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Tropical forests are incredibly dynamic, showing rapid and longer-term changes in growth, mortality, and net primary productivity (NPP) [1,2,3]. Tropical species may be highly sensitive to temperature increases associated with climate change because of their narrow thermal tolerances. However, at the ecosystem scale the competing effects of temperature, light, and precipitation on tropical forest productivity have been difficult to assess. Here we quantify cloudiness over the past several decades to investigate how clouds, together with temperature and precipitation, affect flower production in two contrasting tropical forests. Our results show that temperature, rather than clouds, is critically important to tropical forest flower production. Warmer temperatures increased flower production over seasonal, interannual, and longer timescales, contrary to recent evidence that some tropical forests are already near their temperature threshold [4,5]. Clouds were primarily important seasonally and limited production in a seasonally dry forest but enhanced production in an ever-wet forest. A long-term increase in flower production at the seasonally dry forest is not driven by clouds and instead may be tied to increasing temperatures. These relationships show that tropical forest productivity, which is not widely thought to be controlled by temperature, is indeed sensitive to only small temperature changes (1-4° C) across multiple timescales.

Tropical forests play a large role in the global carbon budget, accounting for about 35% of terrestrial productivity [6]. This productivity in turn has important cascading effects on numerous species with about half of the world's species residing in the tropics [7]. Temperature has long been recognized as a fundamental constraint on many biological processes across a wide range of temporal and spatial scales [8]. It has been hypothesized that tropical species are highly sensitive to climate change and temperature increases because of the narrow temperature range that they occupy [9], and because they may already exist near their upper thermal limits [8]. Some however, have suggested that the ecological impacts of increasing temperature in the tropics will be less pronounced than in higher latitudes because tropical regions experience smaller variability in temperature [10,11]. Tropical forests are warm year-round, usually receive ample precipitation, and thus may instead be more strongly limited by light [1]. Solar radiation has been shown to be highly dynamic over tropical regions and there is some evidence that tropical cloudiness has been decreasing over the past several decades [12]. Numerous experimental and observational studies have shown that cloud cover can limit tropical forest productivity because clouds reduce light availability [13–16], thus a decrease in cloudiness should result in increased productivity.

One of the challenges to understanding drivers of change in tropical forests is considering the simultaneous effects of temperature, clouds, and precipitation, in part because long-term changes in cloudiness have been difficult to quantify [3,17]. Here we advance research in this area by using a new globally gridded satellite dataset, NOAA NCDC GridSat, which provides visible and infrared data to directly quantify cloudiness over the past several decades. Our empirical approach is based on rare long-term flower production records from two contrasting tropical forest sites— one seasonally dry, Barro Colorado Island, Panama (BCI) and one ever wet, Luquillo, Puerto Rico (Figure S1 and S2). We focus on flower production because it is an important measure of reproductive activity as well as an indicator of primary productivity [18]. Using regressions of monthly data we examine what the relative effects of clouds, temperature, and precipitation are on seasonal (intra-annual) and year-to-year (interannual) patterns of flower production. We also examine whether there are long-term trends in flower production and associated climate variables.

On a seasonal timescale higher temperatures were associated with greater flower production at both sites, but cloudiness affected flower production in site-specific ways (Table 1, Figure 1).

At the seasonally dry site, flower production decreased with more clouds. In contrast, at the wet site, flower production increased with increased cloudiness, which may be due to the effects of diffuse light. The light-use efficiency of forests can be higher under cloudy or partly cloudy conditions (low irradiance conditions) because diffuse light is scattered more uniformly throughout the canopy and understory, whereas on clear-sky days sunlight comes from a single direction and many leaves remain in shadow [19,20]. Unlike the seasonally dry site, the wet site is located outside the thick deep convective clouds of the Intertropical Convergence Zone (ITCZ) and cloudiness values were on average lower (Figure 1 and 3), indicating fewer and/or optically thin clouds that enhance diffuse radiation [21]. Results suggest that clouds limit light availability at the seasonally dry site by blocking solar radiation but enhance light availability at the wet site by increasing the diffuse fraction of radiation. Even though clouds had divergent effects on flower production, both sites appear to respond positively to increases in light availability.

We further examined the role of direct radiation on flower production by estimating direct light availability. To do this we reduced top of the atmosphere (TOA) insolation proportional to % cloudy values (i.e., incoming minus reflected; see Supplementary Information). We found that flower production increased with direct light availability at the seasonally dry site (Table S1), supporting the role of direct radiation. At the wet site, however, there was no significant relationship between flower production and estimated direct light availability, again suggesting that the primary effect of clouds on flower production may be in altering diffuse radiation (see further discussion in Supplementary Information).

Relationships with climate differed at seasonal (Table 1) and interannual time scales (Table 2). At the seasonally dry site, the positive effect of temperature was still evident at interannual time scales in addition to the positive effect of precipitation (Table S3). Although irrigation experiments have shown that water addition does not affect leaf litter, wood, or fine root production at the seasonally dry site [22,23], a reduction in water availability associated with droughts may lead to water stress, increased tree mortality and decreased flower production [24,25]. At the wet site, the relationship between flower production and clouds became negative while controlling for the effect of temperature (Figure S4; Table S3). This negative relationship suggests that interannual climate variability results in changes in cloud cover that block solar radiation, possibly associated with large storms or hurricanes as opposed to more predictable seasonal variability.

The seasonally dry site exhibited significant long-term increases in flower production at an average rate of 3% more flowers per year ($R^2 = 0.84$, df = 21, $p<0.001$, Figure 2; see Supplementary Information). At the wet site there was no long-term trend in flower production after accounting for the effects of Hurricane Hugo in 1989 (Figure S2). Decreases in cloudiness and concomitant increases in solar radiation reaching tropical forests have been hypothesized to drive long-term changes in tropical forests [3]. Contrary to these hypotheses [3,12] our results show that the lack of significant long-term trends in cloudiness at either site indicates that clouds and light availability are likely not contributing to long-term directional changes at these tropical forest sites (Figure 3). Instead, the trend at the seasonally dry site may be attributed to increasing maximum temperature ($0.03° \mathrm{C}\ \mathrm{yr}^{-1}$ or about 1% of mean monthly maximum temperatures; $R^2 = 0.20$, df = 21, $p<0.05$; Figure 2) or precipitation ($0.17\ \mathrm{mm}\ \mathrm{yr}^{-1}$ or 0.2% of yearly total; $R^2 = 0.23$, df = 21, $p<0.05$), which is also seen in our interannual analyses of flower production (Table 2, Figure S4). The ~$0.03\ °\mathrm{C}\ \mathrm{yr}^{-1}$ temperature increase is similar to changes across the entire tropical forest biome (~$0.024\ °\mathrm{C}\ \mathrm{yr}^{-1}$) [3], whereas changes in cloudiness are regionally variable.

Our results demonstrate that clouds and light availability affect flower production on a seasonal basis, whereas temperature is a major driver of flower production across several timescales (seasonal, interannual, and the long-term trend at the seasonally dry site). Although the most recent IPCC projections show that temperature increases in the tropics will be smaller in magnitude compared to higher latitude regions [26], our results demonstrate that the productivity and reproductive activity of both seasonally dry and wet tropical forests are sensitive to temperature changes of just 1-2 °C in interannual analyses and 2-4 °C in seasonal analyses (Figures 1, 2, and S1) .

Other studies have suggested that tropical forests are already near their temperature threshold [4,5], however our results based on flower productivity do not show evidence of this—relationships with temperature were always positive at both sites (seasonal, interannual, and long-term trends). Increasing temperatures may enhance flower productivity through both a direct effect on photosynthesis or indirect effects such as increasing rates of litter decomposition and nutrient cycling [27]. Nonetheless, if temperatures continue to increase, it is likely that the productivity of these forests will decline because of increasing rates of respiration or direct cell damage [17,28].

We focused on the role of climate to help answer how tropical forests may respond to climate change in the future but other factors are known to affect forest dynamics. Patterns of flowering phenology in the tropics are affected by biotic interactions such as competition for resources and the timing of peak pollinator activity [29]. Disturbance events such as hurricanes and El Niño-Southern Oscillation are also important to understanding long-term forest dynamics, threshold responses and resilience to disturbance. Additionally, rising atmospheric CO_2 concentrations have been suggested as a potential driver of directional change in tropical forests.

However the wet site shows no directional trend, which would be the expected response to rising CO_2 (although CO_2 does not vary substantially across regions, it is possible that disturbances have masked this effect). Results from other tropical forest sites are also inconsistent with a pantropical increase in productivity associated with rising CO_2 concentrations [30].

Our work addressing climatic drivers of tropical forests highlights the need for further efforts to tease apart the relative importance of the direct and indirect effects of temperature and clouds. We used an unparalleled set of satellite data and ground observations, but completely disentangling competing effects will require physiologically-based experiments to complement our results. Additionally, while measures of diffuse radiation are lacking, our results show that these measurements are crucial for the accurate prediction of tropical forest response to global change. In order to advance our understanding and improve predictions of climate change impacts on tropical forests, efforts to combine and synthesize results from process-based experiments and measurements with longer-term ecosystem-scale observations will be critical.

Methods

We examined the relative effects of clouds, temperature, and precipitation on flower production using regression analyses and monthly averaged data. Because observations in time series data are often serially correlated and therefore non-independent, we fit appropriate error correlation structures (autoregressive and moving average components). Flower production was log-transformed to reduce heteroscedasticity. We used Akaike's Information Criterion (AIC) to assess model fit in a full model, which included each predictor and all two-way interactions (model A in Table 1), compared to reduced models (models B-E in Table 1). Models explained primarily seasonal variation in flower production, therefore to address interannual variation we performed regressions using de-seasonalized monthly data (year-to-year anomalies from the monthly mean for each month). Finally we examined whether there were long-term trends in flower production and associated climate variables using year to predict mean values each year. See Supplementary Information for further details about study sites, remote sensing of clouds, and statistical analyses.

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Author contributions

S.P., B.I.C., E.M.W., and S.J.W. developed and designed the primary analyses. S.P. and J.R. analyzed satellite data and developed cloud detection algorithms. J.K.Z., C.J.N., and S.J.W. curated and assisted with interpretation of the flower production and meterological data. S.P. performed all analyses and wrote the first draft of the manuscript. All authors discussed the results and helped edit the manuscript.

Figure Legends

Figure 1. Empirical relationships between flower production with clouds and temperature at BCI, a seasonally dry tropical forest (a) and Luquillo, a wet tropical forest (b). Data were averaged to monthly values across several decades. Solid points are the observed data with colors indicating differences in temperature (increasing with darker shade). The plane is fitted using a multiple regression with autocorrelated errors, which explained primarily seasonal variation in flower production (all $p < 0.05$; see Table 1 and Supplementary Information). Precipitation was never significant except in its interaction with clouds at the seasonally dry site (Figure S3).

Figure 2. Long-term trends in flower production (solid line) and maximum temperature (dotted line) at BCI from 1987-2009. Flower production was calculated as the number of flower presences for each species in each trap-census combination and averaged to monthly values. Daily temperature was recorded at a meteorological tower above the forest canopy. Both flower production and temperature were averaged to yearly values and regressed against 'year' to examine long-term trends (flower production: $R^2 = 0.84$, df = 21, $p<0.001$; temperature: $R^2 = 0.20$, df = 21, $p<0.05$).

Figure 3. Seasonal and interannual variation in cloudiness at BCI, a seasonally dry tropical forest (a) and Luquillo, a wet tropical forest (b). Data are from NOAA NCDC GridSat-B1, which provides visible (6μm) and thermal infrared (11μm) data every 3 hours since 1980 at 8-km grid cell spatial resolution. Daily data were used to calculate '% of the day cloudy' and then averaged to monthly values.

Table 1. Models of seasonal flower production at a seasonally dry (BCI) and wet (Luquillo) tropical forest using monthly values. The full model (model A; includes clouds, temperature, and precipitation and their two-way interactions) was compared to reduced models (B-E) based on Akaike's information criterion (AIC). Shading indicates equivalent best-fit models. Clouds and temperature were always included in the best-fit models. The main effect of precipitation was never significant in any of the models at either site ($p > 0.05$; see Table S2). These models explained primarily seasonal (not interannual) variation in flower production (see Supplementary Information). To account for autocorrelated errors in monthly data, all models included an autoregressive parameter and models for Luquillo included an additional moving average parameter (see Supplementary Information).

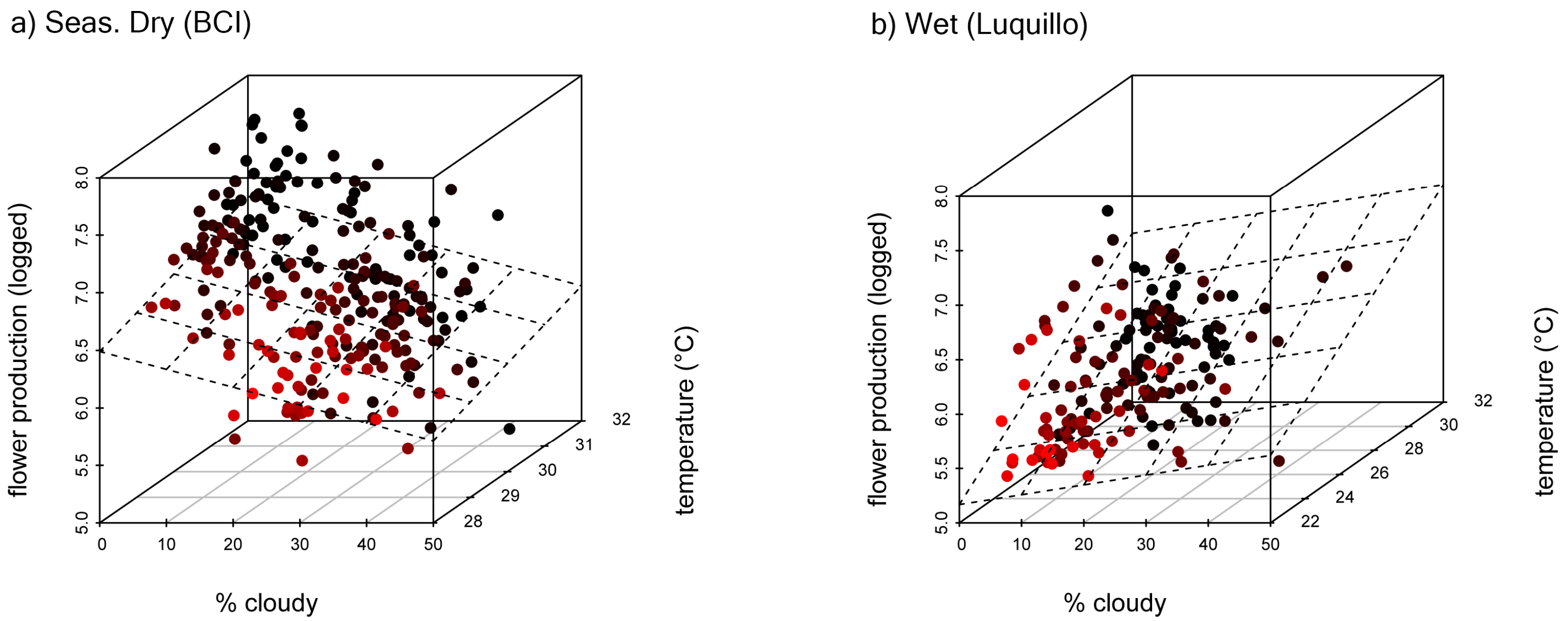
BCI flower production	**Parameters**	**AIC**	**psuedo R^2**	**k**
A) full model	cloud1 + temp + precip + cloud1*temp + cloud1*precip + temp*precip	150.93	0.42	9
B) without interactions	cloud1 + temp + precip	151.47	0.43	6
C) clouds and temperature	cloud1 + temp	149.65	0.43	5
D) clouds and precipitation	cloud1 + precip	165.72	0.30	5
E) temperature and precipitation	temp + precip	193.29	0.28	5
Luquillo flower production				
A) full model	cloud1 + temp1 + precip + cloud1*temp1 + cloud1*precip + temp1*precip	157.45	0.12	10
B) without interactions	cloud1 + temp1 + precip	154.29	0.10	7
C) clouds and temperature	cloud1 + temp1	155.89	0.08	6
D) clouds and precipitation	cloud1 + precip	185.28	0.04	6
E) temperature and precipitation	temp1 + precip	157.90	0.09	6

"cloud" = % of the day cloudy; "temp" = temperature; "precip" = precipitation; "1" indicates the preceding month's value (all data were aggregated to monthly values); "pseudo R^2" = the squared correlation coefficient of observed against predicted values for flower production; "k" = number of model parameters.

Table 2. Models of interannual flower production at a seasonally dry (BCI) and wet (Luquillo) tropical forest using de-seasonalized monthly values (Figure S4). The full model (model A; includes clouds, temperature, and precipitation and their two-way interactions) was compared to reduced models (B-E) based on Akaike's information criterion (AIC). Shading indicates equivalent best-fit models. Clouds and their interactions were never significant in any models at either site when using all available data for both sites (Table S3). For post-1994 Luquillo data (excluding the effect of Hurricane Hugo), clouds were significant ($p < 0.05$; see Table S3) with the additive effect of temperature (model C) and no other variables were significant in any of the other models. De-seasonalized monthly values were calculated as observed monthly values minus the mean value over all years for the appropriate month.

BCI flower production	**Parameters**	**AIC**	**adj R2**	**k**
A) full model	cloud+ temp + precip + cloud*temp + cloud*precip + temp*precip	3812	0.07	8
B) without interactions	cloud + temp + precip	3806	0.07	5
C) clouds and temperature	cloud + temp	3817	0.04	4
D) clouds and precipitation	cloud + precip	3820	0.03	4
E) temperature and precipitation	temp + precip	3805	0.08	4
Luquillo flower production - all data				
A) full model	cloud+ temp + precip + cloud*temp + cloud*precip + temp*precip	2363	0.11	8
B) without interactions	cloud + temp + precip	2362	0.10	5
C) clouds and temperature	cloud + temp	2372	0.05	4
D) clouds and precipitation	cloud + precip	2371	0.05	4
E) temperature and precipitation	temp + precip	2361	0.11	4
Luquillo flower production - post-hurricane				
A) full model	cloud+ temp + precip + cloud*temp + cloud*precip + temp*precip	1787	0.01	8
B) without interactions	cloud + temp + precip	1781	0.03	5
C) clouds and temperature	cloud + temp	1779	0.03	4
D) clouds and precipitation	cloud + precip	1781	0.02	4
E) temperature and precipitation	temp + precip	1782	0.02	4

Figure 1.



a) Seas. Dry (BCI)
flower production (logged)
5.0
5.5
6.0
6.5
7.0
7.5
8.0
0
10
20
30
40
50
% cloudy
28
29
30
31
32
temperature (°C)
b) Wet (Luquillo)
flower production (logged)
5.0
5.5
6.0
6.5
7.0
7.5
8.0
0
10
20
30
40
50
% cloudy
22
24
26
28
30
32
temperature (°C)

Figure 2.

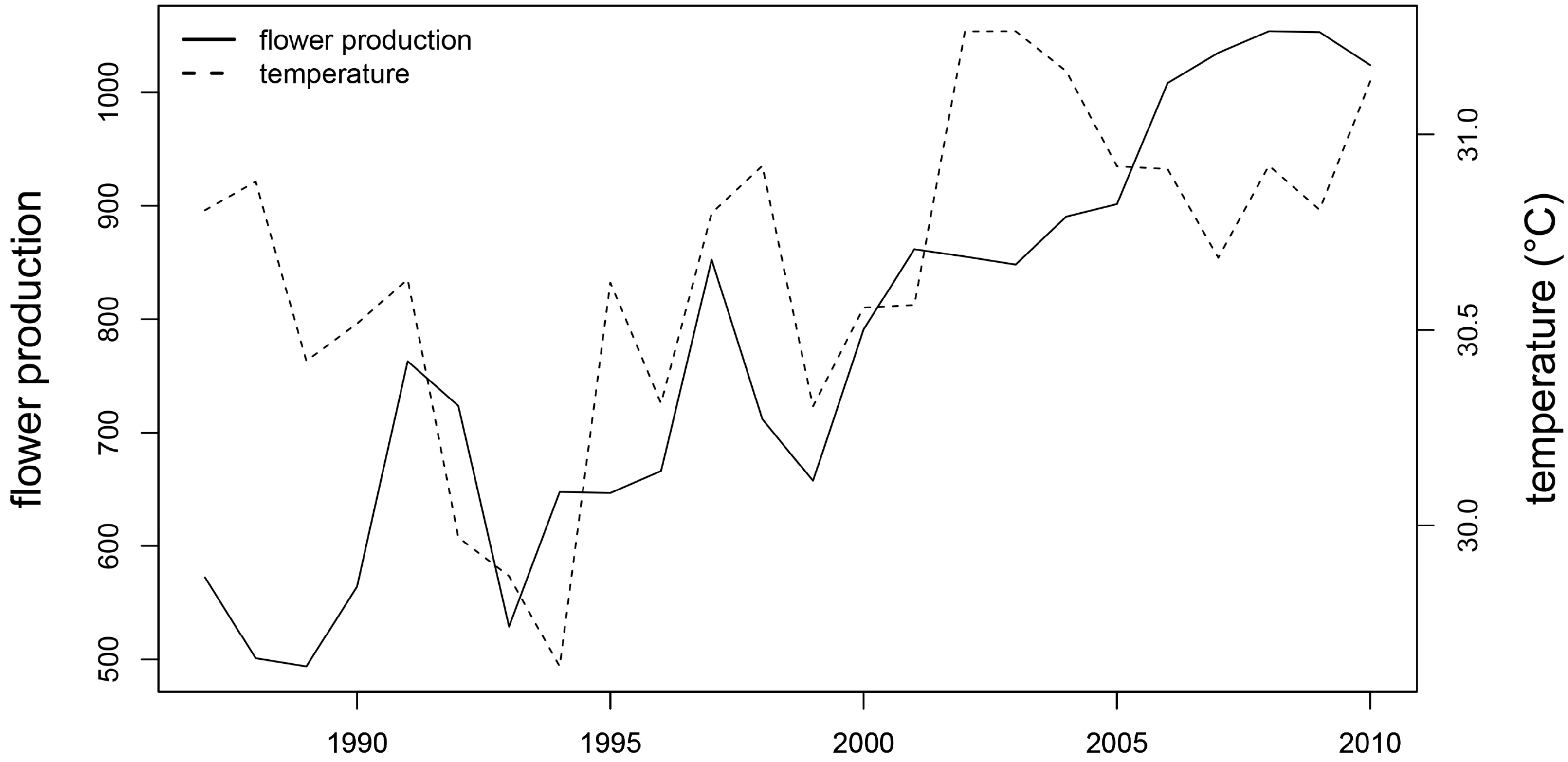
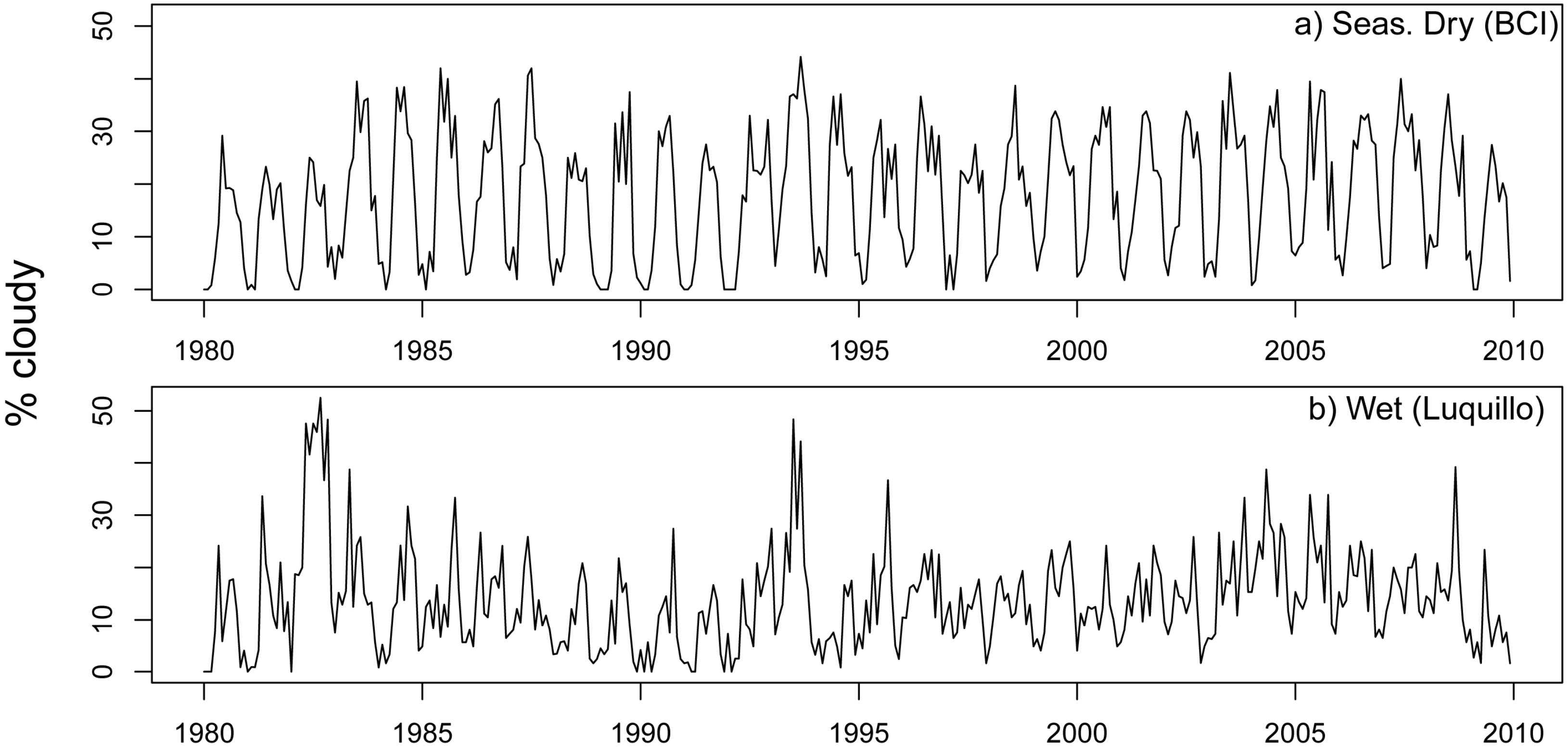

flower production
temperature
flower production
temperature (°C)
500
600
700
800
900
1000
30.0
30.5
31.0
1990
1995
2000
2005
2010

Figure 3.


% cloudy
a) Seas. Dry (BCI)
b) Wet (Luquillo)
0
10
30
50
1980
1985
1990
1995
2000
2005
2010