of just 0.7 ha. This large genetic variation for growth potential in a small area suggests that there might be a genetic basis for strong individual heterogeneity observed in our study population.

Genetic variation in performance is something that has been analysed in numerous studies on short-lived crops (*e.g.* Strigens *et al.* 2012 showed heritability of growth parameters to be high in 285 dent inbred lines of maize), and to a somewhat lower extent in long-lived cultivated species (*e.g.* Clement 1995 found high heritability for growth parameters in in peach palm). Genetic variation in crop varieties, however, is strongly influenced by breeding practices and does therefore not provide much information about genetic variation within natural systems. In natural systems, genetic variation for quantitative traits has been quantified for a wide range of mostly short-lived species. For example, Poorter *et al.* (2005) estimated broad-sense heritability of relative growth rate to be 0.22 in $F_3$ offspring of two lines of *Hordeum spontaneum* from habitats with different productivity. These type of studies suggest that genetic variation in performance is large in short-lived species, and could, therefore, cause individual heterogeneity in performance. However, relatively less is known about the heritability of quantitative traits in natural populations of long-lived plant species. Most work has been done for particular temperate species [*e.g.* genetic variation in resistance and tolerance to herbivory in Aspen (*Populus tremuloides*) has been shown to be substantial (Stevens, Waller & Lindroth 2007)]. For natural populations of plant species in the tropics, information on genetic variation for quantitative traits is more scarce, but some studies exist. For example Bonal *et al.* (2010) estimated heritability of several growth-related traits in a population of the shade-tolerant rain forest tree *Sextonia rubra* to range from 0.23 to 0.28 (which is lower than what we estimated in our study system). Although the few studies on the quantitative genetics of long-lived tropical plant species that are available suggest genetic variation in performance is relatively large, more studies would help to clarify to what extent individual heterogeneity can be explained by inherited characteristics.

*Trade-offs and genotype x environment interactions*

Life history theory predicts that there exists a wide range of strategies that are viable for plant and animal species. These strategies – life histories – may differ strongly in lifespan, age at first reproduction, number of offspring and other important demographic characteristics (Stearns 1992). In many cases, different life-history strategies involve trade-offs, for example, the trade-off between size and quantity in the production of offspring (Stearns 1992), or a trade-off between maximum growth rate and the ability to defend against pathogens (Fine *et al.* 2006). These trade-offs are widespread between species (Salguero-Gómez *et al.* 2016), and have been studied extensively. For example, Muller-Landau (2010) could explain the maintenance of diversity in seed size between tree species due to the trade-off between tolerance to environmental stresses and fecundity. Similarly, a trade-off between maximum growth rate and mortality in the shade is common among tropical tree species (Wright *et al.* 2010).

For these trade-offs between species to have evolved, variation in life histories should also be present within populations (Whitehead & Crawford 2006). Within-population trade-offs may be important in explaining the maintenance of within-population genetic diversity (Bolnick *et al.* 2011), and were studied in Chapter 4. In that Chapter , we tested for genetic variation for a trade-off between growth and tolerance to defoliation, by applying a defoliation treatment to half of the seedlings in the greenhouse experiment that we mentioned above. We expected

that individuals from families that grow fast without the stress of leaf loss, would perform relatively less well under the stress of defoliation, due to less investment in stem reserves, a trade-off that has been shown to exist between species (*e.g.* Kobe 1997), and also within species (Camargo, Tapia-López & Núnez-Farfan 2015), although positive relations between tolerance and growth have also been found (McNutt *et al.* 2012). However, even though we found high genetic variation for growth rate, this variation was not related to response to defoliation. Genotypes that grew fast without stress, were generally still the fast growers when under the stress of defoliation. Therefore a trade-off between growth and tolerance could not explain the maintenance of high genetic variation for growth within the small population that we studied.

It is quite possible though, that there are other trade-offs that we did not test for, like the trade-off with performance in under certain environmental conditions and performance under different conditions (*i.e.* genotype x environment interactions). An example of such a GxE interaction in the supposed trade-off between shade and drought tolerance, the former requiring relatively more and the latter less shoot mass (Smith 1989). If strong GxE interactions exist in the population that we studied, then the genotypes that performed best in our greenhouse experiment are not necessarily the same genotypes that would perform best in a situation with different environmental conditions. These GxE interactions are very well studied for many cultivated plant species (*e.g.* Basford & Cooper 1998; Manrique & Hermann 2000), livestock species (*e.g.* Wallenbeck, Rydhmer & Lundeheim 2009), and for some fish species (*e.g.* Dupont-Nivet *et al.* 2008). Plant and animal breeders use this genetic variation to create new varieties that are adapted to different environmental conditions. Within species, these GxE interactions are also studied, but this often involves comparison of different populations to estimate the probability of *e.g.* invasion success of non-native populations (Colautti, Maron & Barrett 2009).

GxE interactions could explain the maintenance of within-population genetic variation for performance characteristics (Stearns 1992). In a relatively uniform, constant, environment (like the greenhouse in our experiment), only certain genotypes tend to perform well, which would lead to very persistent performance differences, and eventually the superior genotypes would outcompete the others. In a spatially heterogeneous environment however (but one that is stable over time), different genotypes would perform well, and the differences in performance would be very persistent. In this case maintenance of the genetic diversity is already possible if there are GxE interactions. In Chapter 3 of this thesis we show that environmental variation is very variable both on the temporal and spatial scale. In this case, different genotypes would perform best at different times, and the variation in performance between individuals due to genotype (in interaction with the environment) would only persist for a certain amount of time. Using a theoretical model, Gillespie & Turelli (1989) showed that GxE interactions can indeed maintain genetic diversity within populations. It would be interesting to extend this model by including the relation between the genetic diversity, through performance, with demographic processes. This topic is further discussed in the next section of this discussion.

## 3. The demographic and evolutionary consequences of individual heterogeneity

In the previous two sections, I explained that individual heterogeneity is large and widespread and generated by a combination of environmental and genetic factors. Individual heterogeneity also has consequences at higher levels of aggregation. Population dynamics and its effect on selection and evolution are influenced by individual heterogeneity. In this section, I will discuss what these consequences are, how these consequences depend on the underlying causes of individual heterogeneity, and how ecological processes, demography, selection and evolution are interlinked.

*Demography*

When studying demographic processes, in many cases population mean vital rates are used. This ignores differences between individuals and implicitly assumes the contributions of all individuals (at least those within a given age or size class) to population growth to be the same (Levin *et al.* 1997; Bolnick *et al.* 2011). In Chapter 2 I constructed a model in which the persistent performance differences between individuals were incorporated. Using this model, we showed that individuals are not equally important, but that certain keystone individuals exist that are much more important for the growth of the population than others: super-performing individuals (in this case the 50% fastest growing individuals) were almost two times more important than the 50% slowest growing individuals. The importance of such keystone individuals has also been shown for a tropical tree species (Zuidema, Brienen & During 2009).

But to what extent does individual heterogeneity influence population processes, *i.e.* in which cases are population mean vital rates not an adequate descriptor of population characteristics? I did not explicitly study this in this thesis, but as explained in Vindenes & Langangen (2015), studies have shown that demographic parameters as for example optimum flowering size (Rees 2000) and mortality (Vaupel, Manton & Stallard 1979) are not always well predicted by models based on population means. Furthermore, it has been shown that when short-term performance differences persist over time, and performance is size dependent, population growth rate is strongly influenced by individual heterogeneity (Pfister & Stevens 2003).

Individual heterogeneity could also play an important role in population responses to environmental change, for instance in determining their resistance to disturbances [*e.g.* storms, fire or disease (Harrison 1979)]. In Chapter 4 and 5 we studied the response of individuals to experimental defoliation, and tested if this was related to growth in an unstressed situation. In Chapter 4 we did this by applying a defoliation treatment to seedlings of different families in a greenhouse experiment. In Chapter 5 by applying a defoliation treatment to randomly selected individuals from a natural population. In both chapters we found no relation between growth rates under control conditions and responses to defoliation, *i.e.* fast growers keep on growing fast even under the stress of defoliation. This indicates that keystone individuals are disproportionately important in determining the ability of populations to resist defoliation events [for understorey palms *e.g.* due to falling canopy

debris after a storm, or due to an invasion of leaf cutter ants (Martínez-Ramos, Anten & Ackerly 2009)]. If however, the opposite would have been true, and different individuals perform best under stress than under favorable conditions, then under-performers in unstressed situations might be the ones that drive population resistance to disturbance.

Population resistance is just one example of an ecological process for which individual heterogeneity is relevant, but there are many others. For example, individual variation in infectiousness has been shown to strongly influence disease emergence (Lloyd-Smith *et al.* 2005), and individual variation in phenotype reduces extinction risk (Fox 2005). What is clear is that individual heterogeneity influences many ecological processes (Bolnick *et al.* 2011), and should therefore not be ignored.

*Selection and evolution*

To understand the role of individual heterogeneity in demography and evolution it is important to consider the causes of this heterogeneity. For example, the factors that most strongly determine differences in life performance of individuals, also determine which individuals contribute most to the future generation and thus where selection pressure will lie.

Furthermore, the temporal scale of individual heterogeneity at which the causes underlying individual heterogeneity work is important to consider when evaluating the demographic and evolutionary consequences of it. This is illustrated by the results of Chapter 3. As explained in the previous section, I show in Chapter 3 that for long-term performance differences, not only spatial heterogeneity in environmental conditions is important, but also the persistence of the environmental heterogeneity over time. Light was most important for short-term performance differences, so one might conclude based on this that better adaptation to light would mean outcompeting other individuals within the population and that there would thus be a selection pressure on adaptation to performance based on the use of light availability. In our study light was actually most important for long-term performance differences (and therefore for differences in life-output) as well, so this conclusion would have been plausible. Our simulations showed, however, that this does not always need to be the case. As explained in section 2, a factor with just a small effect on short-term performance would have been dismissed as unimportant for individual heterogeneity if the persistence of the factor had not been considered. However, we showed that such a factor could still importantly determine long-term performance differences if it persists over time. Therefore, when studying the environmental factors that drive individual heterogeneity , it is important to not only evaluate the environmental drivers of short-term performance differences (as is often the standard practice in ecological research) but to also determine the degree to which spatial variation in such environmental factors persists over time.

Individual heterogeneity is not only relevant for adaptation of individuals to small-scale variation in environmental conditions, but also to large-scale changes over time, like global climate change (Bolnick *et al.* 2011). If temperature and rainfall patterns change over time, it is possible that the genotypes that perform best in the current situation are not the ones that perform best in the future. In Chapter 4 we estimated genetic variation for tolerance to leaf

loss and compensatory growth responses to be low. This suggests that this population might have limited ability to adapt to changes in disturbance events that entail leaf loss. Furthermore, in section 2 I discussed that possibly genetic variation is maintained within populations due to the combinations of GxE interactions and small-scale variation in environmental conditions. If this is the case, the genotypes present in the population will be adapted to a variety of environmental conditions. If the environment changes on spatial scales that encompass the whole population (if for example annual rainfall increases in an area due to global warming), it is likely that some genotypes present within the population are already better adapted to these new wetter conditions. It is, therefore, likely that over generations, the genetic composition would shift towards more individuals that are better adapted to wetter conditions. This shift would mean that a larger part of the population would keep performing well, and therefore the population growth rate would be maintained. This example shows the importance of individual heterogeneity for the resilience of populations.

The importance of genetic variation and GxE interactions for the resistance, resilience, adaptability, and persistence of populations to changing environments has been studied to quite some extent. For example, Lande & Shannon (1996), have shown that genetic variation can be critical for the adaptation of populations to a changing environment. Fox (2005) and Schemske *et al.* (1994) recognize the importance of genetic variation for population persistence, and Lacy (1997) for population resilience.

The examples in this section show that the ecological processes that cause individual heterogeneity, demographic processes, and evolutionary processes, are all interlinked. In many studies, only one of these aspects is considered. But, as explained in Vindenes & Langangen (2015), Smallegange & Coulson (2013) and Coulson, Tuljapurkar & Childs (2010), many ecological, demographic and evolutionary processes (such as the response of populations to a changing environment) can only be analyzed well if all these aspects are combined. Therefore, in order to understand eco-evolutionary demographic processes, an integrated framework is necessary that combines environment, genetics, and population dynamics. Smallegange & Coulson (2013) and Vindenes & Langangen (2015) present such a framework. The more explicit incorporation of the temporal persistence of the environmental drivers of individual heterogeneity that I suggested, could, as explained in the previous section, very well be included in this.

## 4. Individual heterogeneity and the management of populations

In the previous three sections, I have made clear that individual heterogeneity is widespread, and has clear implications for demography, selection, and evolution. But differences between individuals could also be used to improve the management of natural populations. In this section of the discussion, I address what would be the potential of taking individual differences into account in the management of natural plant populations. I discuss several management aspects: enrichment & selection, harvest estimations and differentially

harvesting. I will conclude with a short discussion on the relation between science and practice.

*Selecting super-performing individuals*

Many forms of population management involve planting of individuals. The most obvious and extreme form in this respect are plantations and crop fields. But there are also intermediate forms in between plantations and natural populations, like agroforestry systems or enrichment planting in secondary- or primary forest (Putz *et al.* 2001). In all these cases a selection can be made of which individuals to plant, with the general goal of maximizing the desired properties. Selection is a very common practice in agriculture that has been practiced for thousands of years (Mazoyer & Roudart 2006) and is widely applied in forestry (Ceccon 1999). For many products that are currently mostly harvested from natural populations, first attempts of enrichment planting might resemble methods in very early agriculture. Studies like the one presented in Chapter 4 of this thesis, where genetic variation for certain characteristics within populations is analyzed, are a good starting point for selection practices. Another study that provides similar information, is for example Callister & Collins (2008), who estimated broad- and narrow sense heritability of several growth-related parameters in teak (*Tectona grandis*).

But is it enough to simply select seeds from the individuals that perform best in natural populations, or in a common garden experiment (like we did in Chapter 4)? Here I argue that there are several complications. As I discussed in section 2 of this discussion, genotypes that perform well in one environment do not necessarily perform well in another (*i.e.* there could be GxE interactions). If this is the case, then selection based on performance would only work if the new individuals are placed in a similar environment. However, what we showed in Chapter 2, is that within natural populations, environmental variation can be very large in both space and time, which would make it hard to determine which genotype to place where. Therefore, when planting in heterogeneous environments, it is probably best to maintain a large amount of genetic diversity to ensure that genotypes that are adapted to different environmental conditions are present. Generally, the importance of genetic variation in planting in natural environments is recognized (Namkoong *et al.* 1996).

But does this mean that when planting individuals in a plantation, where it is often much more easy to create relatively homogeneous environmental conditions, selecting for one genotype would be the best option? This is what has been done for many crops. In fact, the last decades of crop breeding have focussed almost exclusively on creating plant types that function optimally under homogenous highly controlled conditions (Machado 2009), and yields of most crops have concomitantly increased substantially, though this increase is slowing down (Long *et al.* 2006). However, it also creates systems that are highly vulnerable to disturbance and pests (Horrigan, Lawrence & Walker 2002) and require a lot of external input (Machado 2009). As explained in the third section of this discussion, systems are often much more resistant when genetically diverse (Fowler & Mooney 1990). Therefore, to create resilient systems, in any situation (whether it be enrichment planting or a plantation), it is

recommendable to maintain a sufficiently large degree of genetic variation, although a certain degree of selection might be possible.

Another aspect that is relevant, but possibly conflicting, when selecting individuals, is to determine which traits to select for. Traits that drive high production and a good quality product, are not always the same traits that generate the highest fitness. For example, in the case of *C. elegans*, large green leaves and high leaf production rate are not necessarily positively correlated with fitness measures in the habitat where the leaves are collected. When all these traits are positively genetically correlated, choices are easy, but in many cases, this will not be the case. How to tackle these kind of issues has been studied extensively for crops, and many selection methods are available (Bos & Caligari 2008). However, one should keep in mind that, in contrast to agricultural crops, when planting in natural populations (like in the case of enrichment planting), it is important that individuals are still competitive, and highest production is not always positively correlated with best competitive ability (Anten & Vermeulen 2016). When desired traits conflict with competitive performance, planted individuals might be quickly outcompeted by other species present (not many crops would perform well outside of an agricultural field). Therefore selection might work best for traits that do not influence fitness too much. In understorey palms, this could, for example, be the shape of the leaf.

In conclusion, when individual heterogeneity within populations has a genetic basis, selection could be valuable, and methods available from agriculture could be a great guidance on how best to approach this. However, the environmental heterogeneity of natural populations and the desired resilience of systems should always be kept in mind, to prevent problems with homogenization that occurred in classical crop selection.

*Harvest estimates*

As discussed in section 3 (and shown in Chapter 2), individual heterogeneity influences many population characteristics. This importance of individual heterogeneity for demographic processes is increasingly recognized by demographers but has so far rarely been taken into account in the management of populations. However, it is very likely that individual heterogeneity also influences the for management relevant characteristics like biomass production or extinction risk. This raises the question to what extent predictions on harvest and sustainability are influenced if one ignores individual heterogeneity. We did not specifically test this in this thesis, but Brienen & Zuidema (2007b) showed for a tropical forest selective logging system, that estimates of timber yield increased with 36-50% when persistent growth differences between individuals were taken into account. Also Free *et al.* (2014) argue in a study on mahogany (*Swietenia macrophylla*) that incorporation of individual variation and autocorrelation in growth rate into harvest models could help to improve management practices. I think that, in general, estimates of yield and sustainability of exploited natural populations could significantly improve by taking individual heterogeneity into account. I, therefore, recommend further studies that explore the influence of individual heterogeneity on for management relevant population characteristics.

*Smarter harvesting: sparing individuals*

In the previous paragraphs I explained that taking individual heterogeneity into account can improve harvest estimations, but possibly there is also potential to actually increase harvest by selecting which individuals to harvest and which individuals not to, based on individual differences.

In Chapter 2 we showed that some individuals are more important for population growth rate than others. In Chapter 5 we explored if leaf yield could be improved by explicitly sparing individuals with certain characteristics. To determine which individuals this could best be, we analysed which individuals are most important for the growth of the population, and simulated leaf yield in a business as usual scenario (when leaves are harvested from all individuals), and a scenario in which leaves are not harvested from those individuals that are most important for the growth of the population. We found that reductions in population size due to leaf harvesting can to a large extent be prevented by sparing the 40% most important individuals for population growth, with only a 8% reduction in total leaf yield. Furthermore, we showed that yield of leaves of commercial size can increase by three-fold if individuals with leaves of non-commercial size are spared.

Deciding from which individuals to harvest and from which not based on their contribution to population growth is something that has not often been applied in the management of plant populations, although some communities are known to apply this concept in the management of bromeliads (Ticktin, personal communication). In the management of animal populations, however, selective hunting is much more common practice (Milner, Nilsen & Andreassen 2007).

The idea and methods that we present in Chapter 5 are applicable to a wide range of species and products, in theory, to any natural population from which it is possible to harvest selectively per individual. This could, for example, be harvest of fish, meat, timber or any non-timber forest product where either the whole individual or a part of the individual are harvested, as long as harvesting has an effect on performance. Furthermore, differentially harvesting is a method that can be applied in combination with other population management tools. It is for example also possible to change harvest intensity, or harvest frequency [see Ticktin (2004) for a more complete overview]. Models can be a useful tool to analyze the potential of these different management options and a combination of them, for improving harvest practices.

*From science to practice*

How to get information from scientific papers to conservationist and practitioners in the field? As Laurance *et al.* (2012) point out, scientific papers are not necessarily the best means to do this, in many cases outreach using other means of communication are much better. In any case, it would require investment in good relations with government officials, NGOs, managers, and other stakeholders. Even though this takes time and effort, it could make the difference between a study that 'only' has an influence in the scientific arena and one that changes the actual management. A good example of this is work by Ticktin *et al.* (2002),

where active participation of local communities in a study that evaluated the effects of different harvest regimes for leaf and ramet harvesting of the bromeliad *Aechmea magdalenae*, lead local communities to switch to more sustainable harvest regimes and even to the implementation of a local law that protected remaining primary forest. Another study with clear impact is an evaluation of high logging intensities on Brazil nut production in Peru (Guariguata & Rockwell 2015; Rockwell *et al.* 2015), because of which Peruvian law now better protects Brazil nut trees against high logging intensities (Manuel Guariguata, personal communication).

My thesis is part of a larger, more than a decade long, research effort lead by Miguel Martínez-Ramos of the National Autonomous University of Mexico. This research effort aims to understand the ecology and management of *Chamaedorea* leaf harvesting practices. This already resulted in numerous scientific publications (*e.g.* Anten, Martínez-Ramos & Ackerly 2003; Martínez-Ramos, Anten & Ackerly 2009; Hernández-Barrios *et al.* 2012; Jansen *et al.* 2012; Lopez-Toledo *et al.* 2012; van Lent *et al.* 2014; Hernández-Barrios, Anten & Martínez-Ramos 2015). The large extent of information obtained so far can make a significant contribution to the improvement of harvesting management. The next step in this project, therefore, is to communicate the scientific findings to policy makers and harvest practitioners. The large number of people involved from the country where *Xate* is harvested from most, make that this research has large potential to make a difference outside of the scientific community if the results are communicated well to all stakeholders.

Furthermore, two-directional communication types will in many cases be beneficial. Firstly, communication with stakeholders like NGO's and governments could help to identify those research questions that are most important for conservation and management practices, and answering particularly those questions will have the largest impact (Laurance *et al.* 2012). Secondly, management plans can directly benefit from for example local knowledge: Ticktin & Johns (2002) actually quantified for *Achmea magdalenae* that higher yields and lower costs can be obtained by implementing traditional management practices into resource management plans. Construction of these type of management plans in collaboration with local populations would also be a very interesting next step in *Chamaedorea* leaf harvesting research. It would combine the extensive available scientific knowledge, with the experience of harvesters, and therefore has the potential to lead to management plans that are practical and realistic while making optimal use of the ecological properties of *Chamaedorea* palm populations. Furthermore, Mangel *et al.* (1996) argue that for effective conservation, interactive communication is essential. The general message from these studies is clear, for science of natural population management with societal impact, collaboration between scientist and all other stakeholders is essential.

## 5. Methodological notes

In the four questions of this discussion, I have made clear that individual heterogeneity is widespread among plants and animals, and that it can have important ecological,

demographic, and evolutionary consequences. But how can you measure individual heterogeneity? And how can individual heterogeneity be best included in models? Those are the questions that I will answer in this methodological part of the discussion.

*Measuring individual heterogeneity*

Short-term differences in performance can relatively easily be measured by standard measurement methods. This could, for example, be measuring performance of individuals in annual censuses, which is what we did in this thesis. Quantifying long-term performance differences, however, is not straightforward, because information over long time spans is necessary to determine this.

The ideal way to obtain information on long-term performance differences are long-term detailed studies that monitor individuals over long time spans or even the whole lifetime. For long-lived organisms, such studies tend to take a prohibitively large amount of time, money, and effort. Although not common, some studies have used this approach to quantify long-term performance differences in plant species. For example, Grogan & Matthew Landis (2009) showed autocorrelation in growth rate in bigleaf mahogany (*Swietenia macrophylla*) to be strong and persistent in a study that included a decade of annual censuses. Long-term studies are much more often used to quantify long-term performance differences in animals (*e.g.* Steiner, Tuljapurkar & Orzack 2010; Orzack *et al.* 2011). Furthermore, we are aware of several projects that have the potential to analyze long-term performance differences in plants, because they have been monitoring tree communities in some cases for up to decades. These are for example the Pasoh and Barro Colorado Island 50ha plots (see *e.g.* Condit *et al.* 1999), and several secondary forest plots in Mexico and elsewhere (*e.g.* Rozendaal 2016). Although several decades is not as long as the whole lifespan of a large tree, this data could still provide important insights into especially the persistence of performance differences. Up to now, however, this data has only rarely been used to analyze the extent to which long-lived individuals differ.

Some plants produce a record of their lifetime performance history (or at least a proxy thereof) providing the possibility to perform a retrospective reconstruction of these histories, giving information over longer time scales without having to perform long-term studies. The most common example of this is annual tree-ring formation in most temperate and some tropical trees (Groenendijk *et al.* 2014). Species that produce clear internodes are another example [such as palms (this thesis) and *Cecropia* spp. (Zalamea *et al.* 2008)]. The length of the internode is representative for the stem length growth in between the production of two leaves, and can, therefore, be used to reconstruct the stem length growth history of individuals. In this thesis, I used this approach, with which I was able to show that growth differences were long-term and persistent. A possible drawback of internode analysis, however, is that unlike the rings of most trees, internodes are usually not annual. Because of this, assumptions have to be made about annual leaf production when estimations of time are included in the growth history reconstruction. This is a clear limitation of the reconstruction of growth histories using internodes. However, growth history reconstruction from internodes does offer possibilities for many non-ring producing long-lived species to obtain information

about long-term growth differences, and this method has been successfully applied to several species [*e.g. Pourouma aspera* (King 1993) and *Cecropia sciadophylla* (Zalamea *et al.* 2008)].

Internode analysis and dendrochronology only provide information on long-term differences in growth rate, not reproduction. In this case, either long-term data is necessary, or a third option can be used, which is using a modeling approach (*e.g.* Tuljapurkar, Steiner & Orzack 2009). With modeling techniques, it is possible to estimate long-term differences based on short-term data. This is the approach that we used in Chapter 3. Based on annual estimations of growth, survival, and reproduction, we simulated individual reproduction trajectories, from which we estimated long-term differences in reproductive output. A disadvantage of such a modeling approach is that it can be hard to validate model predictions. In our case, however, we were able to validate model output by also estimating long-term differences in growth rate, and comparing these estimations to the estimations from internode reconstruction. In cases like this where a validation measure is available, models can be a useful tool to gain insights into the size of long-term differences in performance between individuals of long-lived species. Especially for trees this offers opportunities, as so far very little is known about individual heterogeneity in lifetime reproduction (Petit & Hampe 2006), and tree rings (which are present in many temperate and also tropical tree species (Groenendijk *et al.* 2014), are a great way to validate model output.

*The quantitative genetics of long-lived species*

Obtaining information on genetic variation for quantitative traits can be hard for long-lived species because they take a long time to complete a life cycle. In this thesis, we used a quantitative genetic approach to determine if individual heterogeneity is partly caused by heritable traits. This gave important insights into the heritability of several growth-related traits in a long-lived species. We were able to do this by using seedlings. There are however some drawbacks to this approach. Firstly, reproductive size was not reached, so we couldn't determine the extent of genetic variation for fecundity. Secondly, differences in demographic parameters like growth and reproduction can be driven by differences in functional traits like SLA and leaf nitrogen content (Poorter *et al.* 2008). However, in seedlings, genetic effects in these type of traits can be hard to separate from ontogenetic effects (see introduction Poorter & Pothmann 1992). Therefore, to obtain information on the heritability of fecundity and functional traits that are strongly influenced by ontogeny, for long-lived species, either very long term studies are necessary [which is commonly done for commercial fruit trees, see *e.g.* Noiton & Shelbourne (1992)], or studies that involve molecular techniques so that parents and offspring can be identified to search for genetic correlations between parents and offspring.

*Individual heterogeneity in population models*

A key element for successful analysis of the consequences of individual heterogeneity is how to include individual heterogeneity in population models. What the best approach in this is, depends on the persistence of the individual heterogeneity: are differences fixed, stochastic, or time varying?

When differences are stochastic, a good option is to use standard Integral Projections Models (IPMs, Easterling, Ellner & Dixon 2000). IPMs are an extension of matrix models, a type of model that has been used for much longer than IPMs in the analysis of population dynamics (Caswell 2001). Integral projection models are built from regression results of the relations between vital rates and state variables like size. The integral model is approximated by dividing the model into many small parts, which allows analysis of the model using common matrix algebra. An important difference with matrix models is that differences between individuals in the same state are included in IPMs. These differences are however not autocorrelated over time, but using IPMs to include individual heterogeneity is a good method when differences are stochastic. With such an IPM, it is possible to analyze what are the decisive events that make some individuals much more successful in life. Snyder *et al.* (2016) present methods for this.

In Chapters 2 and 3 I showed that in *Chamaedorea elegans*, growth differences persisted over many years. These differences were therefore not stochastic, but they were also not fixed (*i.e.* although autocorrelated variation varied throughout time. In this thesis, I used two different methods to incorporate such persistent individual heterogeneity in an IPM. In Chapter 2 I used a size x age population model, and I included differences between individuals by using the relation: past growth rate = stem length/age. I based this model on general methods for size x age IPMs (Ellner & Rees 2006). In Chapter 5 I chose for a different approach and included past performance as a separate state variable in the form of mean internode length (corrected for stem length dependence). Methods on how to include extra state variables are presented in Ellner & Rees (2006). Vindenes & Langangen (2015) also explain that extra state variables can be included in IPMs to incorporate time-varying (or dynamic) individual heterogeneity.

The reason that in this thesis I chose for different methods to incorporate time-varying individual heterogeneity, is that when basing past performance on internode reconstructions, assumptions have to be made about leaf production rates to determine past growth rate. In the first model, differences between individuals in leaf production were assumed to be constant, and in the second model differences in leaf production were not taken into account at all. Which of the two methods is best, is hard to tell, because, as we show in chapter 2, differences in leaf production are to some extent persistent, but not fixed, so the truth probably lies somewhere in between, but this truth is very hard to find.

In this thesis, I did not include fixed differences between individuals (which could, for example, have been genotype), but implementation is relatively easy. Methods for this can be found for example in Vindenes & Langangen (2015). In general, most type of analysis that can be performed with IPMs are explained in Ellner, Childs & Rees (2016).

Thus, how to include individual heterogeneity in population models depends on the type of heterogeneity, but for all types, IPMs offer the flexibility to include this. When interested in determining the decisive events that make individuals become successful in the long-term, the methods of Snyder *et al.* (2016), will probably have to be combined with other methods that allow time-varying and/or fixed differences between individuals, which as the authors

indicate, can probably be done easily. This could possibly be combined with the methods that I used in this thesis.

To conclude, I think that IPMs that specifically take into account all aspects of individual heterogeneity are a very useful tool to address many of the eco-evolutionary issues that are addressed in this thesis. I predict that in the coming years much more exciting research will be performed that uses these type of models, to integrate ecology, individual performance, demography, selection, evolution, and management.
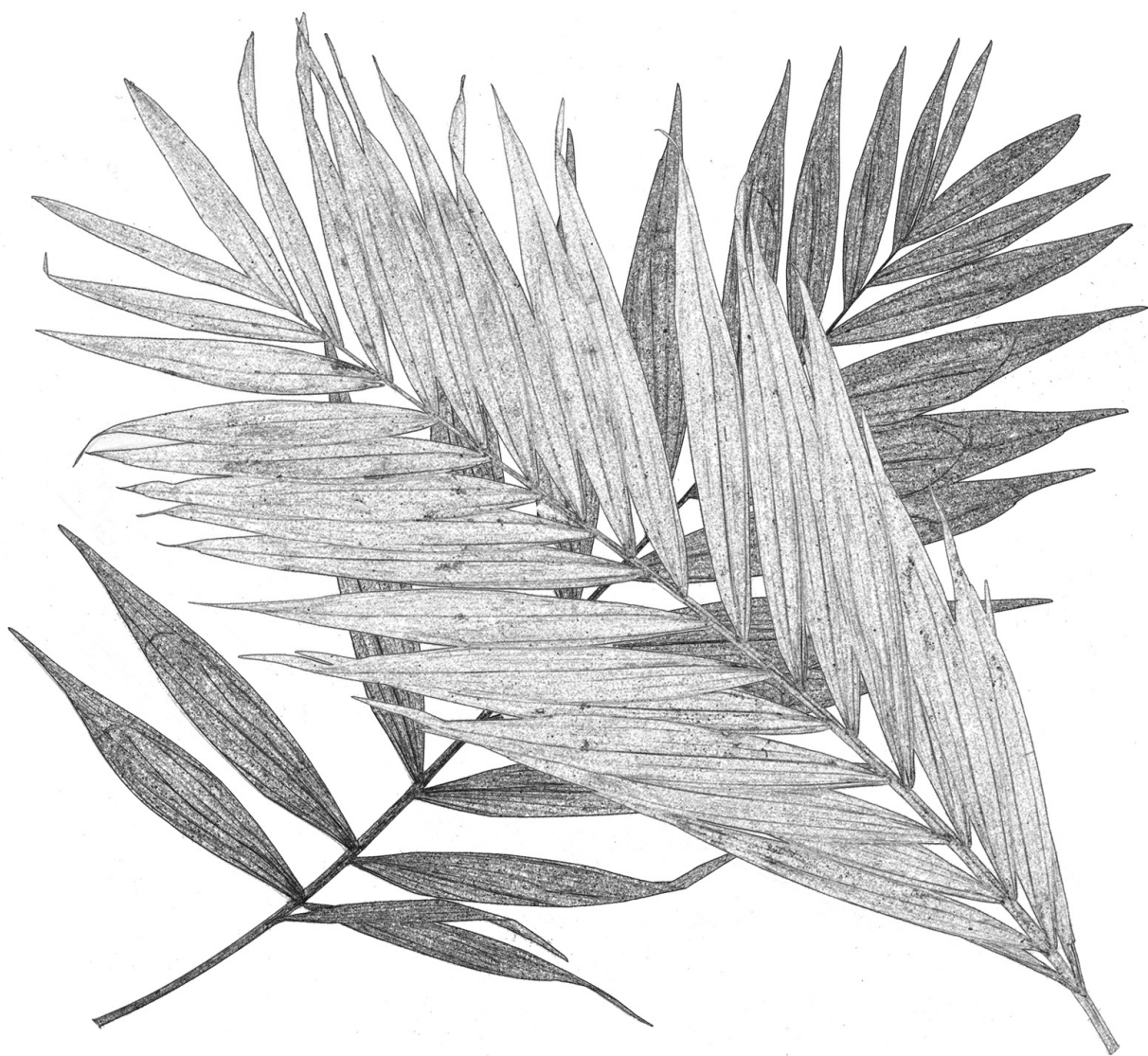
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# Summary

The world is changing rapidly due to anthropogenic disturbance. Effects include: global warming, massive pollution, a changed global nitrogen cycle, high rates of land-use change, and exotic species spread. This has a tremendous impact on both natural and agricultural systems. To understand these impacts, good understanding of ecological systems and underlying drivers is necessary. Ecological systems can be studied at different levels of aggregation. Different levels of aggregation influence each other and are also influenced by external drivers like the environment. The population level is of particular interest, because many important ecological processes occur at the population level, like evolution, extinction, and invasion. Ecologists are increasingly recognizing that population processes are strongly influenced by one level of aggregation lower, the individual level. Individual heterogeneity (*i.e.* differences between individuals in performance), determines many population processes including population growth rate. However, the exact relations between individual heterogeneity, the external drivers of it, and the population level are not always well understood. Furthermore, methods to analyze these relations are not always available.

Individual heterogeneity occurs at different temporal scales, ranging from short- to long-term performance differences between individuals, where short- and long-term refer to the expected lifespan of the species in question. Short-term differences between individuals are relatively easily identifiable and are common in almost all species. But long-term differences are much harder to determine especially for long-lived organisms. Long-term differences between individuals in reproduction have been identified for several animal species, and in growth for several tree species, but less is known about the existence of such differences in other life forms (*e.g.* palms, lianas or clonal plants). Quantifying the extent to which individuals differ is essential for understanding the influence of individual heterogeneity on population processes. Super-performing individuals (*i.e.* individuals that persistently grow faster and reproduce more than others), probably contribute more to the growth of the population and therefore to future generations. Future populations will, therefore, have the genetic characteristics of the super-performers. Which characteristics this will be, depends on the genetic and environmental drivers of super-performance. Full understanding of the influence of individual heterogeneity on population processes, therefore, requires knowledge of the underlying causes of individual heterogeneity.

For many species, it is known that spatial variation in environmental conditions can cause short-term performance differences between individuals, but it is often not clear if the same environmental factors that cause short-term performance differences are also the environmental factors that cause long-term performance differences. Furthermore, genetic variation is known to cause performance differences, but to what extent is not well studied in natural long-lived plant populations. Within-population genetic variation can be maintained in habitats that are characterized by strong temporal or spatial heterogeneity in environmental conditions if the performance of a genotype relative to others depends on the environment it experiences.

Super-performing individuals possibly play an important role in the resistance and resilience of populations to disturbance (*i.e.* maintaining and recovering population growth rate under stress), because super-performers potentially contribute more to the recovery of the population. However, this depends on the relative tolerance to disturbance of super-performers compared to under-performers. A positive relation between performance and tolerance would make super-performers more important, while a negative relation would make them less important. Many types of disturbances entail leaf loss and tolerance to leaf loss is associated with performance being larger than what one would assume based on the amount of leaf area loss. Tolerance can be achieved by compensating for leaf loss in terms of growth rate, which entails either allocating more new assimilates to leaves, allocating new assimilates more efficiently to leaf area (*i.e.* by increasing specific leaf area), or growing faster with existing leaf area (*i.e.* by increasing net assimilation rate). Genetic variation in tolerance and compensatory responses would allow populations to adapt to changes in disturbance events that entail leaf loss.

Individual heterogeneity could also have implications for management. Plant and animal populations are managed at many different levels ranging from harvest from natural populations to modern agricultural practices. When harvesting from natural populations, it might be beneficial to spare the individuals that are most important for future production. Individuals could be spared, either because they contribute most to population growth, because they are tolerant to harvesting (which is relevant when only part of a plant is harvested), or when they start producing less or lower quality product. The productivity of natural populations could also be increased by actively promoting those environmental conditions and genotypes that allow for high productivity, which is the basis of agriculture and common practice in forest management. To determine how this can best be done, knowledge of the causes of individual heterogeneity is necessary.

The general aim of this thesis is to identify and quantify the mechanisms that determine individual heterogeneity and to determine how this heterogeneity, in turn, affects population level processes. This aim was divided into four main questions that I addressed: (1) To what extent do individuals differ in performance? (2) What causes individual heterogeneity in performance? (3) What are the demographic consequences of individual heterogeneity? (4) Can individual differences be used to improve the management of populations? To answer these questions, we used the tropical forest understorey palm *Chamaedorea elegans* as a study system, of which the leaves are an important non-timber forest product that is being used in the floral industry worldwide. We collected demographic data, measured spatial variation in environmental conditions, and applied a defoliation treatment to simulate leaf harvesting, in a natural population in Chiapas, Mexico. Furthermore, we grew seedlings from different mothers from our study population in the greenhouses of Wageningen University, where we also applied a defoliation treatment.

In **Chapter 2** we quantified the extent to which individuals differ in long-term growth rate, and analyzed the importance of fast growers for population growth. We reconstructed growth histories from internodes and showed that growth differences between individuals are very large and persistent in our study population. This led to large variation in life growth

trajectories, with individuals of the same age varying strongly in size. This shows that not only in canopy trees but also in species in the light limited understorey growth differences can be very large. Past growth rate was found to be a very good predictor of current performance (*i.e.* growth and reproduction). Using an Integral Projection Model (*i.e.* a type of demographic model) that was based on size and past growth rate, we showed that fast-growing individuals are much more important for population growth than others: the 50% fastest growing individuals contributed almost two times as much to population growth as the 50% slowest growing individuals.

In **Chapter 3** we analyzed the extent to which observed long-term growth differences can be caused by environmental heterogeneity. Short-term variation in performance was mainly driven by light availability, while soil variables and leaf damage had smaller effects, and spatial heterogeneity in light availability and soil pH were autocorrelated over time. Using individual-based simulation models, we analyzed the extent to which spatial environmental heterogeneity could explain observed long-term variation in growth, and showed that this could largely be explained if the temporal persistence of light availability and soil pH was taken into account. We also estimated long-term inter-individual variation in reproduction to be very large. We further analyzed the importance of temporal persistence in environmental variation for long-term performance differences, by analyzing the whole range of values of environmental persistence, and the strength of the effect of the environmental heterogeneity on short-term performance. We showed that long-term performance differences become large when either the strength of the effect of the environmental factor on short-term performance is large, or when the spatial variation in the environmental factor is persistent over time. This shows that an environmental factor that in a short-term study might have been dismissed as unimportant for long-term performance variation, might, in reality, contribute strongly.

In **Chapter 4** we tested for genetic variation in growth potential, tolerance to leaf loss, compensatory growth responses, and if growth potential and tolerance were genetically correlated in our study population. We quantified compensatory responses with an iterative growth model that takes into account the timing of leaf loss. Genetic variation in growth potential was large, and plants compensated strongly for leaf loss, but genetic variation in tolerance and compensatory growth responses was very limited. Growth performances in defoliated and undefoliated conditions were positively genetically correlated (*i.e.* the same genotypes perform relatively well compared to others, both with and without the stress of leaf loss). The high genetic variation in growth potential and the positive correlation between treatments suggests that the existence of super-performing individuals in our study population likely has (at least in part) a genetic basis. These super-performing individuals, that grow fast even under the stress of leaf loss, possibly contribute disproportionately to population resistance and resilience to disturbance. The low genetic variation in tolerance and compensatory responses, however, suggests that populations might have limited ability to adapt to changes in disturbance regimes that entail increases in leaf loss. Furthermore, the high genetic variation in growth potential could potentially be used in management practices like enrichment planting.

In **Chapter 5** we explore the potential of using individual heterogeneity to design smarter harvest schemes, by sparing individuals that contribute most to future productivity. We tested if fast and slow growers, and small and large individuals, responded differently to leaf loss in terms of vital rates, but found only very limited evidence for this. Using Integral Projection Models that were based on stem length and past growth rate, we simulated leaf harvest over a period of 20 years, in several scenarios of sparing individuals, which we compared to "Business as usual" (*i.e.* no individuals being spared, BAU). Sparing individuals that are most important for population growth, was beneficial for population size (and could, therefore, reduce extinction risk), increased annual leaf harvest at the end of the simulation period, but cumulated leaf harvest over 20 years was much lower compared to BAU. Sparing individuals that produced leaves of non-commercial size (*i.e.* <25cm), therefore allowing them to recover, also resulted in a lower total leaf harvest over 20 years. However, a much higher harvest (a three-fold increase) was found when only leaves of commercial size were considered. These results show that it is possible to increase yield quality and sustainability (in terms of population size) of harvesting practices, by making use of individual heterogeneity. The analytical and modeling methods that we present are applicable to any natural system from which either whole individuals, or parts of individuals, are harvested, and provide an extra tool that could be considered by managers and harvest practitioners to optimize harvest practices.

In conclusion, in this thesis, I showed that in a long-lived understorey palm growth differences are very large and persistent (**Chapter 2**) and that it is likely that long-term differences in reproduction are also very large (**Chapter 3**). I also showed that spatial heterogeneity in environmental conditions can to a large extent explain these differences and that when evaluating the environmental drivers of individual heterogeneity, it is important to take the persistence of spatial variation into account (**Chapter 3**). Individual heterogeneity also is partly genetically determined. I showed that genetic variation in growth potential to be large (**Chapter 4**), and that fast growers keep on growing fast under the stress of leaf loss (**Chapters 4,5**). Therefore it is likely that genetic variation contributes to long-term differences between individuals. Genetic variation for tolerance and compensatory responses was estimated to be low (**Chapter 4**), suggesting that the adaptive potential of our study population to changes in disturbance events that entail leaf loss might be low. I also showed that super-performing individuals are much more important for the growth of the population (**Chapter 2**) and that individuals that are important for future production could be used to improve the management of natural populations (**Chapter 5**).

This study provides improved insight into the extent of individual heterogeneity in a long-lived plant species and its environmental and genetic drivers, and clearly shows the importance of individual heterogeneity and its drivers for population processes and management practices. It also presents methods on how persistent performance differences between individuals can be incorporated into demographic tools, how these can be used to analyze individual contributions to population dynamics, to extrapolate short-term to long–term environmental effects, and to analyze smart harvesting scenarios that take differences between individuals into account. These results indicate that individual heterogeneity,

underlying environmental and genetic drivers, and population processes are all related. Therefore, when evaluating the effect of environmental change on population processes, and in the design of management schemes, it is important to keep these relations in mind. The methodological tools that we presented provide a means of doing this.

# Acknowledgements

Four years working 'alone' on a Ph.D. project can seem like a lonely journey. But it is not, because, in reality, you are never alone. In my case supervisors were always there to help. But also outside of the supervision team a lot of unexpected support came up. Suddenly everyone I needed was there at just the right time and place.

*The supervision team*

Niels, Pieter, Frans and Miguel, the supervision team of my Ph.D. Above all I would like to thank you for helping me becoming the ecologist that I am today, many of the research skills that I have (in the broad sense of the word), I have thanks to you. Together we have developed this Ph.D. thesis. I could not have done it without your help, so thank you!

Pieter, there are very few people with whom I can have as productive work meetings as with you. Many times I came into your office with a doubt or a problem about the analysis that I was doing, and after an hour of discussing and debating all issues were miraculously solved. Niels, your door is always open and you always make time no matter how busy you are. Your clear thinking has been such a valuable contribution to all phases of the research process. Frans, also your advice is very valuable. I really appreciate that you also say what is not okay. Sometimes I didn't believe you at first, but almost always I would find out afterward that you were actually right. Miguel, ecological discussions with you are very inspiring. You always see the broader picture and have many ideas both for experimental approached and analysis. Your input is highly appreciated.

I also want to specifically thank all four of you for your support during the last months of my Ph.D., which is a great example of your dedication as supervisors. When I suddenly decided I wanted to finish my Ph.D. in the middle of the summer holidays you gave me full support (even though several of you thought it would not be possible to finish in the time). Niels, when all others were on holidays, you revised four manuscripts in one week with an average response time of less than a day (I checked). That is impressive, and more than anyone would expect, so thank you! Without the support you all gave me I would not have made it.

It was a great pleasure working with all of you, and I definitely hope we continue collaboration in some way or another in the future! Pieter, I think we are already making a good start in this.

Roy, Arjen and Wopke, the other members of my supervision team. In the end, we didn't collaborate as much as I would have liked to, but the meetings we had were definitely inspiring, and I hope we get the chance to work together more in the future!

*Two experiments in two countries…*

For this Ph.D. two large experiments were set up in different countries. One field experiment in Mexico where we followed the faith of 830 individuals, and an experiment in the greenhouses of Wageningen University, where we grew more than 1400 seedlings from more than 3000 seeds. I did definitely not do this alone, and the help of many different people has been absolutely essential in this.

Greenhouse experiment

I can honestly say the greenhouse experiment would not have been a success without the support of Aad van Ast. Aad advised me and supported a large part of the experiment that we performed in the greenhouse, and coordinated it when I was in Mexico. His experience has been essential.

But I had much more help besides that of Aad. In Wageningen, the people of Unifarm really have been a great help. André, Gerrit, Taede, Herman, Wim, and Ad, thank you for helping me design the practical aspects of the experiment and for making sure my plants got the best possible care! Juan Núñez-Farfan, thank you for the great advice about the setup and the analysis of the experiment, and for your hospitality. Arthur Spruit of Aardam plants, thank you for teaching me how to successfully grow *Chamaedorea elegans* seeds to seedlings. Marcos Malosetti, thank you for your help with the statistics.

I also received a lot of support with data collection in this experiment. Credit definitely goes to the interns Albert, Mitchel, and Ruud, and to Gideon and Stefan, they have measured literally thousands of seeds and plants. But for me, the most valued help of all was that most unexpected, that of many volunteers. When I injured my finger (badly) with climbing, several of my group mates came to the rescue. When I underestimated the time it would take to harvest my experiments, again my groupmates were there. Thank you, Mart, Marcelo, Jorad, and all others that I now forget! But not only group mates came to the rescue. Laura, you saved me when I made it too hard for myself. The support you gave me is much more than can be expected from a friend, and is really highly appreciated! Tabe, thank you very much as well! And Sjoerd, that you voluntarily spend a whole day measuring plants for the good of science really means a lot.

Field experiment

When I was planning to set up the mentioned field experiment in Mexico, my lack of experience made that I had no clue where to start. Jorge Rodriguez-Velázques was my support in Morelia. He helped me very well with the design and practical aspects of the experiment, and initially facilitated contact with the people in Loma Bonita.

Without the fantastic support of the people in Loma Bonita, especially that of Gilberto Jamangapé and Miguel (Tony) Jamangapé, I would not have set up the field experiment and definitely would not have been able to run two experiments in two different countries at the same time. Their support, and that of all others that helped me (especially Fermin, Pascual,

Santos, Audon and Miguel), has been essential, and the hospitality of Lourdes and the other people in the village, and the cheerfulness and positive energy of the many Loma Bonita kids, are highly appreciated.

An important role in the field experiment was played by several MSc students. Sam Muntjewerf, Gerardo Montes de Oca Sierra, Charlotte Watteyn, Sara Vandersmissen, thank you for your help in the design of the experiments, the data collection, analysis, and for the fun we had in Loma! And Gerardo, special thanks to you for making the connection with the village stronger. I hope the village kids still all want to become biologist "just like Gerardo".

Furthermore, Juan Carlos, thank you for coordinating the second defoliation round of my field experiment, help with permits, and many other valuable advice, and Ricardo, thank you for joining the first field trip of my Ph.D., for helping me to get more than 100m of PVC tube and more than 50kg of other field materials to Loma Bonita and setting up the experiments, and above all for making it the most fun trip of all.

To conclude this part, I would also like to thank the Montes Azules Biosphere Reserve for granting me permission to work in the reserve and extract seeds for use in the greenhouse experiment in the Netherlands.

*General thank you' s*

<u>Funding and other support</u>

I would also like to thank PE&RC for allowing me to start my Ph.D. by selecting me in the graduate program, and also for the great support they provide to PhDs (like facilitation a great variety of very useful courses). Especially the course in South Africa on the Science of Conservation has been really important for my personal development.

NWO is thanked for providing the funds necessary for this Ph.D. However, this grant did not cover field costs. I received additional support for this from several private funds (KNAW ecology fund, stichting het Kronendak, the Exploration fund of the Explorers club, the Alberta Mennega stichting, the TREUB maatschappij, and the LEB foundation), and from my two Wageningen University chair groups (CSA and FEM). Thank you all for this!

I would also like to thank Wageningen University for providing funds for printing this thesis.

<u>Non-academic skills</u>

Even though not always generally recognized, some skills that are essential for successful completion of a Ph.D. are of non-academic nature. Many thanks to S.N. Goenka and all the volunteers at the Dhamma Mahi meditation center for teaching me exactly those skills that I needed most during the last stretch of my Ph.D.

<u>My second families</u>

To everybody of FEM. Even though I have not been as a regular visitor of the office as most of you are, I still definitely see you as my FEM family. The support of my fellow Ph.D.'s has

been essential, especially that of my (former) office mates Madelon (not only in Wageningen but also in Mexico, I still got some nice photo's to prove it), Masha, Malene, Kathelyn, Meike, and Danae, that of those that have become climbing partners and therefore provided essential distraction, (again) Madelon, Masha, Juan Ignacio, Cata and Andre (sorry, mentioning you with the wrong group), and that of everyone with whom I have had great discussions with (definitely Federico, Lu, Monique, Mart and Carolina, but I am sure there are more). One thing that for me makes FEM so special is the support of staff members outside of the supervision team. Many of them better know what is going with you, than many of the supervisors of other groups know about their own students. I think this is really extraordinary and makes why so many of the Ph.D. students in our group feel so at home. I think it is the recipe for successful Ph.D. completion, and it definitely led to finding my current postdoc position, thank you Marielos!

Also, CSA has been a great group to be in. The door of both students and staff is always open (figuratively speaking though in the case of students because of Radix design), and I had many fruitful discussions with many of you that helped me a lot during my Ph.D. Whenever I had a modeling challenge there was always someone that knew how to solve it (special thanks to Goufang!). The dedication and motivation of everybody in this group are really impressive, and the intellectual level very high. Uta and Franca, thank you for providing distraction when necessary, Sjanie and Nicole, thank you for all the support, you two keep this group of whiz kids running.

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Thank you also, my Mexican friends, especially Juan Carlos and Amaranta, for your hospitality and for making me feel very much at home in Morelia, and all others, for making that I had a fantastic time in Mexico in general and several of you for keeping me company and sharing a house with me in Loma Bonita.

My Dutch friends (this includes my family!), for understanding every time that I again couldn't meet with them because I was (1) abroad (doing field work, at a conference, etc.) or (2) too busy (setting up my experiments, finishing my thesis, etc.) or (3) too focused on climbing. My friends, even though I don't see you as often as I would like, you are great, you provided distraction exactly when I needed it, love you all!

My actual family

Sjoerd, you have been close to me for most of my academic career, but your contribution to my Ph.D. has been mostly of non-academic nature (although you willingness to measure hundreds of palms in Mexico, and face several centimeter long spines is definitely appreciated). You remind me that there are many paths that one can follow in life both within and outside of a Ph.D. I think even though you don't realize this, and probably won't admit it, you actually contributed a lot to the success of my PhD. Furthermore, I would hereby like to officially state my gratitude to your acceptance of the many times that I left for the other side of the world, and for flying to me three times so far! Let the fourth come soon.

# PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

**Review of literature (4.5 ECTS)**
- Super-performers in palm populations: causes and implications for management

**Writing of project proposal (4.5 ECTS)**
- Super-performers in palm populations: causes and implications for management

**Post-graduate courses (6.1 ECTS)**
- Survival analysis; PE&RC (2013)
- Linear mixed models; PE&RC (2013)
- Bayesian statistics; PE&RC (2014)
- The science of conservation; PE&RC (2016)
- Workshop demography symposium; BES (2014)

**Laboratory training and working visits (1.2 ECTS)**
- Advise on quantitative genetic research and analysis methods; Instituto de Ecología, UNAM (2012-2014)
- Collaboration; IIES, UNAM (2012-2015)

**Invited review of (unpublished) journal manuscript (2 ECTS)**
- Biotropica: influence forest fragmentation on tree population dynamics (2014)
- Biotropica: influence of fruit harvesting on tree population dynamics (2015)

**Competence strengthening / skills courses (1.5 ECTS)**
- Project and time management; PE&RC/Valley Consult (2014)

**PE&RC Annual meetings, seminars and the PE&RC weekend (1.5 ECTS)**
- PE&RC Weekend (2013)
- PE&RC Midterm weekend (2014)

**Discussion groups / local seminars / other scientific meetings (7.8 ECTS)**
- Journal Club; WUR (2012-2016)
- R-users meeting (2012-2016)
- Meetings with other students and/or staff about R and statistics problems; (2012-2016)
- Modelling and Statistics Network; WUR (2013-2016)

**International symposia, workshops and conferences (4.4 ECTS)**
- Demography Beyond the Population symposium of the British Ecological Society; Sheffield, UK (2014)
- Annual meeting of the Evolutionary Demography Society; Lunteren, the Netherlands (2015)

- Annual meeting of the Association for Tropical Biology and Conservation; Montpellier, France (2016)

**Lecturing / supervision of practicals / tutorials (3.3 ECTS)**
- Ecological aspects of bio-interactions (2014)
- Population and systems ecology (2014, 2015)
- Resource dynamics and sustainable utilization (2015)
- Trends (2015)

**Supervision of MSc students**
- Sam Muntjewerf: How do biotic factors influence performance in a Mexican understorey palm?
- Sara Vandersmissen: Environmental control versus super-performance in a tropical understorey palm
- Gerardo Montes de Oca Sierra: Defoliation effects on seed size and the consequences on recruitment of *Chamaedorea elegans* in the *Lacandona* tropical rainforest
- Charlotte Watteyn: Leaf quality and harvest of the commercial palm species *Chamaedorea elegans*

# Short Biography
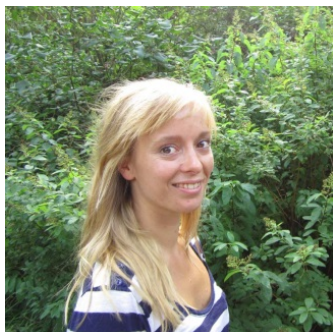
Merel Jansen was born October 10 1986 in Utrecht, The Netherlands. Both primary and secondary education were attended at schools in the Netherlands. From 2005 to 2008 she studied Physics and Astronomy at Utrecht University. She attended one semester of these BSc studies at UC Berkeley, where she obtained part of the credits of her BSc education. She wrote a BSc thesis about phase transitions in the early universe. During her BSc studies, Merel was a member of the Faculty Council of Sciences, and of the Student Government of the Physics and Astronomy department.

After several encounters with tropical forest during travels both during and after her BSc studies, Merel decided to dedicate her life to tropical forest conservation and therefore continued her career in tropical forest ecology. After a short pre-MSc program, she studied Environmental Biology at Utrecht University, where she specialized in Ecology and Natural Resource Management. Her MSc thesis was about super-performance in *Chamaedorea elegans*, and this topic later continued in her PhD research. For this thesis, she collaborated with the National Autonomous University of Mexico, she collected field data in the Montes Azules Biosphere reserve in Chiapas, Mexico, and started with ecological modelling. She also worked in Belgium as an intern at the Centre for Research and Conservation of the Royal Zoological Institute of Antwerp, where she made an assessment of the possibilities for experimental personality research in Okapis in a zoo setting. Furthermore, she attended MSc training courses in underwater research methods, and on general tropical forest research methods. In 2011 Merel graduated with the distinction *Cum Laude*.

To be able to continue the research she started during her MSc, Merel wrote, together with the current advisors of her PhD, a research proposal with which she obtained a personal grant from the NWO/PE&RC graduate programme to perform her PhD research. During her PhD she has set-up experiments in Mexico and the Netherlands, attended several courses on advanced statistics, and participated in a course on interdisciplinary scientific approaches to conservation. Furthermore, she presented results of her PhD work at three different international conferences, she supervised four MSc students and two technical school interns, and extended the collaborations with the National Autonomous University of Mexico.

Recently, Merel started working on a postdoc project at ETH Zurich (in collaboration with CIFOR) on the sustainability of the supply chain of Amazon nuts from Peru to Switzerland.

Merel is fluent in Dutch (mother tongue), English and Spanish, and has a basic understanding of French and German. Outside of her academic career, Merel is very dedicated to rock climbing, scuba diving, meditation and yoga.