The nutrient economy of *Lodoicea maldivica*, a monodominant palm producing the world’s largest seed

Peter J. Edwards¹, Frauke Fleischer-Dogley² and Christopher N. Kaiser-Bunbury³

¹Institute of Integrative Biology, ETH Zurich, 8092 Zurich, Switzerland; ²Seychelles Islands Foundation, Victoria, Seychelles; ³Ecological Networks, Department of Biology, TU Darmstadt, 64287 Darmstadt, Germany

**Summary**

- The iconic *Lodoicea maldivica* palm appears to invest heavily in reproduction, with females bearing the world’s largest seeds and males producing copious pollen. We asked how these palms, which grow in extremely poor soils, obtain sufficient nutrients to support such high levels of reproductive function.
- Our study site was the Vallée de Mai UNESCO Site on Praslin, Seychelles. We measured the trees’ allocations of dry matter, nitrogen (N) and phosphorus (P) to aboveground growth and reproduction, quantified stemflow and throughfall, and measured availabilities of N and P in the soil.
- We show that the nutrient costs of reproduction are very high in male and female plants, and are exceeded those of vegetative growth. We describe how the palm leaves form a huge funnel that intercepts particulate material, especially pollen, which is flushed to the base of the trunk when it rains. In this way, *Lodoicea* improves its nutrient supply and that of its dispersal-limited offspring.
- *Lodoicea* shares many functional characteristics with dominant trees of other monodominant forests in the humid tropics. It also exhibits unique features, including its huge seed, effective funnelling mechanism and diverse community of closely associated animals, suggesting a long evolutionary history under relatively stable conditions.

**Introduction**

Plants of infertile habitats typically use nutrients more efficiently than other species, needing less of them to produce their tissues and resorbing more before they are shed (Aerts, 1996). Nutrients invested in producing fruits and seeds, however, cannot be recovered by resorption, and a low supply of nutrients – especially of nitrogen (N) and phosphorus (P) – can limit reproductive function (Lau & Stephenson, 1994; Poulton et al., 2002). We might therefore expect plants of nutrient-poor environments to allocate less of the most limiting nutrients to pollen and fruits, for example, by having more efficient pollination mechanisms or by producing fewer, smaller seeds (Fujita et al., 2014). Alternatively, we might find them to be particularly efficient in capturing nutrients from their environment, for example, by recovering them from pollen that falls to the ground. Indeed, birch trees (*Betula pendula*) in boreal ecosystems have been shown to recover significant amounts of N and P from the ground through mycorrhizal fungi (Perez-Moreno & Read, 2001).

The iconic coco de mer palm *Lodoicea maldivica* (J. F. Gmel.) Pers. is endemic to two islands of the Seychelles, where it has to cope with very low amounts of soil nutrients. The soils are derived from highly weathered granite containing very little P (0.02–0.03% P₂O₅ content; Ashwal et al., 2002), and are dominated by minerals with a high P-binding capacity such as kaolinite and amorphous iron and aluminium oxides (Dobrovolskii, 1986). Furthermore, many trees grow in boulder-strewn areas with little or no mineral soil. Yet female plants bear the largest seeds in the plant kingdom (individual seeds can exceed 18 kg FW) and males produce huge inflorescences with copious pollen. Although large seeds per se do not indicate high nutrient allocation to reproduction at the plant level (Bazzaz et al., 2000), this may be the case in *Lodoicea* given that female trees can bear a total fruit load of over 100 kg.

We asked how a palm as large as *Lodoicea* is able to maintain apparently high levels of both male and female function in such a nutrient-poor environment (Fig. 1a–d). Field observations suggested a possible answer in that *Lodoicea* trees channel most of the rainwater down their trunks. Indeed, the huge, plicately-folded leaf blades appeared to form an almost perfect funnel, with water being directed into gutter-like petioles, passing unhindered through a split at the base of each petiole, and then splashing down close to the trunk (Fig. 1b–e–g). This stream of water also washed down particulate material on the leaf surface (Fig. 1c), including pollen, perianth parts and the faeces of birds, snails and lizards. Based on these observations, we developed the hypothesis that *Lodoicea* plants improve their nutrient supply (and that of their dispersal-limited offspring) by channelling...
water and nutrient-rich particulate material to the base of the plant.

We investigated this idea in the Vallée de Mai UNESCO World Heritage Site on the island of Praslin, which supports the largest and most intact stand of *Lodoicea* in the Seychelles. First, we quantified the biomass and nutrients allocated to reproduction (in both male and females trees) and aboveground vegetative growth. Second, we quantified the postulated funnelling effect by measuring how much rainfall was channelled down trees and trunkless juvenile plants, and how much fell to the ground at distances of 0.2, 1 and 2 m from the trunk. Third, we measured soil water content and N and P availabilities at different distances from plants of *Lodoicea* and of two other endemic palms, *Phoenicophorium borsigianum* and *Deckenia nobilis*, for comparison. In the discussion, we consider the possible ecological and evolutionary consequences of nutrient capture, not only for *Lodoicea*, but also for the community of animals associated with this keystone species.

**Materials and Methods**

*Lodoicea maldivica*

*Lodoicea maldivica* (J. F. Gmel.) Pers. (Arecaceae) belongs to a monotypic genus within the tribe Borassae (Dransfield...
Lodoicea has a trunkless juvenile phase, during which there is considerable development belowground under the stem base, which forms a massive saucer-shaped structure up to 1 m in diameter known as the ‘bowl’. A remarkable feature of the young plants, especially when growing in the shade, is their greatly elongated petioles, which can be as much as 10 m long (Edwards et al., 2002), so that the leaf blades of even trunkless plants may reach the canopy. The end of the juvenile phase, which probably lasts for several decades in closed forest, is marked by the development of the trunk, which grows incrementally in height with each successive leaf. Trees in the Vallée de Mai usually begin to produce flowers when the trunk is c. 4 m tall. Female trees rarely grow taller than c. 20 m, whereas male trees can reach over 30 m in total height. Apart from this difference in maximum height, there are no obvious differences between the sexes in morphology or vegetative growth. Reviews of the species’ reproductive biology and life history are given by Edwards et al. (2002) and Blackmore et al. (2012).

Lodoicea forest is distinct from other lowland forest communities of the Seychelles in both structure and composition (Vesey-Fitzgerald, 1940). The most obvious difference is the near absence, at least in undisturbed Lodoicea forest, of other tree species, and historical records confirm that the pristine vegetation was very dense and almost monospecific (Fauvel, 1915).

Study site

The fieldwork was conducted in the Vallée de Mai on Praslin, Seychelles. This 19.5 ha reserve, designated a World Heritage Site by UNESCO in 1983, contains some of the finest stands of Lodoicea, although the vegetation is by no means pristine. Describing the area in the 1930s, Vesey-Fitzgerald (1940) wrote: ‘Some very fine specimens of Lodoicea can be seen here, but recent clearing of all vegetation has converted these palm groves into a semi-cultivated plantation’. Since then, there has been extensive planting of seeds, especially in the 1950s, and the trees are more regularly spaced than would have been the case in undisturbed forest. This fact was useful to us, because it made it easier to investigate how soil conditions and throughfall varied with distance from the trunk. Many of the measurements were made in an area of c. 25 × 25 m² containing 10 adults and 36 large juvenile plants that had evidently been planted, perhaps in the 1930s. The trunks of the adults in our sample were 4–8 m tall and had a mean diameter (±SE) of 30.05 (±1.00) cm. Adult trees bore an average of 12 leaves, whereas the juvenile plants had an average of seven leaves arising from the ground.

The Seychelles has a tropical climate and experiences temperatures of 24–32°C and two distinct seasons, the cooler and drier SE Monsoon (monthly mean ±SE rainfall between 2008 and 2013: 103 ± 11 mm) and the warmer and wetter NW Monsoon (185 ± 19 mm). Mean daily rainfall in the dry and wet season is 10.6 ± 1.1 and 17.1 ± 1.2 mm, respectively. Dry periods of up to 2 wk are common in both seasons and are predicted to become more frequent and severe as a result of climate change (Payet & Agricole, 2006).

Nutrient allocation to growth and reproduction

Because of its simple morphology, biomass production by Lodoicea can be estimated by measuring the mean DW of the component parts (leaves, trunks, fruits, male flowers) and the rates at which these parts are produced. Estimates of nutrient allocation can then be obtained using data on nutrient concentrations in the various tissues. Many of these data were available from our earlier studies in the Vallée de Mai or from other sources (Edwards et al., 2002; Fleisher-Dogley et al., 2011; Blackmore et al., 2012), whereas others were collected for this study. The results presented in Table 1 are therefore derived from different random samples of trees, rather than referring to a particular stand.

The rate of leaf production was studied by marking 58 emerging leaves on 15 plants at the ‘bayonet’ stage and monitoring their subsequent development over 4 yr. From these data we estimated that the mean rate of leaf production in young trees with trunks of up to 4 m was 1.20 leaves yr⁻¹. Because the number of leaves on a tree is relatively constant at c. 12 (Fleisher-Dogley et al., 2011), it follows that the production of a new leaf is associated with the abscission of an older leaf. The biomass of leaves was measured by weighing a sample of 10 leaves from randomly selected trees and taking subsamples to determine water content.

Trunk production was estimated by determining the average distance between successive leaf scars on a sample of 50 trees. This yielded an average of 8.6 (± 1.84 SD) leaf scars per metre of trunk, which corresponds to a trunk increment of 12.2 cm per leaf (Fleisher-Dogley et al., 2011). Assuming a mean trunk diameter of 31.1 cm and a mean wood density of 0.299 g cm⁻³ (Edwards et al., 2002), we estimated that 2.77 kg DW of trunk is produced for each new leaf, and 3.33 kg is produced in 1 yr.

Female function was quantified in terms of the resources allocated to fruits. The fruit or ‘nut’ of Lodoicea consists of a single large seed (or occasionally two or three seeds) surrounded by a thick fibrous ‘husk’ formed from the outer pericarp (Romanov et al., 2011). These are borne on massive woody inflorescences that may persist for many years and bear several fruits. A survey in 2001 conducted by staff of the management authorities found that the average number of fruits on all female trees in the Vallée de Mai was 7.03 (Edwards et al., 2002). Because fruits take some 6 yr to develop (Blackmore et al., 2012), this value yields an estimate of 1.17 fruits produced per year. The mean FW of 2450 nuts collected by staff of the Vallée de Mai was 8.48 kg, and the estimated DW was 6.21 kg. We also weighed samples of husks (n = 6) and shells (n = 50). The weight of the kernel (endosperm) was determined as the difference between mean nut weight and the mean shell weight.

The production of male flowers was used as a measure of male function. Male trees bear long-lived (up to 3–4 months), cylindrical inflorescences that produce spirally arranged clusters of
Table 1 Allocations of dry matter and nutrients to aboveground growth and reproduction in Lodoicea maldivica

<table>
<thead>
<tr>
<th>Plant organ</th>
<th>Unit dry mass (g)</th>
<th>Tissue concentrations (mg g⁻¹ DW)</th>
<th>Annual cost per tree (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>N</td>
<td>P</td>
</tr>
<tr>
<td>Leaves</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Living</td>
<td>12486 ± 186 (8)</td>
<td>5.39 ± 0.20 (6)</td>
<td>0.25 ± 0.01 (6)</td>
</tr>
<tr>
<td>Dead</td>
<td>10920 ± 1012 (8)</td>
<td>4.21 ± 0.53 (10)</td>
<td>0.022 ± 0.02 (10)</td>
</tr>
<tr>
<td>Withdrawn</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trunk</td>
<td></td>
<td>2.64 ± 0.21 (30)</td>
<td>0.12 ± 0.01 (30)</td>
</tr>
<tr>
<td>Male flowers</td>
<td>0.0552</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anthers</td>
<td>0.0189 ± 0.0004 (14)</td>
<td>0.25 (5)</td>
<td>34.0</td>
</tr>
<tr>
<td>Perianth etc.</td>
<td>0.0363 ± 0.0032 (6)</td>
<td>9.44 ± 0.22 (6)</td>
<td>0.681 ± 0.08 (6)</td>
</tr>
<tr>
<td>Fruit</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nut</td>
<td>6208 ± 36 (30)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shell</td>
<td>1150 ± 47 (50)</td>
<td>2.16 ± 0.25 (5)</td>
<td>0.064 ± 0.02 (5)</td>
</tr>
<tr>
<td>Kernel</td>
<td>5058</td>
<td>6.67 ± 0.46 (10)</td>
<td>0.78 ± 0.05 (10)</td>
</tr>
<tr>
<td>Husk</td>
<td>1059 ± 131 (6)</td>
<td>2.56 (2)</td>
<td>0.241 (2)</td>
</tr>
</tbody>
</table>

Leaf and trunk data include both male and female trees. Nutrient costs of leaf production are net values, allowing for nutrients retained by the tree when old leaves are shed. Data are mean ± SE values and sample size in parentheses. N, nitrogen; P, phosphorus. Numbers in bold are shown in the flow chart of Fig. 2.

Flowers grow in dense clusters, within deep, pit-like structures. The individual flowers emerge sequentially from the pits and last for a single day before being shed (C.N.K-B, pers. obs.). While open, the flowers attract many animals including lizards and molluscs that feed on the pollen. We counted the number of male inflorescences on trees at different times of year over a period of 4 yr. Based upon 1322 observations, we obtained a mean value of 0.829 flowering inflorescence per tree because we wanted to ensure that no pollen was lost. By contrast, we collected fallen perianth parts from the base of trees (removing the anthers) to ensure that we measured the nutrient concentration in the structures that were actually shed.

In order to determine whether water is channeled to the base of the plant, as our preliminary observations suggested, we studied the spatial distribution of water reaching the forest floor during a rain event (1 December 2010; total rainfall 0.61 mm). We measured the water falling in the immediate vicinity of the trees (i.e. stemflow; Levi & Frost, 2003) by fastening two collectors to each trunk (n=10) using parafilm tape. These collectors were inverted plastic bottles, rectangular in cross-section, from which the base had been removed. The intercepting area was 32.5 cm², and collected water flowing within a radius of 5 cm of the trunk. For the trunkless juvenile plants (n=10), we fixed collectors (plastic bottles with a circular cross-section, again with the bottom removed) into the gutter-like petioles of two leaves, so that any water flowing down the gutter was intercepted. We used bottles with diameters of either 7.5 or 11.0 cm, depending on the size of the petiole. To evaluate the influence of leaf exposure on the amount of rainfall collected in the petioles, we visually estimated the percentage of exposure of all leaves with a fitted collector (n=20). To measure water falling further away from the tree or juvenile (i.e. throughfall), we fixed plastic cups (collecting area 46.6 cm²) in wire stands 20 cm above the ground at distances of 0.2, 1 and 2 m from the trunk (two series of cups for each tree and one series for each juvenile).

Soil moisture and nutrients

We used a portable time domain reflectometer (TDR 100; Campbell Scientific Inc., Logan, UT, USA) to measure soil moisture content (0–10 cm depth) at distances of 0.2, 1 and 2 m from the trunks of seven mature Lodoicea, and two other endemic palms D. nobilis and P. borsigianum. We selected canopy trees throughout the Vallée de Mai that had no other trees or shrubs within a 4-m radius, and made the measurements in December 2010, after an extended dry period that had ended with a heavy shower 2 d earlier. Around each tree we made four sets of measurements in orthogonal directions – one uphill (in cases where the terrain was sloping), one downhill, and the other two left and right along the contour (12 measurements per tree). Because we were interested in how individual trees affected local soil moisture, and not in variation within the study area due to variable soil conditions, we normalised the data so that the mean value per tree was 1.

We measured the availability of N and P in the soil using ion-exchange resin bags (Lundell, 1989; Meason & Idol, 2008). The
5 × 5 cm² bags were made of a fine nylon fabric (60 μM mesh width, Sefar Nitex 03- 60/35; Sefar AG, Thal, Switzerland) and contained 2000 ± 2 mg mixed-bed ion-exchange resin (Amberlite IRN 150, H⁺ and OH⁻ form; Sigma-Aldrich). To saturate exchange sites with K⁺ and Cl⁻ ions before use, the bags were shaken for 2 h in 2 M KCl and thoroughly rinsed with distilled water. The bags were then placed at distances of 0.2, 1, and 2 m from eight adult and eight juvenile Lodoicea, and from four P. borsigianum and three D. nobilis trees (total 69 bags). We cut an oblique slit in the soil with a knife, inserted the bag at a depth of 5 cm, and carefully pressed the soil together. The bags were set out in the field on 2 March 2011 and removed on 9 April 2011. During the 38 d incubation period, 160 mm rain fell in the study area.

On removal, the bags were dried at 37°C for 72 h and sent to Switzerland for analysis. In the laboratory, they were cleaned with distilled water, and the resin was extracted for 1 h in 30 ml 1 M PO₄₃⁻, NO₃⁻ and NH₄⁺ using a continuous flow analyser (AutoAnalyzer 3HR; Seal Analytical). Mean daily N and P adsorption rates were calculated.

We collected soil samples (0–10 cm depth) at distances of 0.2 and 2 m from 12 Lodoicea plants in the main study area to measure soil organic content and total N and P concentrations. Organic content was measured as weight loss on ignition at 550°C. Total N and P concentrations were measured colorimetrically after Kjeldahl digestion using the same methods as for plant material. To determine whether palm pollen could be detected in the soil, we prepared extracts from six pairs of soil samples by heating in dilute sodium hydroxide solution, neutralising with dilute hydrochloric acid, and examining the fraction that passed through a 100-μm sieve under the microscope. We used safranin to stain the pollen.

Data analysis

Stemflow and throughfall All data were expressed as amounts of water reaching the ground relative to rainfall measured in a clearing adjacent to the study plot (mm per unit area). To do this, we assumed that water flowing down the trunk and along the petioles of juveniles reached the ground within 5 cm of the plant base. We combined replicate samples of stemflow or throughfall to give a single value for each distance and plant. In the case of water flowing down petioles, we extrapolated from the data for two leaves to a total value for the plant. Given the non-normality of the data, we used paired Wilcoxon signed-rank tests to analyse differences in water reaching the ground at different distances (0.05, 0.2, 1 and 2 m) from the base of the plants.

Soil moisture Changes in soil moisture with distance from the trunk were analysed with linear mixed effects models (MEM). To compare soil moisture among species and distances we used a fully factorial model with normalised soil moisture as the response variable and main and interaction fixed effects of tree species and distance. The direction of the sampling (downhill, uphill, left, right) from the base of the tree was nested in tree ID and both variables were entered as random effects. Distance was included in the model as a factor with three levels, 0.2, 1 and 2 m from the base of tree. As the critical decline in soil moisture around Lodoicea occurred between 1 and 2 m from the trunk, we tested soil moisture at 0.2 and 2 m against soil moisture at 1 m distance. To test for within-species differences in soil moisture we used MEMs with a similar structure as the fully factorial model but without tree species as a fixed effect. MEM were fitted with the lme function of the nlme package (Pinheiro et al., 2013) in R 3.1.1 (R Core Team, 2014).

Ion-exchange resin adsorption rates The relationships between distance from the trunk and soil nutrient content were analysed with MEM. Phosphate, ammonium and nitrate were entered in separate models as the response variables, with distance from the trunk and species as the main and interaction fixed effects, and tree ID as a random effect. To address the violation of homogeneity of variance assumption in the data, we used the weights argument in the lme function. The phosphate model showed a variance structure with residual spread increasing with distance from the tree and varying across species. The varComb function accounts for complex variance structures by combining the functions varIdent (variance structure per stratum) and varExp (exponential variance structure) and including them as a weight argument in the model (Zuur et al., 2009). Similarly, the residuals of the ammonium and nitrate models varied across species, and the varIdent function was used to account for the variance structure. Optimal model selection was based on the lowest Akaike information criterion (AIC).

Results

Biomass production and nutrient allocation

The mean DW of leaves and trunk produced per tree in 1 yr were 13.1 and 3.3 kg, respectively, with no evidence of any differences between male and female trees. Male trees produced an average of 3.1 kg flowers yr⁻¹, which was equivalent to 16% of measured aboveground production, whereas female trees produced an average of 8.5 kg of fruit, representing 34% of aboveground production. These percentages can be taken as rough measures of reproductive allocation, albeit based only on aboveground structures.

Mean concentrations of N and P in living leaves of Lodoicea were 5.39 and 0.25 mg g⁻¹ DW, respectively (Table 1). However, relatively more P than N was withdrawn from senescing leaves, and the N : P ratio in litter was much higher than in living leaves (191 vs 22). Concentrations of both nutrients were higher in seed endosperm and in anthers than in leaves, but N : P ratios in anthers and endosperm were considerably lower (6.2 and 8.6, respectively; Table 1).

Similar quantities of P were allocated annually to male and female function and to aboveground vegetative growth (4.11, 4.98 and 4.15 g per plant, respectively), whereas allocation of N to reproduction was <50% of that allocated to growth (36.2, 45.5 and 89.5 g, respectively). Because each new leaf is associated
with the death of an old leaf from which nutrients are withdrawn, however, the net nutrient costs of producing leaves are actually much lower. On this basis, reproduction accounted for 86% of all P allocated aboveground in male plants and 88% in female plants, whereas the equivalent values for N were 36% and 42%, respectively (Fig. 2).

Stemflow and throughfall

Stemflow and throughfall were measured following a rain event in 2010, when 0.61 mm rainfall was recorded by a standard rain gauge located in a nearby clearing. Although it was a small shower, so much water flowed down the trunks and petioles that some collectors overflowed, and our values therefore slightly underestimate stemflow. Most rain falling on adult trees either flowed down the trunk or splashed to the ground nearby, with little or none falling at distances of 1 and 2 m from the trunk (Fig. 2).

We calculated the funnelling ratio of trees (Herwitz, 1986; Germer, 2013) as the mean volume of stemflow per tree (2.66 l) divided by the volume of rain falling in an area equal to the mean cross-sectional area of the trunk plus a 5 cm annulus to account for the width of the collectors (0.076 l in 1260 cm²); this yielded a funnelling ratio of 34.4. However, because of splashing as the water gushed down the trunk, this value represented only a fraction of the water reaching the ground close to the tree. We therefore calculated the same ratio for a collecting area extending 30 cm from the trunk. The mean volume of water falling in this larger area (0.64 m²) was 10.5 l, which yielded a funnelling ratio of 26.8. From this value, we calculated the effective collecting area of the water falling to the ground as 17.1 m².

Juvenile plants tended to form even more effective funnels than adults, with almost no water falling to the ground at 0.2, 1 or 2 m distance from the plant (Supporting Information Fig. S1a; Wilcoxon $P = 0.063$ at 0.2 m). Leaves only contributed to the

**Fig. 2** Lodoicea maldivica directs the flow of water, pollen and other organic matter to its base. In this way it improves supplies of phosphorus and nitrogen, which are needed in large quantities to sustain costly reproductive functions.
flow, however, if they were not overtopped by other leaves, and we found a significant positive correlation between the water collected by individual leaves and their estimated exposure above the canopy (Spearman’s $r_s^2 = 0.80, P<0.01$). Because many leaves were not fully exposed, the effective collecting area of juvenile plants was much lower (2.22 m$^2$) than that of adults.

Soil moisture and nutrients

The soil measurements showed that funnelling strongly influenced spatial patterns of moisture and nutrients (Fig. 2). Soil moisture amounts at 0.2 and 1 m distance from *Lodoicea* trees were high and not significantly different (mixed effects models: $t=1.75, P=0.09$), and were significantly lower at 2 m away ($t=-3.09, P=0.004$; Fig. 2). By contrast, soil beneath the two endemic palms used for comparison was wetter at 0.2 m than at 1 m distance (*P. borsigianum*: $t=3.20, P=0.002$; *D. nobilis*: $t=2.73, P=0.009$), but similarly dry at 1 and 2 m away from the plant (*P. borsigianum*: $t=-0.50, P=0.62$; *D. nobilis*: $t=-0.23, P=0.81$; Fig. S1; Supporting Information Table S1). We observed how fine plant debris from structures such as stamens and scale leaves were intercepted by the leaves (Fig. 1c) and accumulated at the base of *Lodoicea* trees. We also found abundant remains of palm pollen in extracts of soil samples collected at 0.2 m from a tree but little or none in samples taken at 2 m. Analyses of paired soil samples taken at 0.2 m and 2 m from *Lodoicea* trees ($n=12$) revealed that the soil close to trees was significantly more organic, and contained higher amounts of total N and total P than samples from further away (mean concentrations ± SE at 0.2 m vs 2 m; % organic matter: $46.5±6.5$ vs $18.8±2.2$; mg N g$^{-1}$: $8.83±1.25$ vs $3.15±0.48$; mg P g$^{-1}$: $0.33±0.06$ vs $0.20±0.03$; paired Wilcoxon test, all $P<0.0025$).

Using ion exchange resins buried in the soil, we recorded over three times as much available phosphate in soil at 0.2 and 1 m distance from adult *Lodoicea* compared with *P. borsigianum* and *D. nobilis*, and no difference among species at 2 m away (Fig. 1c; Table S2a). We found a similar but smaller distance effect for juvenile *Lodoicea* (Figs 2, S1c), but not for the other palms. By contrast, the ion exchange resin studies showed no significant differences in nitrate and ammonium availability with distance among tree species, although soil close to *P. borsigianum* trees showed an elevated mean N content (Fig. S1d; Table S2b).

Discussion

*Lodoicea* leaves have much lower N and P concentrations than most woody plants of the Seychelles, with mean values amounting to 36% and 29%, respectively, of those in 56 native trees and shrubs, most of them growing in similarly poor granitic soils (C. Kueffer, unpublished data). Concentrations are extremely low compared with other tropical rainforest trees, being only 35% and 20%, respectively, of the mean values for such trees in the GLOPNET database (Wright et al., 2004). Indeed, the very few woody plants producing leaves with similar or even lower N and P concentrations are mainly members of the family Proteaceae that grow in exceptionally P-deficient soils in Southwest Australia (Lambers et al., 2011). Even more remarkable were the concentrations of P in recently shed *Lodoicea* leaves (Table 1), which were lower than any previously reported, even for *Banksia* species growing in the poorest soils in Southwest Australia (Denton et al., 2007). Because over 90% of leaf P was withdrawn before senescence, whereas for N the value was 20%, we infer that P was the more limiting nutrient. These results are in line with other work in old, climatically buffered, infertile landscapes, where P has been identified as the more limiting nutrient (Lambers et al., 2008).

Despite this evidence for nutrient-poor conditions in the Vallée de Mai, *Lodoicea* trees appear to allocate relatively high amounts of dry matter to reproduction (Table 1). Although our estimates are based only upon aboveground production, it seems reasonable to conclude that total reproductive allocation in *Lodoicea* is far higher than in most tropical trees, for which values of c. 5% have been reported (Bazzaz et al., 2000), and also in some tropical palms (Cepeda-Cornejo & Dirzo, 2010). Reproductive allocation measured in terms of P is even larger (Fig. 2), even though our measurements do not take account of the nutrients used to produce inflorescences. Such a high proportional allocation of P to reproduction is, however, consistent with data from other areas where this nutrient is in very short supply. For example, P concentrations in *Lodoicea* kernel were in the same range as in Australian *Banksia* species (Denton et al., 2007), some of which are known to allocate an enormous proportion of aboveground P reserves to seeds (48% in *B. hookeriana*; Witkowski & Lamont, 1996). Indeed, the high P requirement for fruit production in *Lodoicea* may explain why many mature female trees in the Vallée de Mai bear few or no fruits (Edwards et al., 2002), whereas trees growing in more fertile conditions in botanic gardens may have as many as 70.

How does *Lodoicea* acquire sufficient P for its reproductive effort? Our results support the hypothesis that funnelling of rainwater significantly improves the local availability of P, and perhaps also of water during dry periods. In this respect, *Lodoicea* is not unique; many trees exhibit funnelling to varying degrees (Herwitz, 1986; Germer et al., 2010; Germer, 2013), and for some species there is evidence that this increases nutrient availability (Enright, 1987; Germer et al., 2012). There appears to be no other tree, however, that forms quite such an efficient funnel as *Lodoicea*, so that almost all water falling on the leaves is directed down the trunk. Indeed, there are intriguing similarities in this respect between the *Lodoicea* palm and so-called ‘tank epiphytes’ such as *Asplenium nidus* and some species of Bromeliaceae, which also grow in nutrient-poor environments. In the epiphytic bromeliad *Werauhia sanguinolenta*, for example, evidence was found for a trade-off between nutrient allocation to vegetative growth and reproduction (Zotz & Richter, 2006). The authors concluded that P was the most limiting nutrient, and calculated that a plant needed c. 2 yr to accumulate sufficient P for a single crop of fruits.

Evolutionary implications

Forest ecosystems dominated by a single species are uncommon but widely distributed in the humid tropics, and their existence
can readily be explained by ecological theory (Hart et al., 1989; Torti et al., 2001; Peh et al., 2011). Such monodominance is usually interpreted as the end-point of a successional process in which, driven by positive feedbacks on site conditions, a multi-species assemblage is gradually replaced by a single species. The exact nature of these feedbacks depends upon the initial site conditions and the functional traits of the dominant tree, which typically produce large, poorly dispersed seeds giving rise to shade-tolerant persistent seedlings (Hart et al., 1989; Peh et al., 2011). Because stands dominated by large-seeded species tend to regenerate and spread more slowly than mixed-forest associations, such vegetation only persists in areas that have not experienced major external disturbance for a very long period.

Although the mechanisms leading to monodominance have been well studied, much less attention has been paid to ecological and evolutionary processes at work within monodominant stands. We argue that monodominance, once attained, can drive the dominant species to change in surprising ways and have important consequences for the ecosystem. In a mixed-forest assemblage, the evolutionary stable strategy for a trait such as seed mass or maximum tree height is influenced in a game-theoretic way by the trait values of the other species present, with the consequence that species making up the community exhibit a range of values (Westoby et al., 1992). By contrast, in a monodominant system, evolutionary change may be driven primarily by ecological interactions among individuals of the same species, which might lead to continuing directional selection for particular traits. This difference in selection pressures could explain not only the huge seed of Lodoicea, but also other aspects of the species’ ecology and nutrient economy. We explore these aspects in the following paragraphs.

Large seed and high pollen production Edwards et al. (2002) suggested that Lodoicea evolved from an ancestral Gondwana palm that produced large, animal-dispersed seeds. As the Seychelles broke away from the continental landmass, the island populations of this palm lost any means for seed dispersal. According to their hypothesis, sibling competition then drove the evolution of large seeds capable of forming persistent, shade-tolerant seedlings. They also suggested that intensified male competition selected for long-lived male plants that produced large amounts of pollen.

Funnelling mechanism and other structural changes The increase in seed size and pollen production would have entailed many physiological and morphological adjustments. One of these was probably the evolution of the funnelling mechanism to meet the increasing nutrient requirements for reproduction. This, in turn, may have been accompanied by the development of a lignified structure at the base of the trunk (bowl), which provides a strong anchorage for female trees laden with fruit, and also breaks the erosive force of water gushing down the trunk during heavy rain.

Low foliage nutrient concentrations Why should the foliage of Lodoicea have such low concentrations of N and P? These cannot be explained by exceptionally low total concentrations in the soil alone, because the values measured at Vallée de Mai lie within the ranges reported for other tropical rain forest soils on granite (Grubb et al., 1994). We suggest that the primary reason is an evolutionary trade-off between allocating nutrients to vegetative and reproductive structures, which in Lodoicea is strongly biased towards reproduction, especially in the case of P. The position of this trade-off, which profoundly affects ecosystem functioning in Lodoicea forest, is clearly different from that reached in other endemic palms of the Seychelles, which have much higher foliar P concentrations (by a factor of 2–4; M. Beaud & C. Kueffer, unpublished data), despite growing in similarly poor soils.

This interpretation is consistent with other studies showing a link between monodominance and low nutrient availability. In northeastern Congo, the litter produced by the monodominant tree Gilbertiodendron dewevrei decomposed much more slowly than litter from mixed forests, thereby slowing nutrient turnover within the ecosystem and reducing N availability in the soil (Torti et al., 2001). Seedlings of smaller-seeded tree species had difficulty in establishing in the deeper litter of Gilbertiodendron forest, which also favoured monodominance (Torti et al., 2001). Both mechanisms are likely to apply in Lodoicea forest. Indeed, the debris from the huge leaves of Lodoicea makes it almost impossible for other trees to establish (Seychelles Islands Foundation, unpublished data).

Clustered recruitment beneath the mother plant In the few areas where natural patterns of regeneration can still be observed, the huge seedlings of Lodoicea usually occur in a dense cluster close to the mother plant. Because of funnelling, nutrient and moisture conditions are favorable there (Fig. 2), but light intensities are often low and seedlings grow very slowly (Seychelles Islands Foundation, unpublished data). As the young plants grow larger, however, they increasingly compete with the mother tree, both by taking up nutrients from the same soil pool and by over-topping the mother’s foliage, reducing her funnelling capacity. This competition between generations could explain why female trees are apparently shorter-lived than male trees and rarely grow above 20 m in height (Edwards et al., 2002).

Resistance to herbivory Another mechanism that may assist a species in achieving monodominance is resistance to foliar damage (Torti et al., 2001; Peh et al., 2011). This is clearly evident for Lodoicea, which appears to sustain no damage from either vertebrate or invertebrate herbivores. This lack of herbivores could reflect a high investment in chemical defences (Torti et al., 2001), but is more likely to be a consequence of the extremely low nutrient content of the foliage (Coley & Barone, 1996). As in other nutrient-poor vegetation such as fynbos in the Cape Province of South Africa (Edwards, 1989), the low concentration of N rather than of P is likely to be the most important factor preventing its utilization by herbivores. This is supported by the observation that trees growing in fertile soil in Singapore botanic gardens often show heavy damage from rhinoceros beetles (P.J.E., pers. obs.).

The wider community Despite this absence of foliage feeders, Lodoicea forests support a remarkable community of animals,
several of which are known primarily from this ecosystem (Beaver & Chong-Seng, 1992; Noble et al., 2011; Reuleaux et al., 2013). Although of limited area, these forests are home to five endemic species of gecko (including one occurring only in Lodoicea forest) and a slug, all of which visit male flowers and feed on their pollen. The leaf litter at the base of trees hosts a recently discovered cricket and a frog, both known only from Praslin. Little is known about these organisms, but all of them probably depend, directly or indirectly, on the stream of resources that originates as pollen in male inflorescences, is intercepted by the foliage, and is funneled to the roots.

In conclusion, our results show that Lodoicea, despite growing in nutrient-poor soils, maintains high levels of both male and female reproductive function. This is achieved through a nutrient economy that allocates a high proportion of N and especially P to reproduction, producing vegetative tissues with very low nutrient concentrations and withdrawing most of the P from leaves before they are shed. The species also shows distinctive morphological features that enable it to improve its nutrient supply by funnelling particulate material to the base of the tree.

At first sight a botanical oddity, Lodoicea shows many functional similarities to other species forming monodominant forests in the humid tropics. However, it also exhibits unique features – notably the huge seed and highly developed funnelling mechanism – that presumably are products of its long evolution as a monodominant species in a stable island environment. This idea is supported by the evident coevolution with Lodoicea of several animal species, whose life histories have been shaped by its capacity to capture nutrients and invest heavily in reproduction.

Acknowledgements

We thank Seychelles Islands Foundation staff for assistance with data collection, and Seychelles Bureau of Standards and Department of Environment for permission to conduct the research and export samples, respectively. We are grateful to N. Bunbury and W. Accouche for coordinating and facilitating the research, and Seychelles Bureau of Standards and Department of Environment for funding the research. We are grateful to N. Bunbury and L. Turnbull, G. McInerney, N. Bunbury and three anonymous reviewers for providing valuable feedback on earlier drafts. We thank W. Accouche for coordinating and facilitating the research, and Seychelles Bureau of Standards and Department of Environment for funding the research. We are grateful to N. Bunbury and L. Turnbull, G. McInerney, N. Bunbury and three anonymous reviewers for providing valuable feedback on earlier drafts. We thank N. Hawtin for designing the infographic, E. Morgan for collecting the flowers, and C. Kueffer and M. Beaud for providing us with the nutrient analyses of Lodoicea foliage. C.N.K-B. was funded by the Swiss National Science Foundation (PA00P3_142204) and the German Research Foundation (KA 3349/2-1).

References


Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Inter- and intraspecific differences of effects of palm trees on spatial distribution of water and soil nutrients.

Table S1 Model results testing the influence of distance to the base of a tree on soil moisture among three plant species

Table S2 Model results testing the influence of distance to the base of a tree on soil nutrients phosphorus and nitrogen among three plant species

Please note: Wiley Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the New Phytologist Central Office.