

**Primary productivity
and its correlation
with rainfall on
Aldabra Atoll**

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Primary productivity and its correlation with rainfall on Aldabra Atoll

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Abstract

Aldabra Atoll, a UNESCO World Heritage Site since 1982, hosts the world's largest population of giant tortoises. In view of recent rainfall declines in the East African region, it is important to assess the implications of local rainfall trends on the atoll's ecosystem and evaluate potential threats to the food resources of the giant tortoises. However, building an accurate picture of the effects of climate change requires detailed context-specific case-studies, an approach often hindered by data deficiencies in remote areas. Here, we present and analyse a new historical rainfall record of Aldabra atoll together with two potential measures of primary productivity: (1) tree-ring measurements of the deciduous tree species *Ochna ciliata* and, (2) satellite-derived NDVI (normalized difference vegetation index) data for the period 2001–2012. Rainfall declined by about 6 mm yr^{-1} in the last four decades, in agreement with general regional declines, and this decline could mostly be attributed to changes in wet-season rainfall. We were unable to cross-date samples of *O. ciliata* with sufficient precision to deduce long-term patterns of productivity. However, satellite data were used to derive Aldabra's land surface phenology (LSP) for the period 2001–2012 which was then linked to rainfall seasonality. This relationship was strongest in the eastern parts of the atoll (with a time-lag of about six weeks between rainfall changes and LSP responses), an area dominated by deciduous grasses that supports high densities of tortoises. While the seasonality in productivity, as reflected in the satellite record, is correlated with rainfall, we did not find any change in mean rainfall or productivity for the shorter period 2001–2012. The sensitivity of Aldabra's vegetation to rainfall highlights the potential impact of increasing water stress in East Africa on the region's endemic ecosystems.

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annual temperature is between 24 and 28°C (Appendix B, Fig. B1), making rainfall the most likely factor limiting GPP. Given the close coupling between rainfall and the productivity of the tortoise turf (Gibson and Phillipson, 1983a), declines in rainfall are inevitably of concern, as this vegetation type hosts the highest densities of tortoises (Turnbull et al., 2015). Forecasted declines in wet season rainfall over eastern Africa could impact Aldabra's GPP strongly enough to jeopardize its tortoise population and other indigenous biodiversity in the future. In this study, we examine whether Aldabra's rainfall is declining, and whether there are detectable impacts on the atoll's GPP.

Several studies have used the normalized difference vegetation index (NDVI), derived from optical satellite sensors to infer land surface phenology (LSP) and its relationship with rainfall fluctuations in Africa (e.g. Eklundh, 2003; Omuto et al., 2010). In some of these ecosystems, dramatic fluctuations in rainfall induce not only seasonal oscillations in NDVI, but also the formation of annual growth rings in the cambium of some tree species (Fichtler et al., 2004). We combine meteorological data, deciduous tree-ring analysis, and NDVI to analyze long-term trends and intra-annual variability of rainfall and productivity proxies. More specifically, we aim to:

1. Investigate long-term trends in Aldabra's instrumental rainfall record.
2. Assess the dendroecological potential of the indigenous tree, *Ochna ciliata* and – if possible – use these measurements to assess long-term changes in Aldabra's mean primary productivity.
3. Investigate the relationship between land surface phenology and rainfall over the short term (2001–2012).

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November 1999 to October 2000). The resulting annual series was then regressed against year using ordinary least squares regression for the period 1969–2012, excluding years 1992 and 1993 (no data) and 1976 (missing October rainfall).

Daily rainfall records have been maintained since the year 2000, coinciding with the operational period of the Moderate Resolution Imaging Spectroradiometer (MODIS) sensors aboard NASA's Terra satellite. The daily rainfall data from 2000–2013 were averaged into a 16 day series to match the temporal resolution of the MODIS NDVI data for subsequent rainfall–NDVI analyses. Rainfall seasonality metrics were derived as described in Sect. 2.4.

2.3 Dendrochronological data and processing

Forty-five *Ochna ciliata* (hereafter *O. ciliata*) trees were sampled at Picard, GTE and GTSC (Grande Terre South-Central) sites in October 2012 (Fig. 1). One radial cross-section was sampled from each tree at breast height. In the laboratory, 32 cross-sections selected for the dendroecological analysis were sanded with progressively finer abrasive paper to reveal the growth zones and ring boundaries. Digital images of the sanded cross-sections were obtained at 1200 dpi using an Epson 10000XL flatbed scanner. Micro-sections of about 15 µm thickness were then sliced from the cross-sections using a sliding microtome after which they were stained with safranin-astra blue solution, dehydrated through an ethanol series (70, 95, 100 %) and clarified in xylol (Rossi et al., 2013). Fixed slides were then prepared by embalming the stained micro-sections in Canada balsam and drying them for 24 h at 60 °C. Digital images of these slides were then acquired at ×20 magnification using a light microscope (Olympus Bx41 microscope, Japan) equipped with a camera (Canon EOS 650D).

Tree-ring chronologies were developed using standard dendrochronological procedures (Stokes and Smiley, 1968). Tree-rings were identified from the micro-section images and their widths measured from pith to bark using WinDendro software Version 2008a (Regent Instruments Inc., 2008). Resulting chronologies were then cross-dated visually by checking anomalies such as false or missing rings observed

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on the micro-sections against digital scans of the respective tree cross-section. We used the percentage of sign agreement in interannual ring width variation to statistically evaluate the degree of congruence amongst chronologies within and across samples (Schweingruber, 1988).

2.4 NDVI data record and processing

The NDVI data product used to derive LSP metrics was obtained from the MODIS sensor aboard the Terra satellite. The product, Collection 5 VI MOD13Q1, was downloaded for the period 2000–2012 (Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC), 2011). The product has a spatial resolution of 250 m and a temporal resolution of 16 days. NDVI is computed as a normalized ratio of the reflectances in the near infra-red (NIR) and red spectral ranges:

$$\text{NDVI} = \frac{\rho_{\text{NIR}} - \rho_{\text{RED}}}{\rho_{\text{NIR}} + \rho_{\text{RED}}} \quad (1)$$

Where ρ is the reflectance integrated between 0.841 and 0.876 μm (NIR, MODIS Band 2) and between 0.62 and 0.67 μm (RED, MODIS Band 1) respectively (Huete et al., 2002).

The product is delivered with the following pre-processing. To minimize the negative bias clouds exert on NDVI, the maximum NDVI value from ca. 10 observations made in each 16 day window is retained to represent that period (Holben, 1986). The MOD13Q1 product is computed from MODIS surface reflectances that have been masked for water, clouds, aerosols, and cloud shadows (Huete et al., 2002). While the product is not corrected for reflectance anisotropy, it comes at the highest spatial resolution (250 m) that MODIS offers; an important advantage when working with spatial extents that are as small and heterogeneous as Aldabra. Quality filtering during pre-processing is done on a per-pixel basis (Huete et al., 2002). Some pixels close to the ocean were inconsistently classified as water or land areas by the MODIS land/water mask.

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series (Jönsson and Eklundh, 2004). Finally, LSP parameters were extracted for each site's NDVI time series for the 12 growing seasons spanning the period 2001–2012 as follows:

- i. Start of season (SOS): day of year at which 10 % of the NDVI range between previous dry season minimum and current growing season maximum is reached.
- ii. End of season (EOS): day of year at which 10 % of the NDVI range between the current growing season maximum and next dry season minimum is reached.
- iii. Length of season (LOS): arithmetic difference (in days) between SOS and EOS.

Value based seasonality parameters were extracted as follows:

- iv. Seasonal maximum: highest raw NDVI value in a given growing season.
- v. Seasonal NDVI mean: an average of all raw NDVI values between SOS and EOS.

The smoothing methodology applied to the NDVI data was also used to derive seasonality metrics from the 16 day rainfall time series. For each wet season, the total wet season rainfall was calculated as the sum of all raw 16 day values that fell between the respective rainfall SOS and EOS. Finally, each rainfall seasonality or LSP metric consisted of a series of 12 data points, one from each season over the 2001–2012 period.

2.5 Rainfall–NDVI correlations

First, we used time-series analysis to study the strength of the association between the 16 day rainfall and NDVI time series. The cross-correlation function measures the similarity between two time series as a function of a time-lag applied to one of them. In this case, it outputs Pearson's correlations between the rainfall and NDVI time series for lags 0 to n (where n is the maximal lag in days) applied to the rainfall series. The

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cross-correlation function is defined as:

$$r_n = \frac{\text{Cov}_n(\text{rainfall}, \text{NDVI})}{\text{SD}_{\text{rainfall}} \text{SD}_{\text{NDVI}}} \quad (2)$$

Where r_n is the cross-correlation coefficient at lag n , Cov is the covariance between the two time series while SD refers to the standard deviation. The cross-correlation analysis was conducted for each site starting with a lag of the NDVI series of 0 (concurrent 16 day window, $n = 0$) up to a lag of 6×16 days (3 months, $n = 6$). The maximum r_n from the resulting pool of lagged coefficients is then taken to represent that site's strongest vegetation response to prior rainfall conditions. To get a finer impression of the spatial variation in the rainfall–NDVI correlation, the cross-correlation analysis was also performed on the NDVI time series of each pixel (i.e., at the 250 m spatial resolution).

In the second part of this analysis, a Pearson's correlation matrix was computed for all the phenological and rainfall seasonality metrics i.e., for each unique pair between a rainfall seasonality metric and an LSP metric, a Pearson's correlation coefficient was calculated.

Finally, to assess the rainfall and NDVI trend over the short-term (2001–2012), each seasonality metric was regressed against year.

A significance threshold of $\alpha = 0.05$ was used for all statistical analyses discussed in this paper.

3 Results

3.1 Long term trends in rainfall

The initial regression of rainfall against time using all available data from 1969 to 2012 (Model I, Fig. 2) yielded a decline of 5.80 mm yr^{-1} in total annual rainfall ($p = 0.06$, adjusted $r^2 = 0.064$, standard error (SE) = ± 2.99 mm). Notably, 1998, which coincides

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with an El-Niño event was extremely wet. It was also the wettest year on Aldabra since 1969. In a second regression model (Model II, Fig. 2), we treated 1998 as an outlier. This analysis yielded a significant decline in total annual rainfall of 6.63 mm yr^{-1} ($p = 0.016$, adjusted $r^2 = 0.12$, $\text{SE} = \pm 2.64 \text{ mm}$); hence this outlier has little impact on the estimate. To assess the possible impact of the missing rainfall data from October 1976, we interpolated this value using a mean based on all available data. This model gave a slope estimate of -5.80 mm yr^{-1} ($p = 0.06$, adjusted $r^2 = 0.064$, $\text{SE} = \pm 2.99 \text{ mm}$). Once again, excluding 1998 from this model yielded a slope of -6.64 mm yr^{-1} ($p = 0.016$, adjusted $r^2 = 0.12$, $\text{SE} = \pm 2.64 \text{ mm}$); hence the estimate is also robust to the inclusion of the 1976 rainfall data.

We further split the annual rainfall into wet season (November–April) and dry season (May–October) totals. For the wet season totals there was a significant decline of -5.74 mm yr^{-1} , ($p = 0.01$, adjusted $r^2 = 0.13$, $\text{SE} = \pm 2.13 \text{ mm}$; excluding 1998), and for the dry season a non-significant decline of -1.42 mm yr^{-1} , ($p = 0.18$, adjusted $r^2 = 0.02$, $\text{SE} = \pm 1.05 \text{ mm}$; excluding 1998). Therefore, the decline in annual rainfall appears to be mostly due to reduced wet season rainfall, a trend that coincides with the wider East African region (Funk et al., 2008; Lyon and DeWitt, 2012).

3.2 Dendroecology

Despite the presence of rings (Fig. 3), absence of clear tree-ring wood anatomical structures and of common and consistent ring-width patterns between samples, within and across sampling sites impeded precise cross-dating. Information such as absolute age of the trees or periodicity of cambial activity in the species on Aldabra would have reduced cross-dating uncertainties, e.g., as shown by Nicolini et al. (2010) with *Acacia seyal* from Niger.

Due to the described limitations, we were unable to link the tree-ring chronologies to the long-term rainfall record (1969–2012) or, use the tree-ring data to assess long-term trends in Aldabra's productivity. However, as outlined in the discussion section,

this result is still of ecological importance with regard to how woody types on Aldabra respond to seasonal and inter-annual changes in rainfall as compared to tortoise turf.

3.3 Rainfall–NDVI seasonality patterns over 2001–2012

NDVI time series of all six sites followed similar annual cycles (Fig. 4). Based on the mean annual NDVI time series (January–December) averaged from 2001 to 2012 data, NDVI minima ranged from 0.44 (Polymnie) to 0.56 (Malabar) while the maxima ranged from 0.58 (GTSC) to 0.71 (Malabar). Similar to the atoll-wide mean NDVI (Fig. 4), all six sites exhibited distinct unimodal seasonality, consistent with the pattern in the rainfall time series. In addition, there is no discernible upward or downward inter-annual trend in rainfall or in NDVI for 2001–2012.

3.4 Rainfall–NDVI correlations

The strongest rainfall–NDVI correlation occurred at a lag of one to four 16 day periods, depending on the site. This means that an NDVI observation from a given 16 day period is most strongly associated with rainfall from either the previous 16 day window (lag 1) or the 2nd–4th preceding periods (lags 2–4). Picard and Polymnie appear to have shorter lag periods than Grande Terre and Malabar. For all study units on Grande Terre, the maximal rainfall–NDVI correlation occurred at a lag of three 16 day periods, corresponding to an approximate six week time difference between rainfall changes and ensuing vegetation responses (Table 2).

Figure 5 shows the spatial variation in the magnitude of rainfall–NDVI correlations (r_n) at the pixel resolution. Spatial patterns in these correlations that correspond to the distribution of different vegetation types and their sensitivity to water stress can be discerned. GTE, which has the highest percentage cover of tortoise turf, has the highest correlation between rainfall and NDVI, suggesting that tortoise turf are particularly sensitive to changes in rainfall. Areas along the lagoon shores (mangrove

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dominated) have the lowest r_n values with the exception of Malabar which unlike other sites, has low r_n values along the lagoonal shores and in most of its inland regions.

Correlation analysis of rainfall seasonality and NDVI-derived vegetation phenological metrics revealed clear spatial patterns in the strength of the relationship between wet season total rainfall and corresponding growing season NDVI (Table 3). Year 2007 was excluded as an outlier because, compared to other years, its growing season mean and maximum NDVI (atoll-wide) were unusually high for the corresponding wet season rainfall amount, e.g. there is a correlation between maximum growing season NDVI (atoll wide) and wet season rainfall ($r = 0.68$, $p = 0.02$, $n = 11$) only with the exclusion of year 2007 (Fig. A2). Correlation between mean growing season NDVI and total wet season rainfall on the other hand borders on statistical significance ($r = 0.58$, $p = 0.06$) when the 2007 season is excluded.

Unlike other years, the 2007 wet season appears bimodal (Fig. 4). Its second “hump” occurs beyond the respective wet season EOS as designated by the Savitzky–Golay smoother (Fig. 4), possibly resulting in an underestimation of the 2007 wet season rainfall and hence the outlier effect (Fig. A2). This illustrates a typical challenge in parameterization of noisy time series by smoothing, i.e., it is sometimes difficult to optimize the smoother’s fit both locally and globally.

Significant Pearson correlation coefficients (between rainfall and NDVI seasonality metrics) are only significant upon exclusion of year 2007 data (Table 3). For brevity, we present and discuss results from four sites, where at least one significant correlation coefficient between an LSP metric and a rainfall seasonality metric was observed. This excludes GTSC and Picard.

We did not find significant temporal trends in any of the rainfall or NDVI seasonality metrics for the 2001–2012 period.

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NDVI data were freely obtained online through the MODIS global subsetting tool at the Oak Ridge National Laboratory Distributed Active Archive Centre.

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Table B1. Total monthly rainfall (in millimetres) on Aldabra based on rain-gauge readings at Picard station. Source: Seychelles Islands Foundation.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1969	153.4	147.2	151.5	393.5	176.3	36.8	39.7	14.3	18.5	11.8	54.9	56.8
1970	47.5	85.2	139.6	210.5	31.7	29.5	33.7	25.7	7.3	20.9	12.7	56.6
1971	244.5	57.4	246.6	192.5	34.7	65.9	14.3	19.1	8.6	6	88.7	200.4
1972	224.5	15	112.2	162.2	28.2	100.3	54.6	75.1	4.2	12.7	25.6	240.2
1973	261	286.8	262.8	56.7	57.1	47.7	81.3	25.2	21.8	33.7	9.2	77.6
1974	290.6	114.5	380.8	346.4	50.4	29.4	51.2	31.8	1.9	1.1	19.4	148.9
1975	131.4	162.8	111.1	166.7	76.7	41.4	16.1	14.9	14.5	2.9	91.7	136.2
1976	357.4	177.4	260.9	87.1	66.6	64.4	65.5	36	4.7	NA	16.7	79.8
1977	262.5	116.3	255.7	239.4	139.6	89.5	82.2	26.8	5	37	63.5	120.8
1978	254	139.2	339	18	54.8	48.1	135.4	22.6	8.7	16.9	191.6	234.4
1979	233.6	108.6	105.2	67.8	140.3	55.3	61.4	33.7	19.4	0.1	52.3	262.2
1980	82.1	151.9	120.8	184.9	19.1	66.1	16.6	40	10	1.6	9.5	123.1
1981	143.5	52.9	238.1	17.8	94.5	26.2	22.1	20.4	12.1	8.6	10.8	337.1
1982	91.4	44.8	121.2	136.8	70.1	106.9	12.9	17.2	40.9	47.5	110.4	34.6
1983	481.4	108.8	140.2	51.4	146	12.4	12	24.6	5.5	30.7	65.3	228.9
1984	81.5	56	137.5	74.4	19.3	48.5	15.1	2.8	1	6.6	27.1	117.3
1985	58.4	212.4	162.3	116.6	24.9	46.9	24.9	18.5	2.8	10.9	38.4	168.3
1986	263.7	10.6	128.4	116.3	118.5	44.2	56.2	11.7	5.7	4.7	92.4	243
1987	78.2	190.5	90.8	126.7	14	23.6	54	48.9	7.6	2.2	125	174.1
1988	195.5	159.6	132.4	15.6	46.7	33.6	22.8	28.5	3.2	5.8	87.6	305.5
1989	85.5	7.2	265	195.9	83.6	32.4	19.3	9.3	5.7	7.8	28.5	194.5
1990	264.2	83.2	35	197.8	28.5	5.7	15.5	6.7	12.7	6.5	99.1	186.7
1991	336.1	50.7	13.8	47.7	33.6	23.2	12.3	13.1	13.1	7.5	38.5	NA
1992	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1993	NA	NA	NA	400	132.2	23	5	25	4	0	7	28
1994	84.4	112	183	63.3	107.8	24.8	14.9	14.5	4.7	235.4	5.3	442.3
1995	53	76.6	306.7	122.4	38.1	18.3	19.6	10.4	10.8	10.4	2	19
1996	145	175.6	301.6	19.7	19.9	36.8	46.5	6.6	3.6	12.4	10.1	70
1997	298.2	0	220.3	48	21.4	19.4	12	9.2	0.8	12.6	227.8	299
1998	332.5	282.6	124.3	246.6	41.2	58.3	37.4	32.6	12.6	8.1	10.2	85.1
1999	246.9	153.7	187.8	4.9	24.9	27.71	28.65	2.9	9.1	4.8	15.7	131.6
2000	50.6	13.4	122	34.4	20	68.4	20.4	21.1	1.7	0.4	22.8	116.3
2001	142.3	229.9	102.3	63.1	42.8	27.3	16.3	41	3.6	80.5	12	102.4
2002	114.2	66	174.8	38.9	9.5	2.7	1.2	2.6	7.4	2.2	35.2	127.5
2003	121.7	44.1	133.9	274	74.4	37.2	31.8	25.7	15.8	4.2	28.5	315
2004	69.5	145.1	11.2	9.1	14.6	7.4	42.9	19	6.2	137	21.5	152.2
2005	249.3	151.85	150.95	170.6	179.45	9.33	38.28	17.58	4.1	5	25.55	77.8
2006	383.3	226	431.4	29.6	43.8	59.2	105.7	83.97	70.91	1.5	87.8	264.9
2007	124.48	22.97	69.11	7.53	17.81	127.8	23.8	16.23	44	5.4	113.8	49
2008	245	51.6	115.9	120.78	6.9	12.6	16.4	5.4	10.7	4.4	76.2	121.7
2009	92	45.9	157.1	91.25	95.5	16	49.6	14.9	5.62	0	10.2	157.55
2010	43.7	243.9	82.66	103.7	70.52	45.24	26.67	20.65	9.65	11.96	6.03	68.31
2011	151.29	149.85	156.31	235.21	85.3	29.38	13.84	21.08	15.7	27.11	96.7	117.65
2012	41.6	262.9	133.6	182	55.7	58.3	27.6	10.3	7.7	2.1	38	183.6

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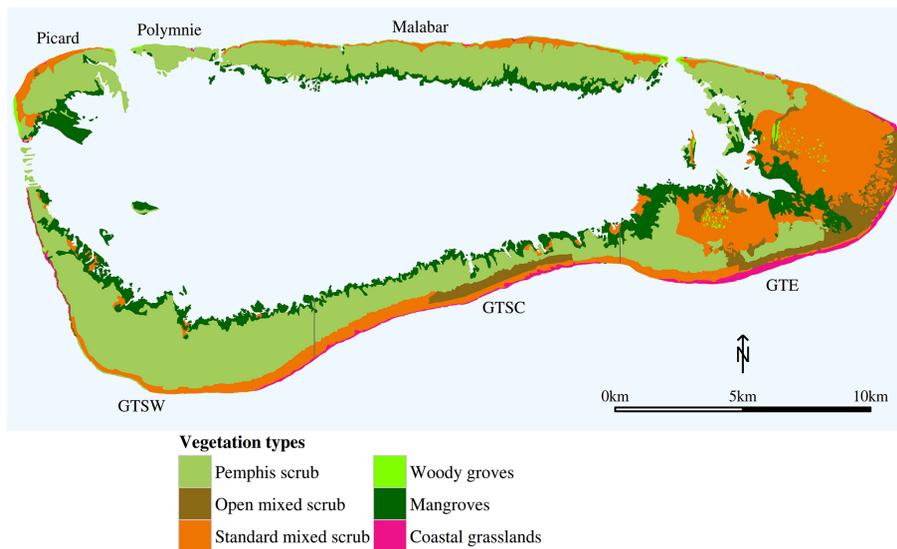


Figure 1. Spatial distribution of vegetation types on Aldabra Atoll based on a 1983 vegetation survey (Gibson and Phillipson, 1983b). This reproduction was prepared by vectorizing the original hard copy. In this study, the southern island of Grande Terre is further split into south-western (GTSW), south-central (GTSC) and eastern (GTE) sub-regions.

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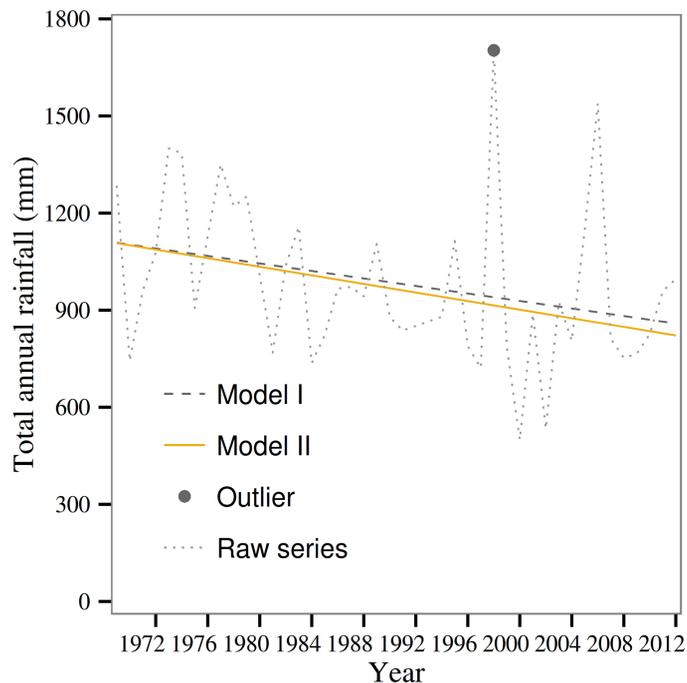


Figure 2. Long term trends in Aldabra’s total annual rainfall from rain gauge readings at the Picard research station over the period 1969–2012. An ordinary least squares regression model was used to model total annual rainfall as a function of time (year) (Model I). The model was then refitted with the wettest year on Aldabra’s instrumental rainfall record, i.e., 1998, excluded as an outlier thus yielding Model II.

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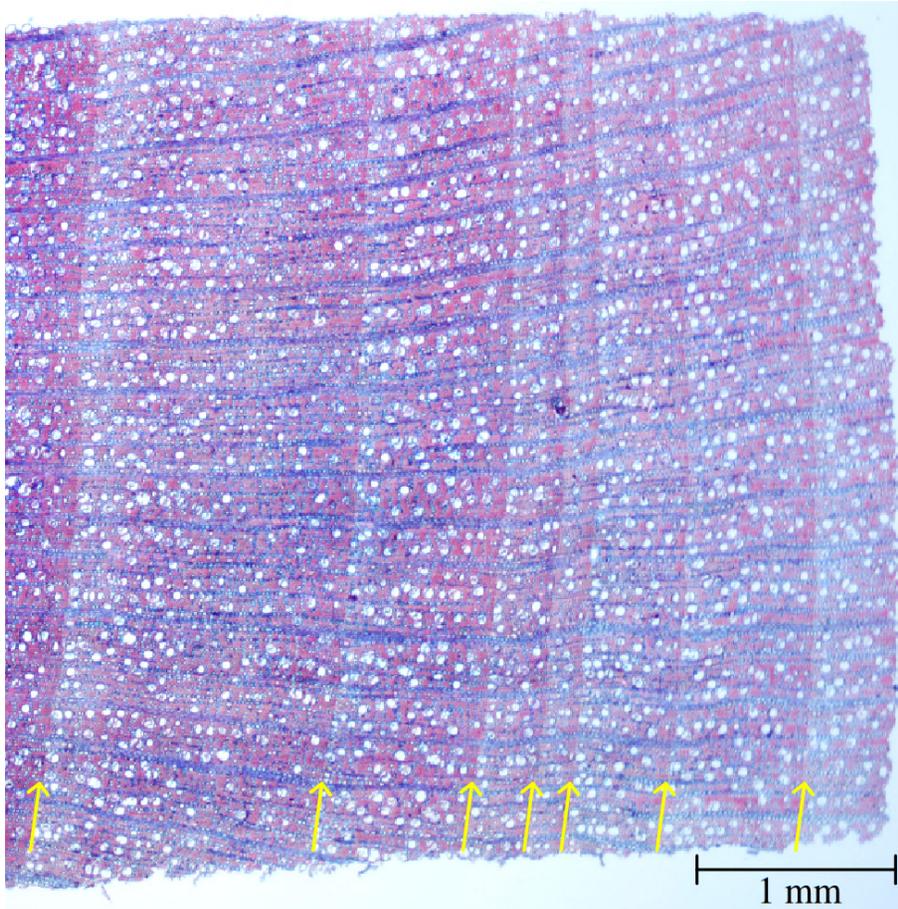



Figure 3. Radial micro-section of an *Ochna ciliata* sample obtained from Picard. Yellow arrows indicate the seven outermost ring boundaries i.e., the image's left to right direction corresponds to the micro-section's pith to bark orientation.

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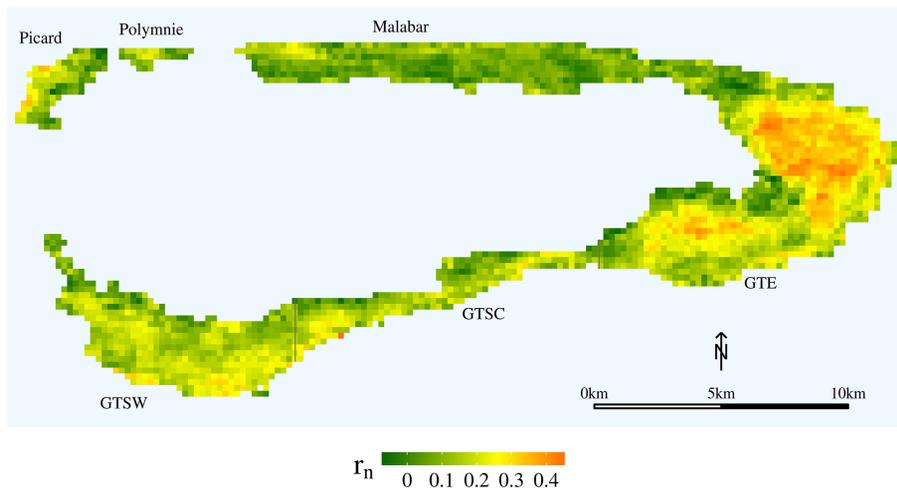


Figure 5. Spatial variation in the strength of rainfall–NDVI cross-correlation (r_n). Coefficients above 0.115 are significant (Fig. A1). Notably, the relationship between NDVI and rainfall is strongest in areas dominated by deciduous types i.e. on GTE. (See Fig. 1 legend for full site names.)

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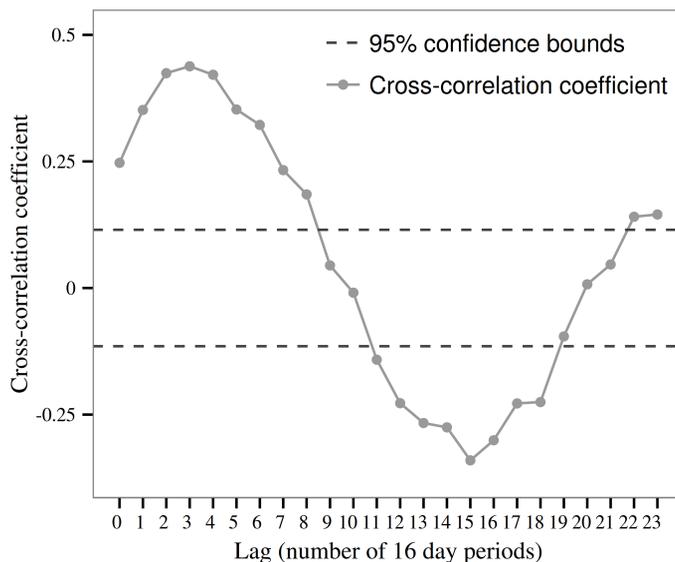


Figure A1. Cross-correlation analysis showing lagged correlation coefficients between rainfall and NDVI (normalized difference vegetation index) time series for up to 23 sixteen day lags (one calendar year). Under the null hypothesis that there is zero correlation between the two time series, the 95% confidence intervals are $0 \pm 2/\sqrt{N}$ where N is the length of the time series (Metcalf and Cowpertwait, 2009). NDVI time series of all pixels had a length of 299 (23 values per year covering 13 years). Confidence bounds therefore correspond to cross correlation coefficient values of ± 0.115 .

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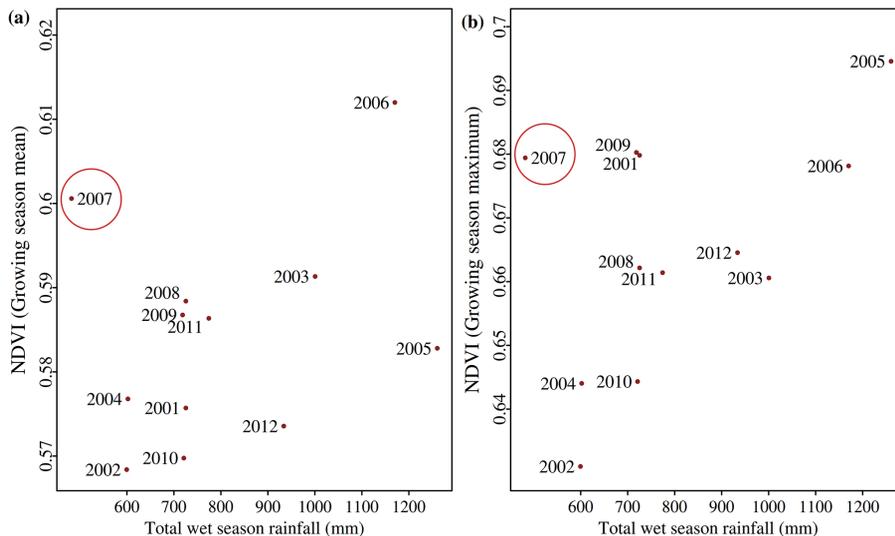


Figure A2. Year 2007's outlier effect in the correlation between wet season rainfall and **(a)** atoll-wide growing season mean NDVI (normalized difference vegetation index); **(b)** atoll-wide growing season maximum NDVI.

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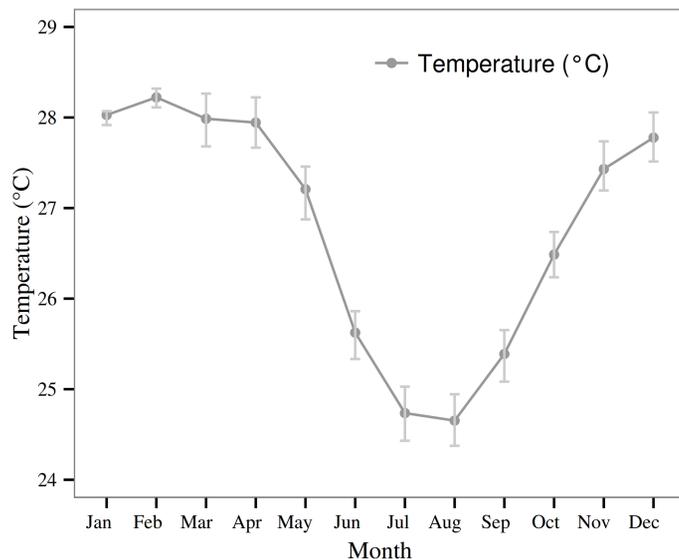


Figure B1. Mean monthly dry-bulb temperatures (\pm standard error) on Aldabra based on the 1968–2008 average and excluding 1992–1999 for which there is no data. Source: Seychelles Islands Foundation.

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