Understanding Plant Phenology and its Drivers in a Tropical Semi-arid Landscape

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CERTIFICATE

This is to certify that this dissertation entitled “**Understanding Plant Phenology and its Drivers in a Tropical Semi-arid Landscape**” towards the partial fulfilment of the BS-MS dual degree programme at the **Indian Institute of Science Education and Research, Pune** represents original research carried out by “**Abinand Reddy K** at **Nature Conservation Foundation, Bangalore**” under the supervision of "**Dr. Suhel Quader, Scientist, Nature Conservation Foundation, Bangalore**” during the academic year 2014-2015.

Dr. Suhel Quader

Date : 25th March, 2015

DECLARATION

I hereby declare that the matter embodied in the report entitled “**Understanding Plant Phenology and its Drivers in a Tropical Semi-arid Landscape**” are the results of the investigations carried out by me at **Nature Conservation Foundation, Bangalore.**, under the supervision of **Dr. Suhel Quader** and the same has not been submitted elsewhere for any other degree.

Reddy

Abinand Reddy K Date: 25th March, 2015

Abstract

Monitoring the phenology of the primary producers of an ecosystem can reveal the dynamics of an ecosystem. This study was conducted in a semi-arid ecosystem in Andhra Pradesh, where moisture is severely limiting, but the landscape still boasts a large diversity.

A total of 18 species of trees and shrubs have been monitored fortnightly at the study site for their leaf, flower and fruit phenology since December 2007. This provided a 6-year long-term dataset to describe phenological patterns and examine the relationship between climate and phenology.

Majority of the plants were deciduous. Deciduousness of all plants was found to be between the months of February and May. Leaf flush followed shortly after. Flowering in most of the species followed subsequently after leaf flush. Fruiting was observed to happened mostly in the monsoons, and ripe fruits of majority of the plants were concentrated in the dry phase of the year.

I further characterised the seasonality in the populations' phenophases. Synchrony and consistency of populations were analysed for their ecological and evolutionary consequences. Leaf flush was found to be more synchronous than flowering and Trees were found to be more consistent than shrubs.

Individual consistencies with respect to the population, were explored to further understand population level synchrony. Most species hinted at some level of individual consistency. Leaf flush of inconsistent populations were positively correlated to the first day of rainfall. An irrigation experiment was conducted on two species to verify causality. No response was observed for irrigation. Monitoring phenology can shed light on the plants relationship with both, the abiotic factors, and their biotic interactions.

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Introduction

Phenology of plants are the periodic events in their life cycle. Leaf flush, deciduousness, flowering and fruiting are some of the important phenophases of plants. The dynamics of an ecosystem are heavily dependent on the phenology of these primary producers. Understanding these phenophases are therefore critical for understanding the ecology of a landscape.

Apart from having direct implications for their vegetative and reproductive survival, phenological characters of plants are the primary resources available for all animals (Shukla and Ramakrishnan, 1982). Herbivores, pollinators and frugivores are some animals directly dependent on the leaves, flowers or fruits of plants as their source of resources. Phenologies of plants and animal feeding behaviour have therefore co-evolved and are vital for the functioning of the ecosystem (Visser and Both, 2005).

Phenology studies have been conducted extensively on tropical ecosystems. While majority of the studies focus on forest ecosystems (Ortiz et al.,2006; Bendix et al., 2006; Mishra et al., 2006; Opler et al., 1980; Frankie et al., 1974; Chapman et al., 1999; Bach, 2002), very few have been conducted on semi-arid landscapes (Donovan and Ehleringer, 1992; Schwinnin et al., 2004), even though arid and semi-arid are the most abundant landscapes, covering over 30 percent of the total land area (Kottek et al., 2006). Semi arid landscapes are highly seasonal and plant phenology patterns are expected to be affected by these abiotic factors, which in turn affect the animals that depend on these seasonal resources.

Seasonality in Phenophases

Plants depend on various abiotic factors such as moisture and sunlight for their raw-materials, to produce tissues for growth and reproduction. Seasonality in the availability of these abiotic factors resulted in seasonality in phenology of plants.

Abiotic cues have been thought to be the dominant proximate cues for phenology while biotic interactions have been hypothesised to be the ultimate factors. Abiotic factors provide constraints on when plants can produce tissues for growth and survival; within those constraints, plants have evolved to time their phenology for key biotic interactions. Abiotic factors that plants are known to respond to include:

rainfall, photoperiod, irradiance, temperature and humidity. Maximal pollination, fruit dispersal and seedling recruitment, conspecific synchronisation of flowering and fruiting, and minimising seed and leaf predation (Bach et al., 2002) are some of the key biotic interactions plants evolve to synchronise to.

The phenology of plants can broadly be characterised as vegetative and reproductive. Plants utilise different strategies and are known to allocate different amounts of resources for the two phases. The two phases can exert either similar or opposing selection pressures on plant phenology.

1. Vegetative Phenology

Evergreen plants do not show a deciduous phase, but can have different leaf flush phenology. Leaf replacement has been observed to be aseasonal and seasonal in different species of plants (Shukla and Ramakrishnan, 1982). In deciduous plants, factors affecting leaf fall is dictated by the habitat. Light limited plants in habitats, without moisture stress, have been observed to drop leaves in times of low photoperiod, poor irradiance and temperature and flushed again with increase in day length, quality of light and temperature (Wright et al., 1994; Sundarapandian et al., 2013). Habitats with seasonal droughts however are driven by moisture availability. Leaf fall has been known to occur in dry season possibly due to drought stress (Wright, 1991). Leaflessness reduces transpiration and can help preserve water, for later use such as leaf flush and flowering. Deciduous periods have been known to be variable depending on the moisture stress.

Onset of leaf flush has been observed in species to happen towards the end of the dry period, either just before moisture became available or immediately after (Singh and Khushwaha, 2006).

2. Reproductive Phenology

Flowering in evergreen forests, like leaf flush, is also not highly seasonal at the community level, with species flowering all through the year. Seasonality is high in deciduous and semi-arid landscapes where resource partitioning between vegetative and reproductive phase is required (Bawa et al., 2003). Availability of pollinators is also a key driver for seasonality in flowering.

Flowering in deciduous forests and semi-arid landscapes has been mostly observed during the dry seasons. While some studies observed flowering during the leafless period (Shukla and Ramakrishnan ,1982), other's have reported flowering after leaf flush (Singh and Khushwaha, 2006). Flowering during the leafless period has been hypothesised as temporal partitioning of the vegetative and reproductive phase (Singh and Khushwaha, 2006). It is also speculated that relief from water stress after leaf drop could trigger flowering (Bawa et al., 2003). Proximal visibility of flowers on leafless branches has also been reported as an advantage of flowering during the deciduous phase (Bawa et al., 2003).

High efficiency of converting new organic matter to organs rather than storing for future use is one of the key advantages of flowering after leaf flush (Zimmerman et al., 2007; Hamann, 2004). Timing of flowering is also controlled by the factors that can affect fruit phenology. If selection is stronger for fruiting in a certain time, it could change the flowering phenology as these phenophases are linked strongly physiologically.

Species in evergreen forests have either seasonal or aseasonal phenology and are driven primarily by biotic interactions. Seasonal fruiting has been studied for many species, especially congeners that have known to diverge their fruiting phenology to avoid competition for fruit dispersers (Wheelwright, 1985; Snow 1965). Biotic and abiotic factors are ultimate reasons for the timing of fruiting. Synchronising with biotic factors is key for efficient fruit dispersal and with abiotic factors for seedling survival.

The level of biotic interactions is dependent on the mode of dispersal of its fruits. Wind dispersed fruits are seen to fruit in leafless periods so as to be able to disperse large distances, without obstructions (Hamann, 2004; Aravind et al., 2013). Animal dispersed fruits are known to be fleshy and requires the plant to put in more resources into these to successfully attract animals and are therefore known to fruit during or following wet seasons (Thompson and Willson, 1979; Chapman et al., 2005). Timing fruiting for maximising dispersal however is futile if there is no adequate seedling recruitment and many fruit phenologies have been observed to synchronise to the timing of rainfall for maximum seed survival. The same species in two different locations have been known to fruit at different times based on the onset of rainfall there (Aravind et al,2013). Temperature has been speculated to be one of the major cues for timing of flowering and fruiting (Kimura et al., 2009; Mishra et al., 2006).

The various phenology studies conducted, have found different seasonalities and different relationships between the phenophases and biotic interactions, in their study areas. While there are results, broadly applicable across ecosystems, many are unique and contingent on the study site, due to the variability of the multiple factors responsible for shaping the phenophases.

Characterising phenology - Population and Individual level patterns

Characterising seasonality has been key to understand population and community level processes and their implications. Seasonality has been further understood under population synchrony and consistency.

1. Population Synchrony within a year

Synchrony has been studied greatly at the community and population levels (Franklin and Bach, 2006; Freitas and Bolmgren, 2008). Inter-specific synchrony at the community level is the overlap of different species showing the phenophase of interest, it is of particular ecological consequence when the different species share common pollinators or dispersers. Intra-specific synchrony of the species' phenology can be qualitatively defined as the overlap of the phenophase of the various individuals of a population.

Synchrony in leaf flush is known to help in satiating herbivores and thereby reducing the overall predation (Franklin and Bach, 2006). Asynchronous flushing may also be advantageous as asynchrony could help support different animals in the community (Crawley et al., 1988).

Inter-specific synchrony in flowering is thought to be disadvantageous as it increases competition for pollinators. It also causes pollen wasting and stigma blocking as pollinators move from species to species (Wheelwright, 1985). Community synchrony in fruiting however can be both beneficial and detrimental. While asynchrony can reduce competition for dispersers, synchrony helps in satiating predators and better dispersal of seeds as dispersers move between species

(Wheelwright, 1985). Inter-specific asynchrony is observed greatly in moist forests, especially among congeners who share dispersers (Snow, 19665). In semi-arid landscapes however, fruiting phenology is mostly synchronised, due to the seasonality in moisture availability.

At the species level, synchrony and asynchrony of the reproductive phenophases have been shown to have unique advantages. Synchrony of flowering is vital for the population as it maximises out-crossing leading to high genetic variation, which is highly selected for. Synchronised populations can also attract more pollinators. Asynchrony of flowering on the other hand, could prevent risk spreading and reduce competition if species abundance is high (Bolmgren, 1998). Synchrony of fruiting similarly attracts more dispersers or satiate seed predators, while asynchrony could decrease competition and probably increase seed survival at the population level if factors such as moisture are not temporally consistent (Bolmgren, 1998).Apart from advantages and disadvantages, synchrony could just be constrained based on seasonal resource availability and similarly asynchrony could also be an artefact of varied microhabitats which enforce differences. This thesis will restrict itself to intra-specific synchrony and discussions on synchrony will be only addressed at the population level hereafter.

2. Population Consistency across years

Consistency of timing of populations' phenology from year to year also has great ecological consequences. Inconsistency of phenology may be advantageous for populations that are dependent on variable environmental cues and plasticity in phenophases can help cope with variability. Phenologies of animals however are synchronised to that of plants and inconsistency can lead to mismatch of these phenologies which could have great repercussions (Petanidou et al., 2014; Stenseth and Mysterud, 2002).

Understanding the variability in consistency is of great interest as it is it could give us insights as to which abiotic factors plant phenologies could be correlated to. Photoperiod is known to be the primary cue for phenology as it is the most faithful variable of climate, that does not vary from year to year. Plants however may vary in how strongly they are matched to the photoperiod due to effects of other variable abiotic factors such as moisture, humidity and temperature. Based on this we expect differential inter-annual variation in phenology among species and phenophases. Tracking consistency of species' phenology has been of interest for many studies in the recent past that have tried to understand consequences of global warming and climate change (Korner and Basler, 2013; Miller-Rushing et al., 2008).

3. Individual consistency across years

While studies have hypothesised on ultimate advantages and disadvantages of synchrony and asynchrony, few have dwelled on the proximal causality. If a species respond to a certain cue, which is experienced by all individuals, why do plants differentially respond? In these asynchronous populations, do the individuals maintain their order, in onset of phenology? Consistency of onset of phenology, for different individuals, with respect to the population could give insights to these underlying reasons of asynchrony.

Consistency of individuals may be due to genetic differences, which may reflect the genetic diversity in a population. Consistency could also be because of differences in microhabitats that facilitate or delay phenophases. Only one study has been found that looked into individual consistency of asynchronous oaks and found that they maintained their time of leaf flush with respect to the population. This was reported to be important for the community, as the trees supported different species compositions as a result of their inconsistency (Crawley and Akhteruzzaman, 1988). This study aims at characterising and understanding individual consistency, among different species and phenophases to explore the reasons of population asynchrony.

Drivers of Phenology

The seasonality in the weather and plant phenologies begs the question, as to how they might be correlated and what changes in weather might cause changes in phenology. Populations consistent across years maybe correlated to a more invariable component of weather, while inconsistent populations may be driven by variable aspects. While invariability makes it intrinsically hard to correlate to a true causal factor, variable populations can be compared to different factors to find correlations.

Instances with high degree of correlation could then be used to investigate causality. Lab experiments to establish causality may not be applicable to phenological behaviour on field as green houses may have different environmental conditions and cannot account for all the variable conditions of the field (Wright 1991). Therefore field manipulative experiments are essential in testing whether correlations established are really cues plants respond to.

Irrigation experiments conducted have showed varying results. Some cases have yielded no perceivable change due to manipulation, while others have shown flushing and flowering. Wright (1991) suggested that there might be endogenous circannual rhythms in plants that may control phenology rather than abiotic cues or a combination.

In this thesis, I use a unique long-term (6-year) dataset of marked individuals of 18 species from a semi-arid ecosystem to (a) determine seasonality in phenological patterns, (b) further characterise first leaf flush and flowering, as consistency and synchrony to understand the drivers that trigger these phenophases, and (c) examine the relationship between inter-annual variation in phenology, both vegetative and reproductive, and inter-annual variation in weather, predominantly rainfall, the most variable factor. I also conduct a field experiment designed to test causal relationships between dry-season precipitation and timing of leaf flush.

Methods

Study site:

Located in the Chittoor district of Andhra Pradesh, Rishi Valley School (16'63' N, 78'45' E) lies at the foothills of Horseley Hills, the highest mountain range of the state. The valley lies at an elevation of 700 metres above sea level. It is surrounded by hillocks, which are predominantly covered by granite boulders and sheet rocks. The overall landscape is largely semi-arid, covered with scrub vegetation. The campus itself is a patchy, dry, deciduous forest which is a result of reforestation efforts of the school.

The climate of the valley can broadly be classified into 4 periods: a cool dry period from December to February, a hot dry period from March to May, the Southwest monsoons from June to August and the Northeast monsoons from September to

November. The average monthly temperatures and rainfall for the last 14 years are as shown in Fig. 1 and Fig. 2 respectively

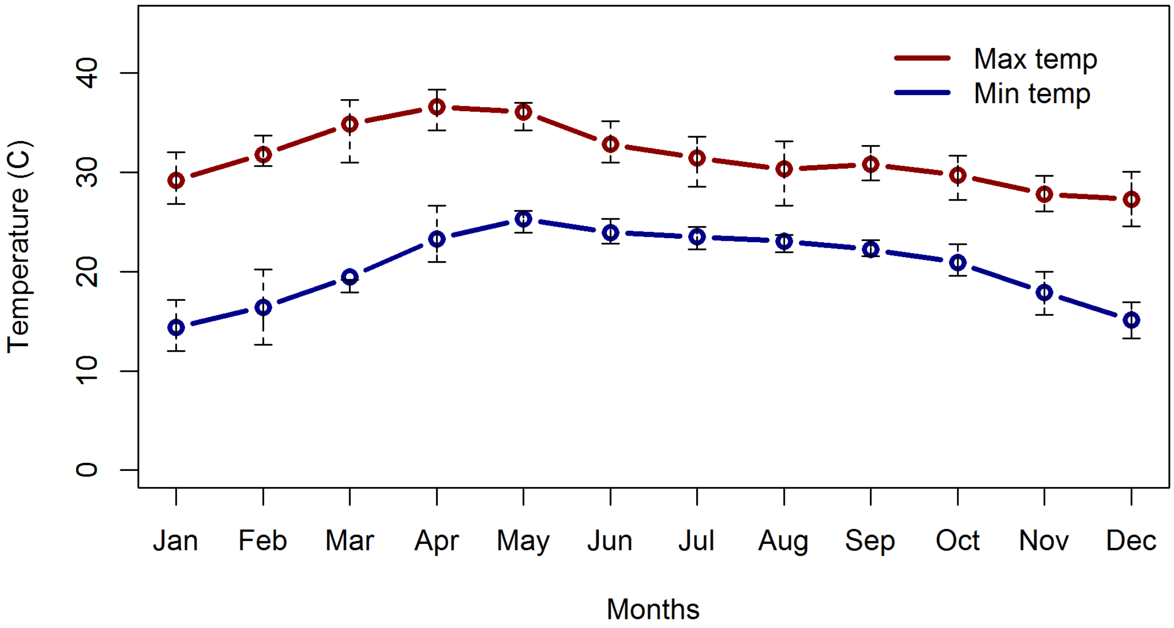


Fig. 1. Mean monthly maximum (red) and minimum (blue) temperatures in Rishi Valley since January 2000 recorded by the school's manual weather station. (Whiskers show range of variation in mean monthly temperature)

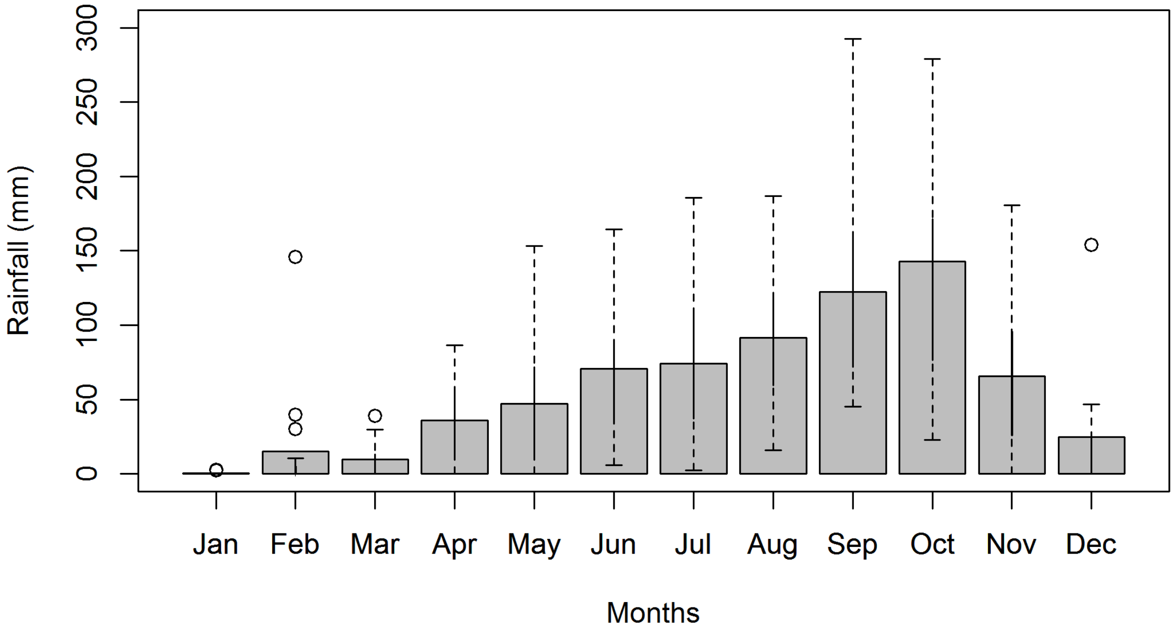


Fig. 2. Average monthly rainfall in Rishi Valley since January 2000 recorded by the school's manual weather station.(Whiskers represent range in variation and open circles represent outliers)

Being fairly elevated from mean sea level, the minimum temperature can go down to as low as 8ºC and as high as 41ºC in the summer. Rainfall in the valley is both scanty and erratic. While both monsoons reach the valley, most of its moisture is received from the Northeast monsoons (Fig. 2.).

While there is variation in temperature in a single year, monthly temperature does not vary dramatically from year to year. Rainfall on the other hand, experiences high intra-annual as well as inter-annual variation. The valley goes through regular drought years with a few intermittent years of good rain (Fig. 3.). in 2014 the valley experienced its 9th continuous drought year, with the lowest recorded rainfall in the last 15 years. Poor rainfalls have pushed local farmers to extract water from the ground for cultivation, and the prolonged drought has led to insufficient recharge and depletion of ground water in the valley. Despite the poor abiotic conditions, the valley is biotically diverse. The valley is a recognised bird preserve, with over 220 species of birds and 12 species of mammals inhabiting it. The valley is also home to a variety of reptiles, invertebrates and plants, but they have not been actively monitored or recorded for confident reporting.

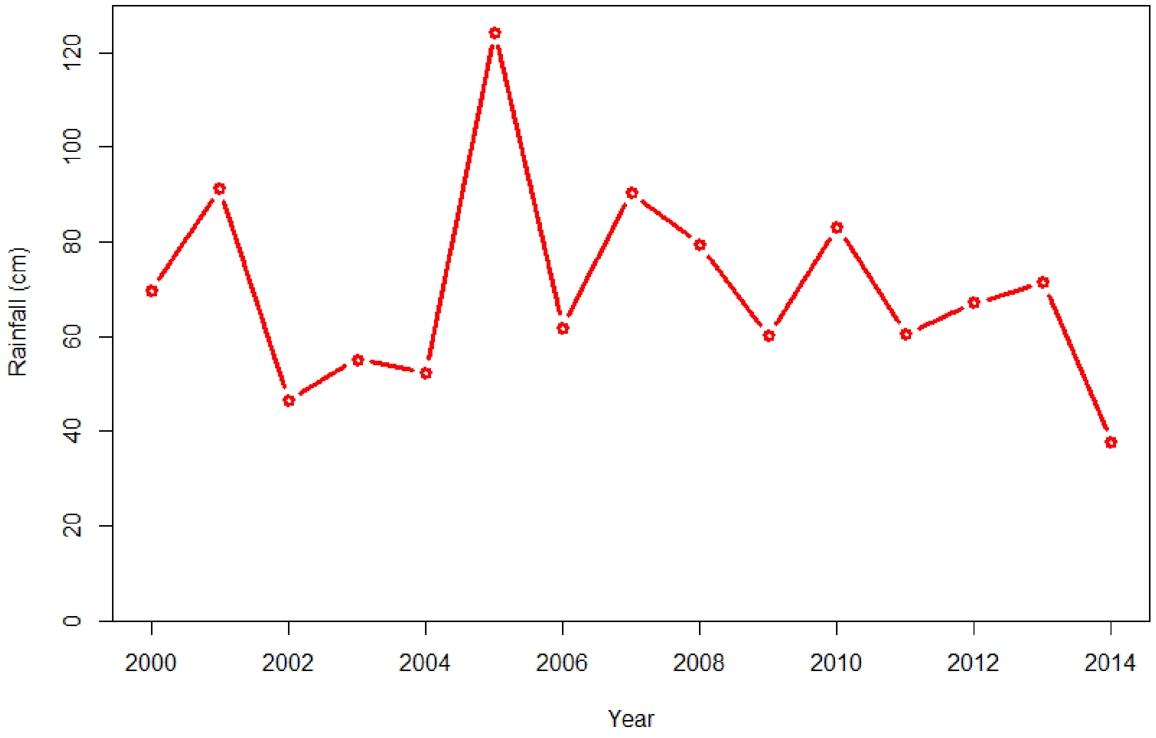


Fig. 3. Annual rainfall across 14 years in Rishi Valley

Data collection:

Weather data:

Weather data has been acquired from the school, who monitor it through a manual station. Maximum and minimum temperatures are recorded using a standard Six's thermometer placed in a Stevenson's screen and rainfall is monitored using a regular rain gauge. Readings are collected every day in the morning, except on Sundays and records exist since January 2000. Since data is collected in the mornings, while minimum temperature recorded is of the day readings are taken, maximum temperature is of the previous day's and rainfall reflects that of the previous 24 hours or last checked. An automated weather station has been installed in December of 2013 that monitors multiple weather variables every 15 minutes.

Table 1. Plant species monitored, and their details in the long term phenology project.

Species	Type	Origin	Individuals
Tamarindus indicus	Tree	Exotic	40
Peltoforum pterocarpum	Tree	Exotic	40
Azadirachta indica	Tree	Native	40
Santalum album	Tree	Native	40
Delonix regia	Tree	Exotic	40
Ficus religiosa	Tree	Native	20
Ficus benghalensis	Tree	Native	12
Albizzia amara	Tree	Native	40
Wrightia tinctoria	Tree	Native	40
Erythroxylon monogynum	Shrub	Native	40
Chomelia asiatica	Shrub	Native	40
Lantana camara	Shrub	Exotic	40
Pongamia pinnata	Tree	Native	40
Acacia leucophloea	Tree	Native	40
Randia dumetorum	Shrub	Native	40
Strychnos nux-vomica	Shrub	Native	40
Flacourtia sepiaria	Shrub	Native	40
Ficus tomentosa	Tree	Native	15

Long term phenology monitoring data:

Eighteen plant species have been monitored in the valley since December 2007. Species names and number of individuals of each are provided in **Table 1**. Species selected were those that were abundant in the valley, and included both native and exotic species, of tree and shrub classes. All the individuals selected were in the campus of the school (~ 1.5 km^2) except a few individuals from 2 *Ficus.* species, which were present adjacent to the campus. Individuals of a species selected were separated by a minimum of 20 meters. The species were selected arbitrarily at the inception of the study based only on abundance, and are not representative of the community. The valley consists of other thorny shrubs, woody plants and also exotics that were introduced for ornamental and afforestation purposes.

The monitoring of phenology has been conducted since December of 2007. Data is collected fortnightly at the first and third week of every month and all the data has been collected by a single observer. Six phenological characters were monitored : (i)fresh leaves, (ii)mature leaves, (iii)flower buds, (iv)open flowers, (v)ripe fruits and (vi)unripe fruits. Initially only presence or absence of the mentioned characters were noted, but as of October 2011 a three class system has been used, were '0' denotes absence, '1' denotes presence of the character in less than 33 percent of the branches and '2' for greater than 33 percent. The three class system was implemented to gain better resolution of phenological responses . All the data however was collapsed to a measure of presence or absence for homogeneity. Ripe fruits, such as pods of *Delonix regia* that may remain on the tree for long periods of time are noted as present till a new fruiting season starts. A tagged individual that died, was replaced by an individual of the same species with a different tag. Binoculars were used when required to scan canopies of taller trees.

Irrigation experiment:

An artificial watering experiment was conducted on field, based on analysis of the long term phenology data (Fig. 8). The experiment was conducted between the second week of February and the second week of March in 2015. 6 species, 4 shrubs (*Erythroxylon monogynum, Randia dumetorum, Flacourtia sepiaria* and *Lantana camara)* and 2 trees (*Wrightia tinctoria* and *Albizzia amara)*, showed phenological responses to a single 4cm off-seasonal shower in February 2008. A simulation of an equivalent amount of water from the shower was to be provided to individuals, to monitor their response more quantitatively. While extent of roots could not be measured, the water received by an individual was assumed to be proportional to its canopy cover.

Because of both time and resource constraints the experiment was conducted only on two species: *Randia dumetorum*(RD) and *Flacourtia sepiaria*(FS). Due to water constraints, the two tree species were dropped as a 4cm rainfall, over a radius of 1m canopy, translates to over 100 litres of water. *Erythroxylon monogynum* could not be used due to the lack of abundance in the field site. *Lantana camara* was an interesting option, to understand its invasive nature, but was dropped in fear of repercussions of the experiment on the ecosystem.

The field site for the experiment was a fallow step cultivation land (0.2km^2) at the base of a hillock, beside the Rishi Valley School. The land was recently bought over by the school, from local farmers, for reforestation purposes. Reforestation was attempted by planting trees and preventing grazers from entering, but has been unsuccessful, due to the extended drought. The landscape is therefore an undisturbed, open scrub. Plants are predominantly present on bunds, beside sheet rocks and other patches where cultivation had not been possible.

The experiment had 3 treatments: (i) watering an equivalent of 4cm of rainfall (ii) watering an equivalent of 2cm of rainfall and (iii) a control with no watering. 20 triads of RD and 15 of FS were identified. Individuals in a triad were not closer than 3m but not further than 20m. Individuals of a triad were size matched as far as possible and were selected on relatively flat areas, such that restricted watering was possible. Once the triads were selected, individuals in a triad were assigned one of the three treatments at random. No individual tagged for the experiment was a part of the long term phenology monitoring.

The shrubs were assumed to have an average spread of 0.5m radius, which translates to an approximate equivalent of 30 litres and 15 litres of water, for the 4cm and 2cm rainfall respectively. Due to the lack of information of the root systems of the species, intensity of the rainfall event, to calculate the runoff or soil moisture data, accurate estimates of the moisture received by the individuals could not be established. However, the moisture provided by the artificial watering, was assumed to be equivalent if not more than the natural event. 17 triads of RD were watered on the 11th of February, the rest were watered on the subsequent day. All individuals of FS were watered on the13th of February. Watering was done with the help of students from the school and all watering was done in the evening after 5pm to minimise evaporation. Water was poured slowly at the base of the shoot and runoffs were restricted to a 0.5m radius from the centre, as much as possible.

5 branches were tagged for monitoring on each individual plant. A thread was tied at 20cm from the apex of each branch for RD, and at 10cm for FS for each branch and the number of fresh, mature and senescent leaves were counted and noted between the apex and the thread. Data was collected once before watering and subsequently collected twice a week at regular intervals for 4 weeks. A 1.8cm rainfall event occurred on the 3rd of march. Getting soil moisture data was attempted using a probe, but the equipment was highly inaccurate and the terrain restricted the possibility of using the gravimetric method. Lack of this data considerably reduces the confidence in the interpretation of the results.

Data analysis:

Data from December, 2007 to December, 2013 is analysed in this study. The long term phenology monitoring data consists of over 10,000 rows. The programming language R was used to analyse the data for its statistical power.

1. Seasonality

Although data was collected on the first and third weeks of every month, to normalise for variation in days data was collected on, across the years, date of data collected on the first week were set to the first of that month and data collected in the second half of the month were set to the 16th. General patterns in phenophase seasonality were first tested for by plotting the proportion of the population showing a particular phenological character on a given fortnight. Proportions of individuals in leaf flush, deciduousness, flowering and fruiting were plotted. Seasonal phenophases were interpreted as those that showed a period of dormancy between two years, for at least 4 of the 6 years, at the population level. Phenophases that didn't were interpreted as independent of abiotic seasonal cues and therefore aseasonal. Deciduousness was characterised by absence of both fresh and mature leaves, flowering was plotted as presence of either flower or bud, only unripe fruits were used to asses seasonality in fruiting due to the extended presence of ripe fruits in certain cases as mentioned earlier.

2. Synchrony and Consistency

Seasonal phenophases of plants were then analysed for population level synchrony and inter year consistency of first day of showing phenological character in a season. First day of phenological character of an individual, was established as the day the character was first observed in a year. Since phenophases can extend through two calendar years, the beginning of a phenophase in a year was established as the fortnight at which the proportion of population showing the phenophase of interest, fell to less than 5% since the previous season's. Failing to meet that condition that year's data for the population was not considered. Species with more than 3 years of such missing years would have automatically be considered aseasonal. To look at population level synchrony and consistency of both reproductive and vegetative phases, first day of leaf flush and first day of flowering of individuals were used for analysis. Yearly cumulative graphs of the first days of flowering and leaf flush were plotted against Julian days, starting from the 1st of January of every year to the 31st of December. The cumulative graphs were scaled to a 100% of individuals showing the character in the given season (because not all individuals necessarily flowered or fruited in each season).

Qualitatively the slope of the curves in the scaled cumulative graphs hint at the synchrony of the populations. A steeper slope indicated simultaneous, synchronous flushing or flowering of a population, while a gentler slope indicated asynchrony. The consistency can be visualised from the graphs as the spread of the plots (Fig. 5a,b).

More quantitatively, the mean number of days between 25% and 75% of the population to show the phenophase was used to understand synchrony. Only the median 50% was used to exclude outliers. Consistency was measured as the difference between the median day, of first leaf flush or flowering of the population, of the earliest year from that of the latest.

3. Individual consistency across years

Asynchronous populations were then investigated, to check if individuals in the population were consistent in their timing of phenology with respect to the population from year to year. Species that showed a minimum of 30 days difference between the first flower or leaf of 5% and 95% of the population flushing or flowering that year were considered. A difference of less than 30 days, were considered synchronous, and could not be analysed as the resolution of the data constrains it. The 5% and 95% cut-off was implemented to disregard possible outliers.

Individuals in a population were ranked based on the day they first show the phenophase of interest. Individuals that did not show the phenological character for more two years were disregarded in the analysis. Ties were given the average rank of that class. Median ranks of individuals across years were ordered and plotted. To see if the ranking was non-random, simulations were conducted assigning at random, the ranks of each year, to individuals, for all 6 years. Their median ranks were then ordered. Simulations were iterated 10,000 times and observed individuals with median ranks that lay outside the 2.5th or 97.5th percentile of the simulated medians were considered non-random and consistent individuals. Species that were synchronised under 30 days, would yield only 2 ranks and would not be very informative and were therefore disregarded.

This method however could only distinguish individuals that were consistently early or late, since the observed medians had to intersect the simulated ones in between, the consistency of the middle individuals could not be interpreted.

4. Weather correlation

Inconsistent populations were then correlated to weather. Rainfall was used as it is more variable than temperature and because moisture is likely to be the limiting factor in this landscape. Based on preliminary analysis, population leaf flush was correlated with the first rainfall in the year. The populations median day of first leaf flush was plotted against the first rain in that year which was greater than 1cm in a day. A 1cm threshold was established, based on the assumption that a lower amount of rainfall would not provide enough moisture to enable a response and species were observed to respond to at least 2cm of rainfall from the data. Owing to the resolution, species whose variation in median days between years was less than 30 days were classified as relatively consistent and no attempt was made to examine their phenology in relation to yearly variation in rainfall.

Proportions of phenology, measured how many individuals of the population were showing the phenophase of interest at a given time. The area under the curve represented the number of individuals showing the phenophase and for how long. A large area for a year, implied that a large proportion of the population, displayed the phenophase for an extended period of time. A small area however, suggested either a poor number of individuals showed the phenological character or individuals expressed the character for a short duration or a combination of both. The area under the curve therefore was taken to be a proxy for the effort the population put into a phenophase in a year. If plants were primarily limited by water, years with good rainfall should have led to a greater effort in phenophases by plants as opposed to a year with poor rainfall. Total amount of rainfall in year was plotted against the total vegetative and reproductive effort of species in a year. The area under the curve of the flowering proportion and mature leaf proportions were used as measures of reproductive and vegetative efforts respectively.

The timing of fruiting was compared to the timing of rainfall using circular statistics. The year was divided into 24 bins, based on the two halves of each month data was collected. Number of individuals fruiting on a particular fortnight was added to each bin. Rainfall was treated similarly. Rose diagrams were plotted along with their circular means and compared to see if mean fruiting was synchronised to coincide with the monsoons for greater chances of seed survival.

5. Irrigation experiment

The proportion of mature leaves present on a particular day as compared to the number of mature leaves before the watering, was plotted and compared for all three treatments to see if the watering aided in leaf persistence. Presence of fresh leaves was plotted as a function of time to see if the watering aided in flushing of leaves.

Results

Being a semi-arid landscape driven by seasonal climate, the species present were mostly seasonal for all phenophases.

Vegetative phenology:

Apart from 2 species (*Chomelia asiatica, Santalum album)* , 16 of the 18 species shed their leaves in the dry season (Fig. 4.). Of the remaining 16, all the shrubs and one tree (*Wrightia tinctoria*) had prolonged deciduous periods of complete leaflessness as compared to the remaining trees that had shorter or no period of complete leaflessness. The duration of deciduousness varied considerably between years. Trees with short spans or no deciduousness was a result of leaf flush coinciding with the leaf fall. Deciduous periods of all species was during the late cool and dry phase or early weeks of the warm dry periods.

only one species(*Chomelia asiatica)* showed no seasonality in leaf flush. Three species (*Peltoforum pterocarpum, Santalum album* and *Ficus* tomentosa) showed partial seasonality with maximum individuals flushing in the warm dry period and a majority flushing through the year that only declined before the peak of the subsequent year. All others had a dormant period after the monsoons, through the cooler months and flushed leaves during the hot dry periods. All species continued to flush leaves through the monsoons and was either extended or bimodal, with peaks coinciding with the two monsoons. Leaf flush was generally lower during the wetter north-east monsoons. Proportions flushing leaves through the monsoons varied greatly from year to year for all species, onset of leaf flush was much less varied.

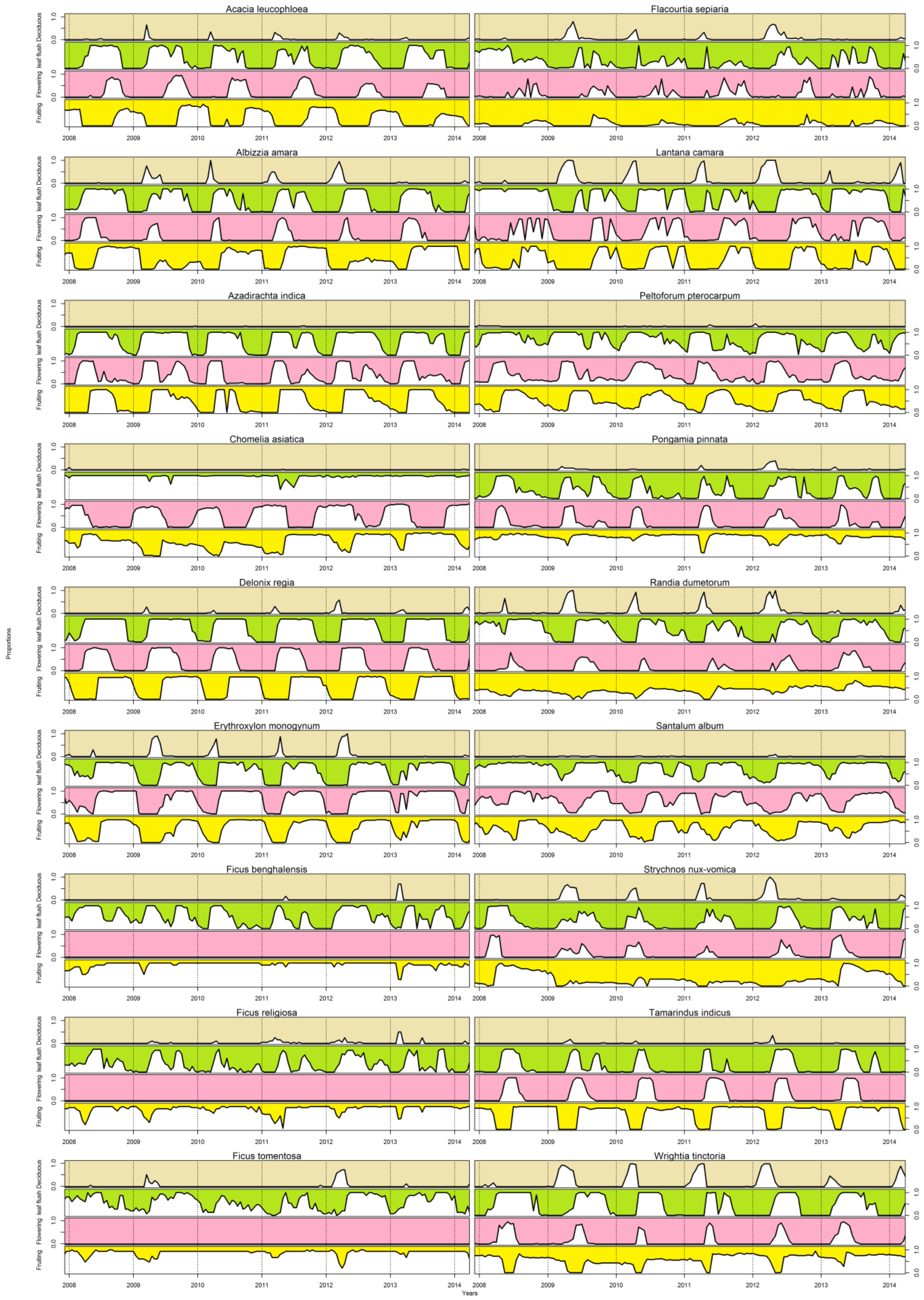


Fig.4. Proportions of the deciduousness (brown), leaf flush (green), flowering (pink) and fruiting (yellow) phenophases of the 18 species across 6 years of the long term monitoring study. Proportions are plotted from bottom up (white portions).

Reproductive Phenology:

All flowering species showed seasonality in flowering. Flowering data for *Ficus* species was not collected due to their lack of that phenophase. 11 of the 15 flowering species put out buds soon after flushing leaves during the warm dry summer. 4 of these 11 species had short pronounced flowering periods, while the remaining had extended flowering that continued through the monsoons for some species. *Azadirachta indica* was the one species that showed a pronounced bimodal seasonality, that coincided with the two wet periods; the second flowering effort was always weaker than the first . *Peltoforum pterocarpum* was the only species with

partial seasonality with more than 5% of its plants flowering at any given point of the year. Only one species (*Chomelia asiatica*) flowered exclusively during the dry months. The remaining three species flowered predominantly during the north-east monsoons. 5 species (3 shrubs, 2 trees) had individuals that did not flower annually, while all other species' flowering reaches a proportion of 1 every year.

The *Ficus.* species did not show seasonality in fruiting. While all species were seasonal in flowering, with pronounced durations, fruiting was more varied. Most species showed presence of fruit for extended periods of time. Presence of unripe fruits was observed till the subsequent fruiting season for 4 species, which had all flowered before the monsoons. 8 of the summer flowering species held fruits through the monsoons, of which 2 continued through the cool dry periods. The late flowering species all developed fruits during the late monsoons and persisted through the cool dry period.

Characterising Seasonality:

Scaled cumulative graphs were use to characterise both vegetative and reproductive phenologies (Fig 5a,b.). The one evergreen shrub and the 3 species with extended leaf flush were excluded from the vegetative graphs, while the *Ficus* species and *Peltoforum pterocarpum* were excluded from the reproductive graphs. The seasonality was characterised by synchrony and consistency. Synchrony looked at the variation between timings of the phenology within a year whereas consistency looked at the variation of the population across years.

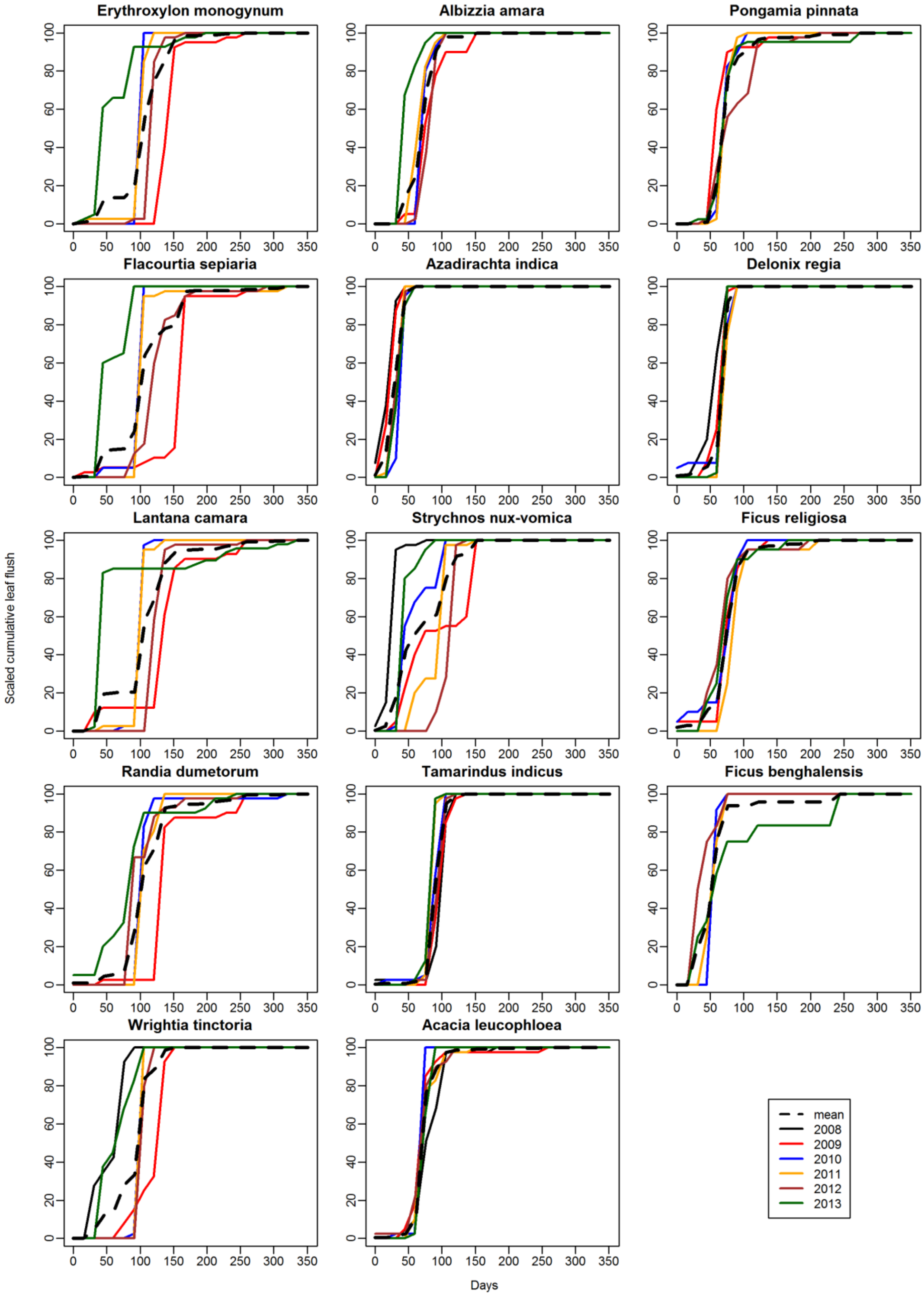


Fig. 5a. Scaled cumulative frequency of onset of leaf flush for 13 of the 18 species to assess population synchrony and consistency. Day 1 starts from the 1st of January of each year. Legend is provided in the bottom right panel.

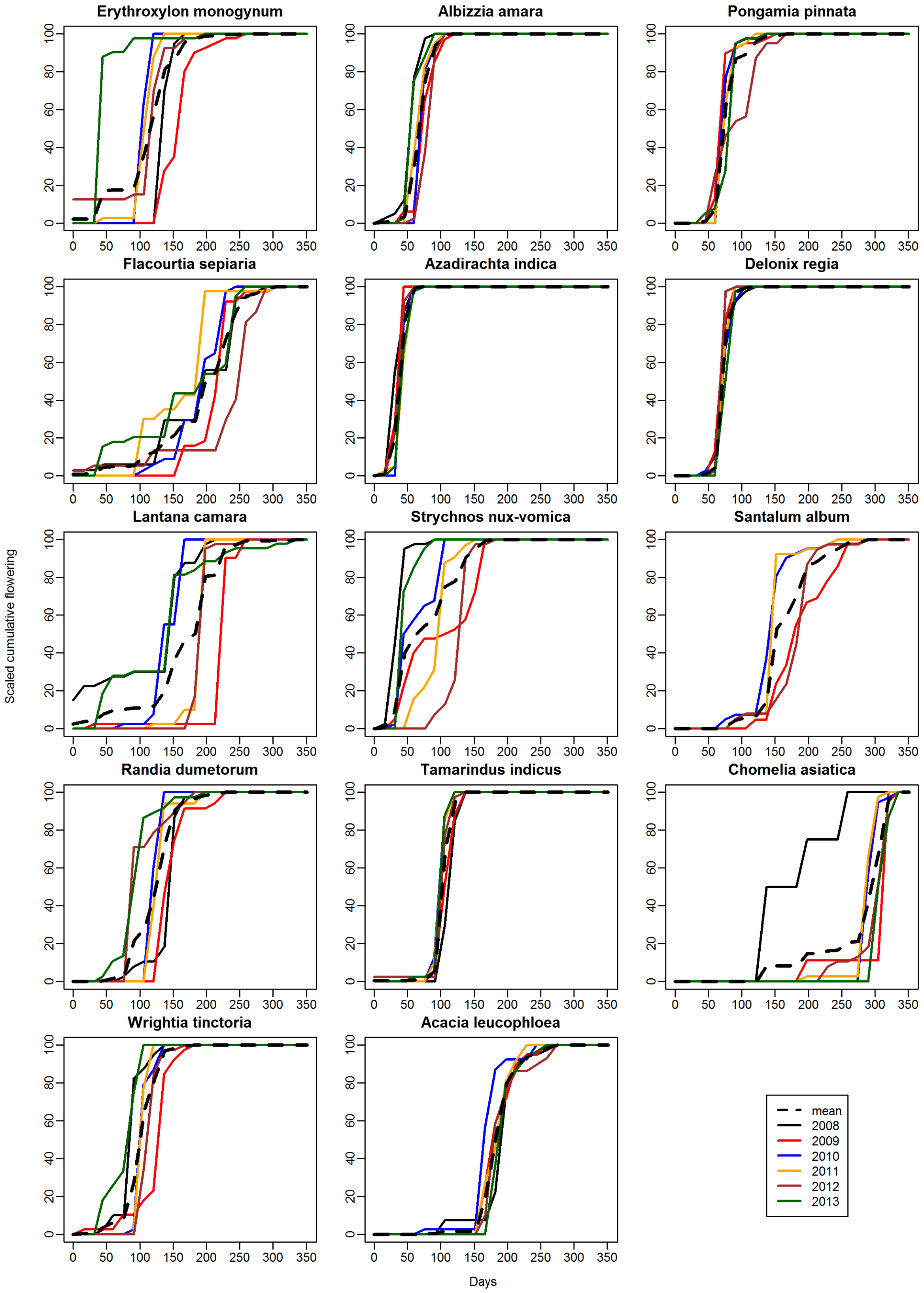


Fig. 5b. Scaled cumulative frequency of first flower for 13 of the 18 species to assess population synchrony and consistency. Day 1 starts from the 1st of January of each year. Legend is provided in the bottom right panel.

1. Synchrony

The mean number of days between 25% and 75% of the population to show the phenophase was used to understand the synchrony of the onset of a population's phenophase. Populations that flushed or flowered in fewer days, were considered synchronous whereas ones that took longer were thought to be asynchronous. Two species (*S. nux-vomica and F. benghalensis)* , were found to be asynchronous (> 30 days) in flushing leaves (Fig. 6), while The remaining species were synchronous (< 30 days).

Flowering was found to be more asynchronous as compared to leaf flush (Fig. 6), where 5 species(*F. sepiaria, L. camara, S. nux-vomica, S. album* and *C. asiatica*) were asynchronous (>30 days) . The rest were synchronous (< 30 days). While only the median 50% was measured for synchrony, apart from few highly synchronous species(*A. amara, A. indica, T. indicus and D. regia*) most species had individuals that flushed or flowered even months after the first one had in the population.

2. Consistency

Consistency was measured as the difference between the median day of onset of the population's flowering and leaf flush, of the earliest year from that of the latest. A population with greater differences, were considered inconsistent and ones without where considered consistent.

Seven species, 4 shrubs and 3 trees,(*R. dumetorum, F. sepiaria, L. camara, E. monogynum, S. nux-vomica, A. amara* and *W. tinctoria*) were found to be inconsistent from year to year (> 30 days) in leaf flush (Fig. 6.). The same species apart from *A. amara* were also inconsistent in flowering along with *S. album* and *C. asiatica.* The 5 trees (*A. indica, T. indicus, D. regia, A. leucophloea* and *P. pinnata*) were highly consistent for both phenophases between years. Unlike synchrony most species that were consistent at flushing leaves, were also consistent at timing of flowering.

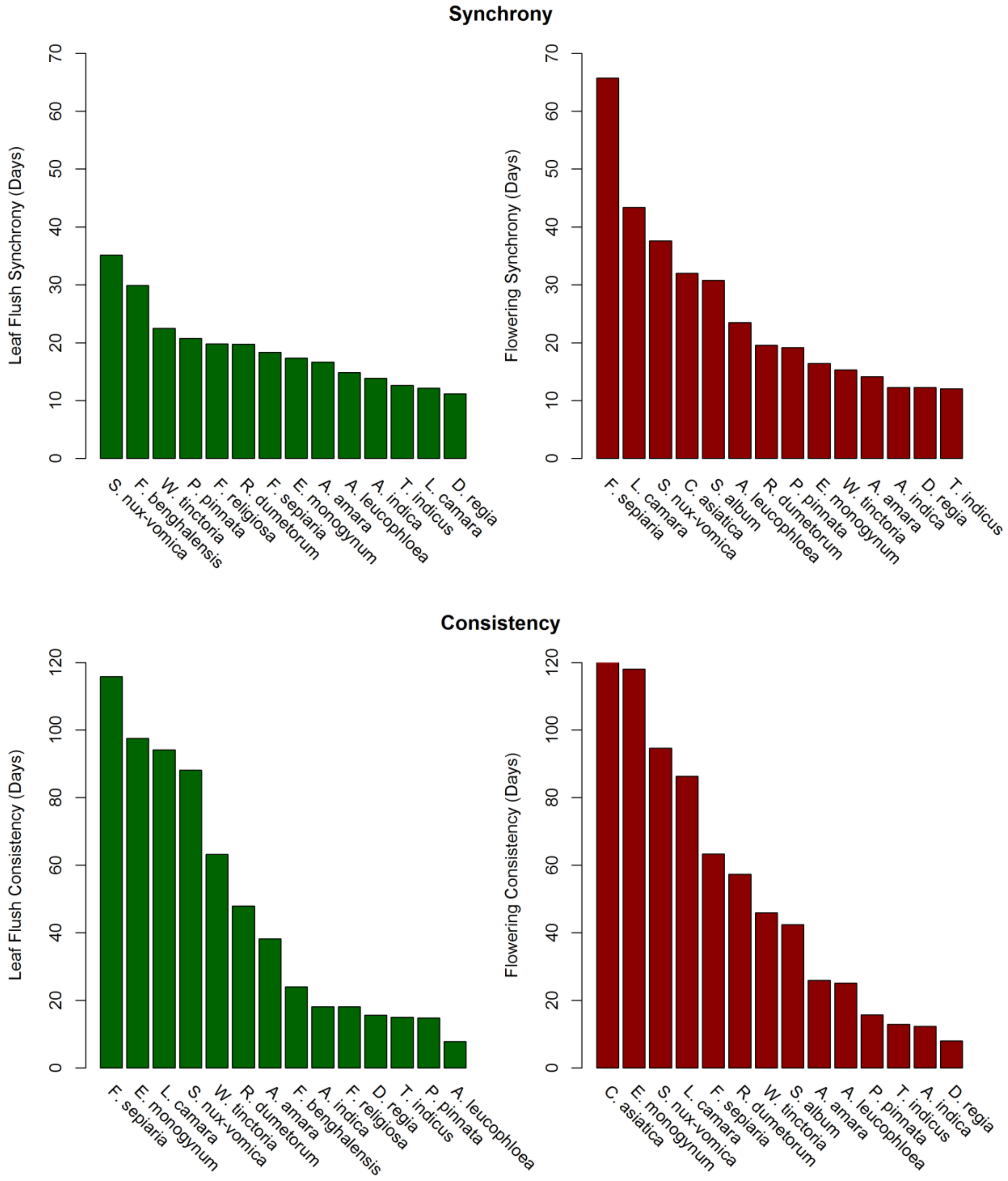


Fig. 6. Top two panels show the synchrony of leaf flush and flowering of different species, measured as the mean number of days between onset of phenophases of 25% and 75% of the population. Consistency of species is depicted in the bottom two panels, as the range of median onset days of the phenophases across years. The green and red bars represent leaf flush and flowering respectively. Species missing in the graphs, were aseasonal for that phenophase.

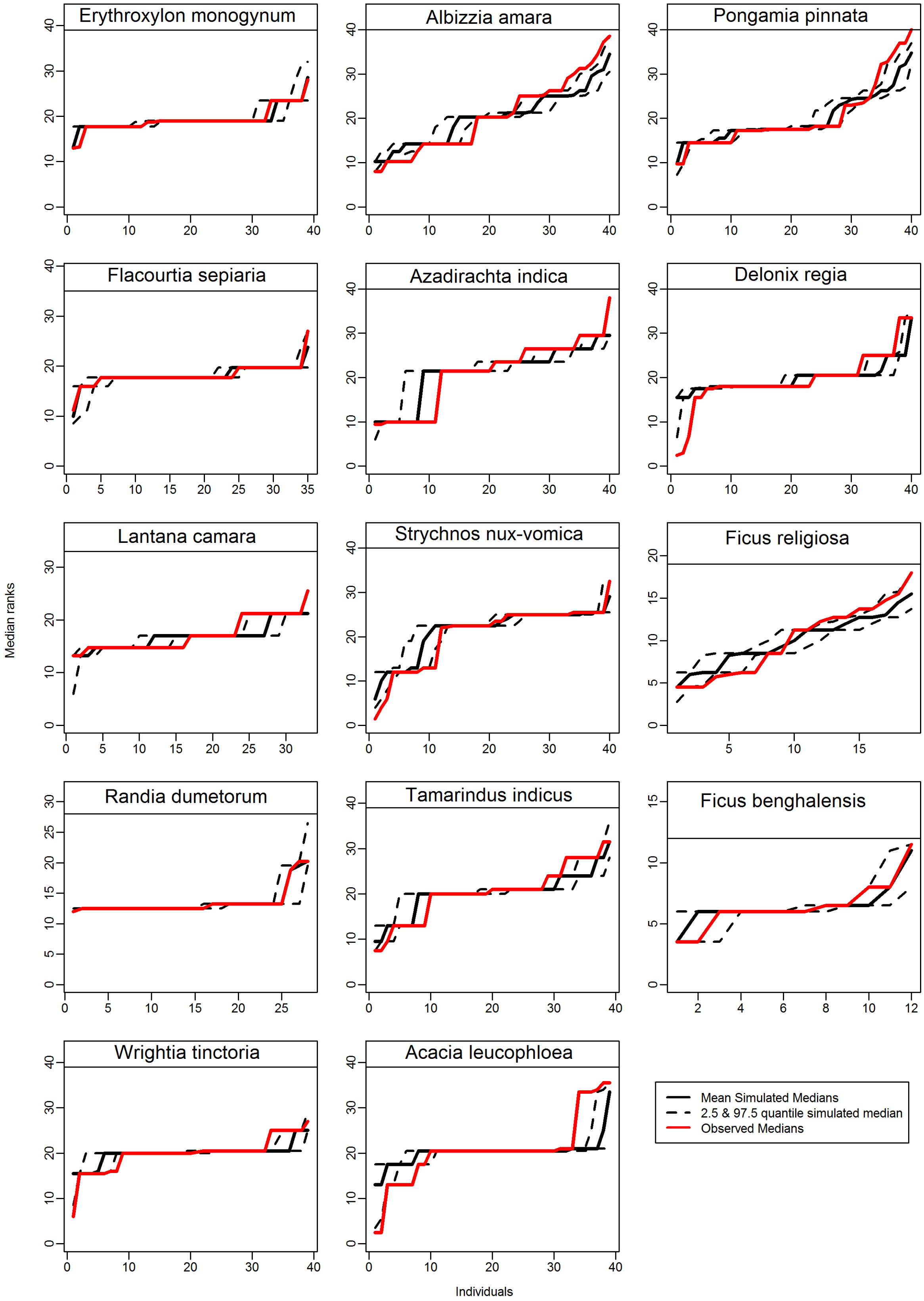


Fig. 7a. Ranking of individuals based on first leaf for 14 of the 18 species to assess individual consistency with respect to the population. Legend is provided in the bottom right panel.

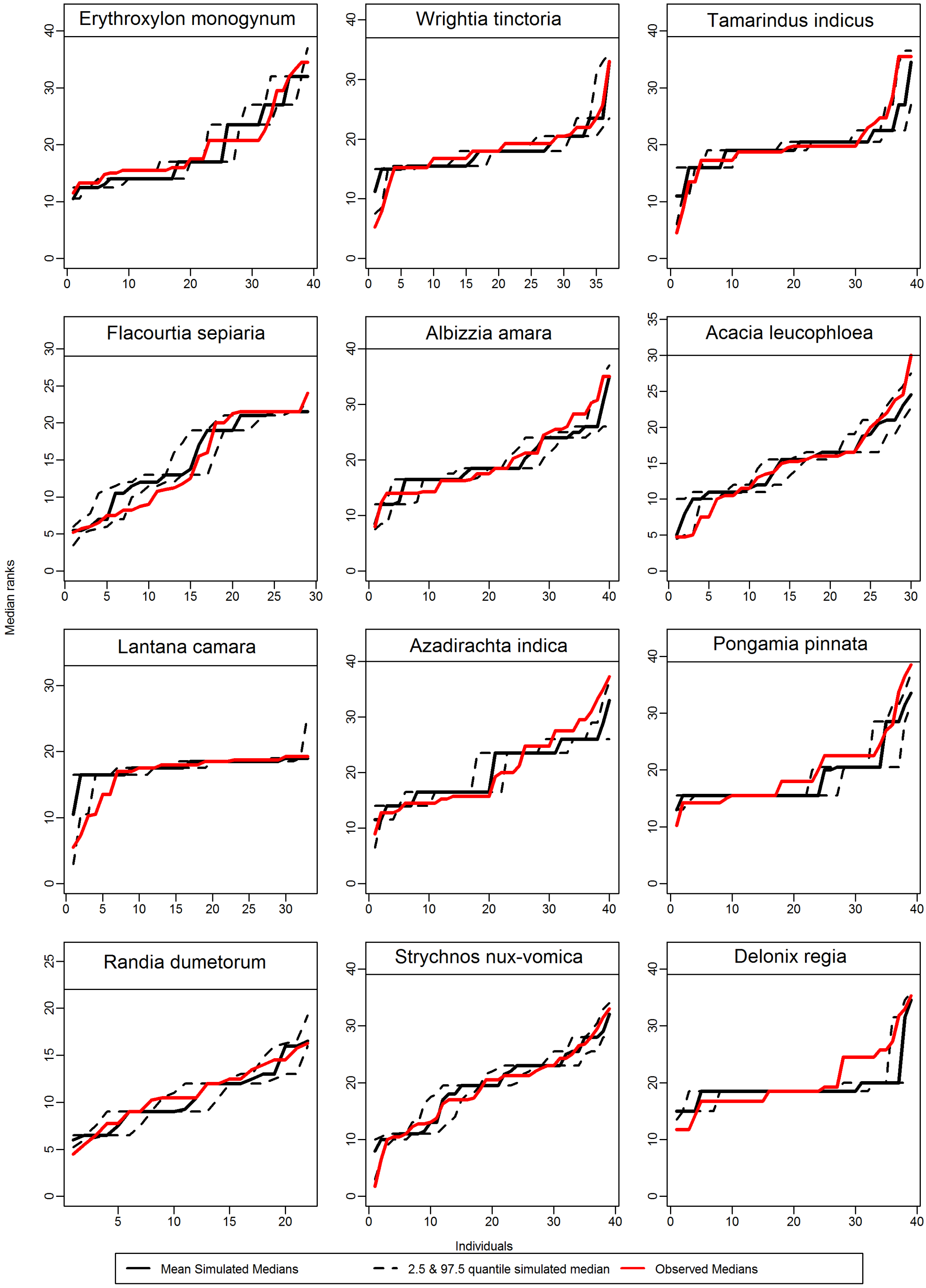


Fig. 7b. Ranking of individuals based on first flower for 12 of the 18 species to assess individual consistency with respect to the population. Legend is provided below the plots.

3. Individual consistency:

Populations that were asynchronous, were so because some individuals flushed or flowered later than the others. Even synchronous species had outliers which were much earlier or later than the rest of the population. Individuals whose observed medians fell outside the 2.5 and 97.5 quartiles of the simulated medians, were believed to be consistent, with respect to the population for that phenophase.

Of the asynchronous species, *F. benghalensis* was the only species that showed complete inconsistency at the individual level. Only early flushing individuals of *S. nux-vomica* and *W. tinctoria* consistently flushed early with respect to the populations across years, while all individuals of *P. pinnata* seemed to be consistent in flushing with respect to their population. Of the synchronous species, the 4 trees (*D. regia, A. leucophloea, F. religiosa and A. amara)* showed high consistency at the individual level with respect to the population whereas the shrubs were inconsistent.

Of the flowering species, data from individuals of *C. asiatica* and *S. album* were not represented adequately across years, and where therefore not included in the rank analysis. Of the remaining asynchronous species, individuals of *F. sepiaria* were consistent, while only early flowerers of the remaining 2 populations were consistent (Fig. 7b.). Of the synchronous species, *R. dumetorum* was inconsistent. Two species (*A. amara and T. indicus*) had consistent outliers whereas only the late flowerers of the rest of the species were consistent.

Weather and Phenology

1. Correlation to rainfall

Seasonal inconsistency of populations had to be linked to some variable a-biotic factor which prompted the variation in timing of the phenophases. Population median days of first leaf flush and flowering of inconsistent species were correlated to first rainfall event of the year(Fig. 8.).

Onset of flowering was not influenced by the timing of rain. Leaf lush of the inconsistent species however was correlated with first rain (Fig. 8.). 2 of the 7 species were moderately correlated (*R. dumetorum* $r = 0.72$, $p = 0.17$ and *S. nux-vomica* $r = 0.71$, $p = 0.11$) while the other 5 species were strongly correlated (r >

0.95, p < 0.05). Responses of 5 of the 7 species were immediate, while 2 species (*r. dumetorum* and *W. tinctoria*) had delayed flushing responses.

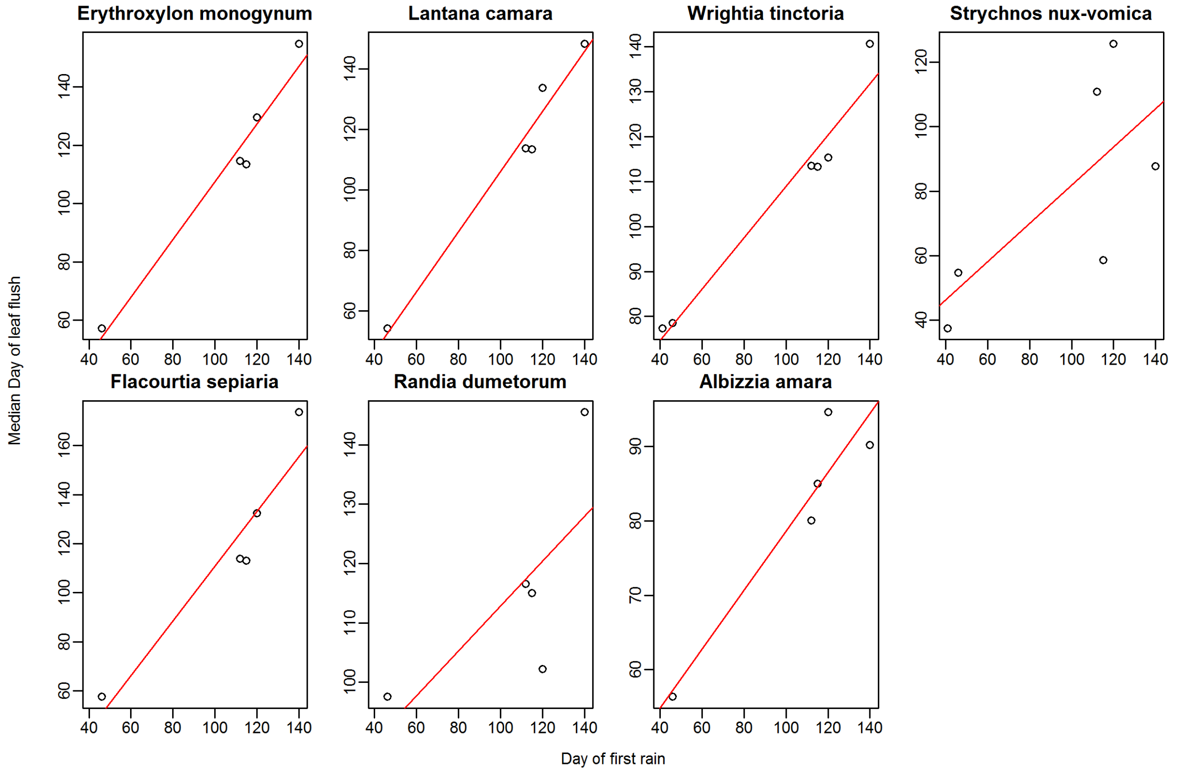


Fig. 8. Correlation of populations' median day of leaf flush and first day of rain greater than 1cm. Days on both axis are in Julian days with the first day of each year as day one (The species above were those considered for the irrigation experiment).

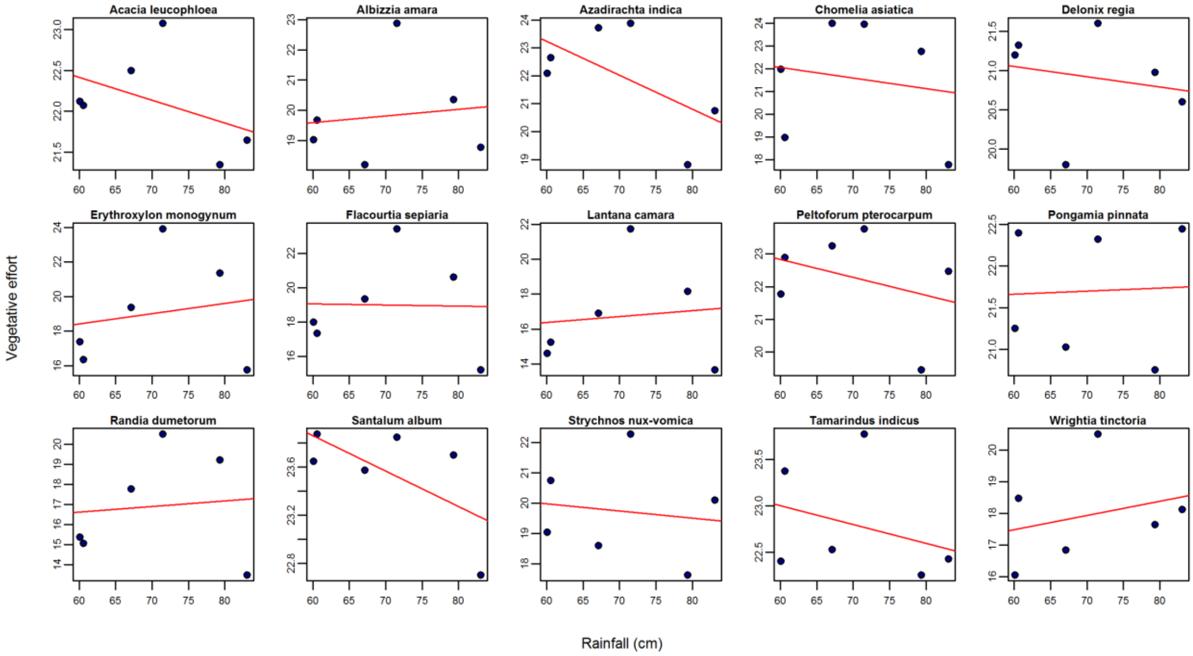


Fig. 9a. Comparison of total vegetative effort and total rainfall in a year.

2. Total reproductive and vegetative effort:

For a landscape limited by moisture and driven by the monsoons, total duration of flowering and leaf presence was correlated to total rainfall in a year (Fig 9a,b). Neither the vegetative effort or the reproductive effort was correlated to the moisture available in a year for any species. Smaller efforts in general reflected shorter durations of the phenophase, with narrower peaks, rather than decrease in individuals showing that phenophase.

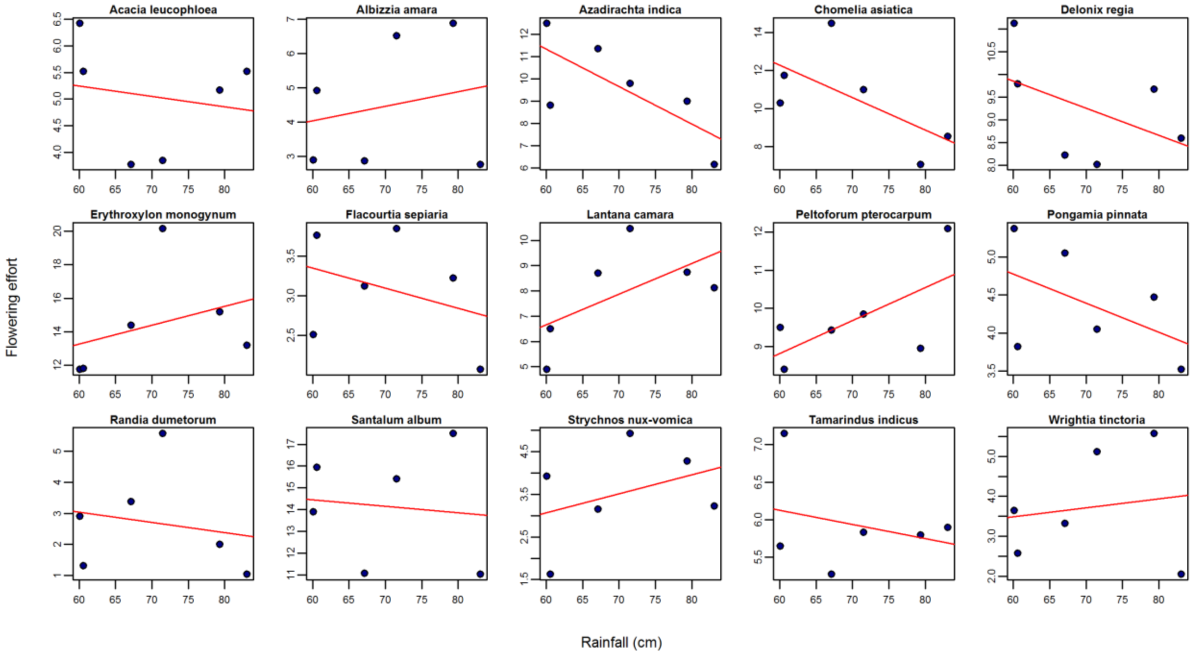
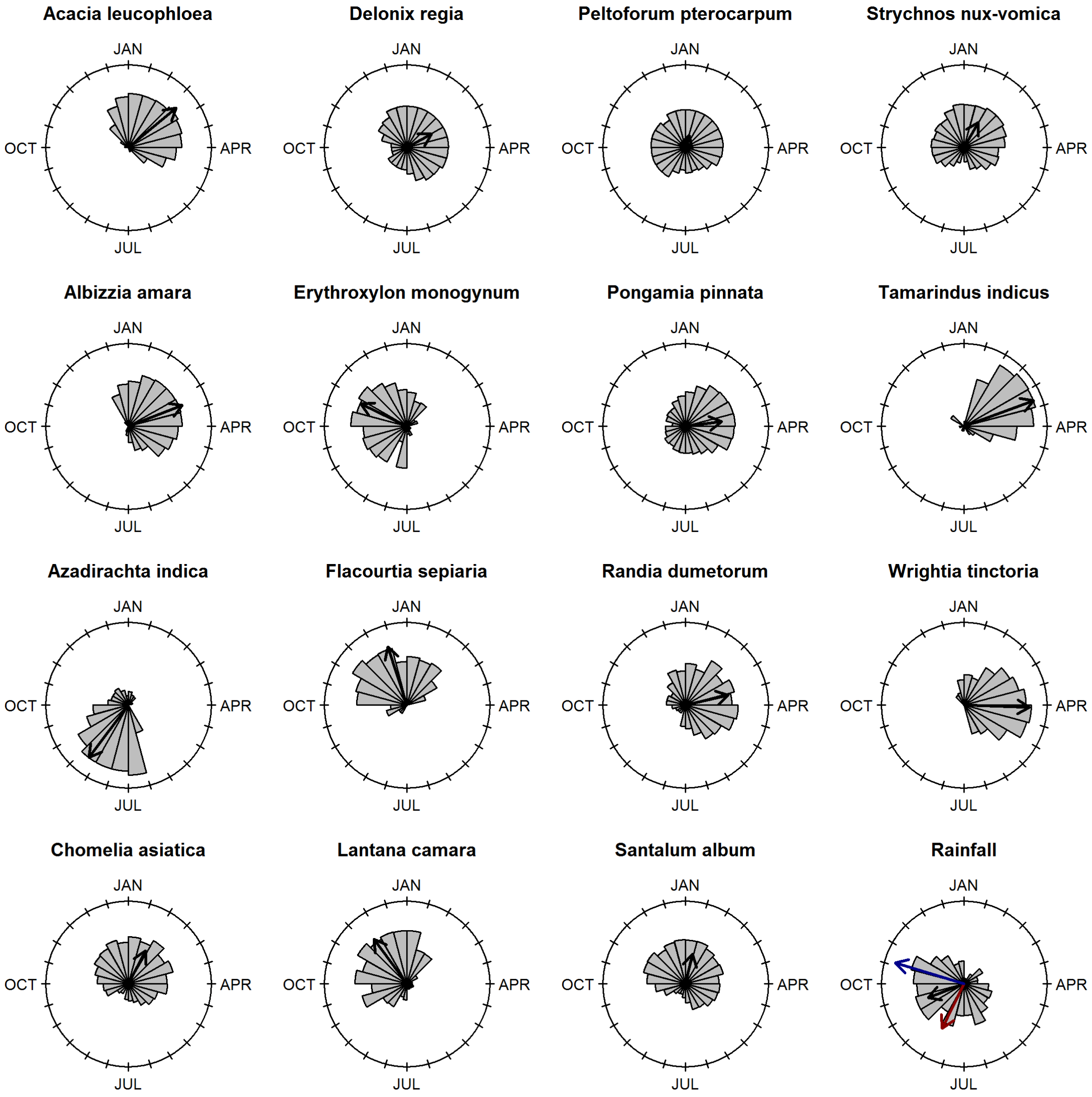


Fig. 9b. Comparison of total reproductive effort and total rainfall in a year.

3. Timing of mature fruit and the monsoons:

Mean fruiting days of a population from all years were compared to the mean of the south-west and north-east monsoons (Fig. 10.). *Ficus* species were excluded as they didn't show seasonality in fruiting. *P. pterocarpum* was the only other species that didn't show seasonality in the presence of its pods but was included in the analysis. *A. indica* and *E. monogynum* were the only two species that were truly synchronised with the monsoons. *A. indica*'s fruiting occurred and finished within the span of the monsoons, with its mean occurring between the two monsoons, while the latter's mean was synchronised with the north east monsoons. *L. camara* fruits matured through the north-east monsoons and peaked just after. The remaining 11 species' means were during the dry periods although in some cases fruit maturation set in by the late north-east monsoons.



Acacia leucophloea
Delonix regia
Peltoforum pterocarpum
Strychnos nux-vomica
Albizzia amara
Erythroxylon monogynum
Pongamia pinnata
Tamarindus indicus
Azadirachta indica
Flacourtia sepiaria
Randia dumetorum
Wrightia tinctoria
Chomelia asiatica
Lantana camara
Santalum album
Rainfall

Fig. 10. Circular plots of Mature fruits for 15 of the 18 species. Black arrows depicts the vector of mean direction and mean resultant length of the circular data. Bottom right panel is the circular plot of the annual rainfall. Red arrow is the resultant vector of the south-west monsoons and the blue arrow is that of the north-east monsoons.

Irrigation experiment results:

Neither of the two species showed any response to either of the treatments. There was no flushing of leaves as anticipated by irrigation (Fig. 11.). As expected in the dry season both species slowly shed their leaves through the course of the experiment, but there was no observable change in leaf persistence either on provision of moisture. Leaf persistence was unaffected in both treatments for both species as compared to the control. The brief rainfall event however that interrupted the experiment led to profuse leaf flush in the *Flacourtia* species with even

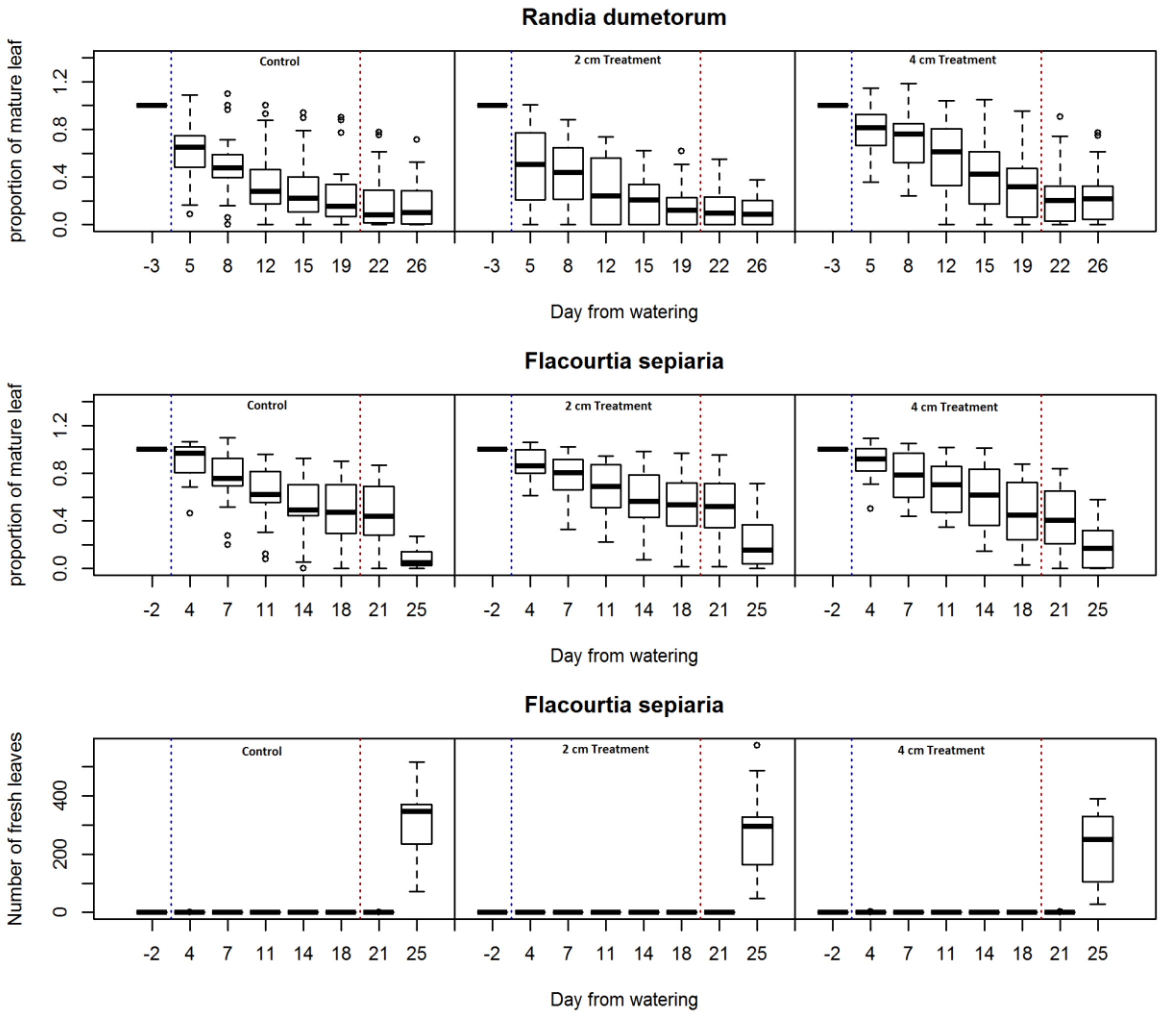


Fig. 11. First two graphs show the number of mature leaves as a proportion of the number before watering through the period of the experiment. Third plot is the number of fresh leaves observed for *Flacourtia* species through the experiment. Left panels are control, middle ones are of the 2cm treatment and right panels are of the 4cm treatment. Blue dotted line depict timing of irrigation, red dotted line show the timing of the 1.8cm rainfall. (Boxes represent the inter-quartile lengths, the bold lines represent the medians, whiskers represent the range and the open dots show outliers)

appearance of flowers in certain individuals. Response of the three treatments to the rainfall was also not observably different from each other. Flushing of leaves was accompanied by the high shedding of mature leaves as compared to the rate of leaf loss before. Putting out of fresh leaves was also observed in certain individuals of *Randia* species but the experiment was concluded before conclusive observations could be made on the population.

Discussion

Phenology of Rishi valley has been found to be highly seasonal, agreeing with typical deciduous, moisture limited landscapes.

Vegetative Phenology

Deciduousness of majority of the plants seems to be congruent to the moisture limitation of the landscape. Deciduousness seems to be limited to the late cool dry and the early hot dry phase. Drought stress is a significant phenomenon during dry seasons and plants may want to reduce the stress by shedding leaves in this phase. Lack of leaves reduces moisture loss through transpiration. By the later part of the cool dry season, temperatures during the day is quite high and humidity is low, with no cloud cover, all of which raises transpiration rates in leaves.

Although moisture may not be as limiting as later in the hot, dry season, all the plants shed their leaves then, rather than later. This maybe because of the reduced photoperiod during the cool dry phase. Total irradiance is possibly lower, during and following the winter equinox, as compared to the summer, when photoperiod and irradiance progressively increase. Plants may want to capitalise on periods of higher energy availability and conserve water for later use by shedding their leaves early. Deciduousness has therefore probably evolved to minimise water stress but at the same time maximise on irradiance.

Leaf flush in the moisture stressed, high irradiance dry phase, also occurs possibly because photosynthetic assimilation is highest in fresh leaves (Zimmerman et al., 2007) and plants want to utilise this during the cloudless periods. Flushing continued through the monsoons when neither light nor moisture was limiting and tapered off by the end of the monsoons as photoperiod reduced. Trees in general seem to have a shorter deciduous phase, possibly owing to the fact that they might have deeper roots and larger root surface area, as compared to shrubs, which makes more moisture available to them, reducing drought stress.

Reproductive Phenology

In majority of the flowering species, flowering happened immediately after leaf flush, contrary to observations in most other studies. Majority of Indian species however seem to show such flowering phenology (Singh and Khushwaha, 2006), the major advantage being that organic matter synthesised by the fresh leaves can be efficiently utilised in flowering. Leaf flush before flowering may also aid in increasing insect populations that could help in greater pollination. Development of many insect species are known to be dependent on fresh leaves (Visser and Both,2005) . This speculation however should be limited to entemophilic plants. The lack of plants using other pollination strategies, in this study, did not allow for comparison. Flowering of species at other timings could be due to several reasons. Competition for pollinators may be lesser for these species, they may not be as efficient as coping with water stress and flowered after adequate moisture availability, or selection on timing of fruiting has had stronger selection pressures. Regardless of the reason, these species help provide resources for insects at different times of the year and is beneficial for sustaining the community.

There was no observed seasonality in *Ficus* species but studies have shown that different *Ficus* species may have different peaks of fruiting intensity (Kuaraska et al., 2012), which has not been measured in this study. Yearlong availability of fruits with staggered peaks may be vital for maintaining frugivores in the landscape, during seasons of low resources. Majority of the fruiting occurred during the wet season. This may primarily because, plants have exhausted all their resources in the dry season on leaves and flowers and are unable to develop fruits as well, so as to drop them during the monsoons. Especially fleshy fruits are known to require high investment of moisture for proper development (Shukla and Ramakrishnan, 1982), so as to attract dispersers. Extended fruiting maybe a consequence of plants trying to drop fruits throughout the year, trying to cover as many periods of the erratic rainfall as possible so that at least a few seeds may survive (Bolmgren, 1998).

Mature fruits predominantly occurred during the dry season rather than around the onset of either of the monsoons. Advantage of fruiting in this time is unclear for mechanically dispersed seeds such as pods. The time delay to the monsoons may help in dispersal of seeds to greater distances before moisture is made available. For fleshy fruits this may be advantageous as resources are low in the dry season and may attract a high number of dispersers. Breeding season of birds predominantly happens in summer, during the south-west monsoons, and these potential seed dispersers switch to a more insect rich diet (Thompson and Willson, 1978) . Limited dispersers during this period may have also restricted plants to fruit post monsoons. From the above speculation, bird dispersed species should predominantly fruit before or after the breeding season as compared to the others. However even mechanically dispersed plants, fruit around the same time, which could also be for separate dispersal advantages, as mentioned earlier. Understanding the diet content of frugivores, during and after breeding, to see if there is a switch might justify the speculation. Most plants depend on various species for their dispersal, however, comparing the phenologies of a specialist and its unique disperser might show the exclusive relationship between the phenologies of the two species. While these biotic interactions may not have been causal in the shaping of the fruit phenology, they definitely benefit from it.

Competition for dispersers during the winters may not really occur, as Rishi Valley receives a large number of winter migrants. Species richness in the valley, may be a consequence of availability of ample resources even in the dry conditions. The winter migrants may also greatly reduce invertebrate populations in the winter, which could have also led to the majority of flowering phenology to follow flushing rather than precede it. Observing insect and bird population dynamics could help verify these speculations. Like correlating plant phenology to the weather it depends on, all these speculations may be verified by understanding the phenologies of animals and correlating them to phenologies of plants they depend on. However since most plants and animals coevolve, understanding causality may be a lot harder.

Synchrony

Synchrony of leaf flush was found to be much higher than flowering, in general, suggesting asynchrony in flushing may not be advantageous; even if plants had developed synchrony they may not have been selected for. Asynchrony in leaf flush would lead to some plants capitalising on high irradiance days and gathering more resources, outcompeting the others. The low levels of asynchrony observed, may be due to differences in micro habitats of the individuals. Asynchrony in leaves may also be due to water stress and how efficiently individuals had shed their leaves before the dry season, leading to how much of their resources they had allocated for the following season.

Presence of species showing both synchronous and asynchronous flowering strategies suggests possible advantages of either strategy. Synchronous plants maximise on genetic exchange and maintain the health of the populations. Competition for pollinators may lead to asynchrony. All the highly synchronous species, were the larger trees, possibly because of access to more resources. Large trees are also comparatively lower in number as opposed to shrubs, forcing them to synchronise for maximum outcrossing. Smaller trees and shrubs are more abundant, and asynchrony may not really translate to poor gene exchange, it may however restrict it.

The duration of flowering has also not been considered which would shed light if asynchronous species truly have lesser scope for genetic exchange, extended flowering species may not see this as a hindrance. The intensity of the reproductive characters have also not been considered, true quantitative synchrony would be a measure of the number of reproductive characters overlapping (Freitas and Bolmgren, 2008). Species asynchronous in the onset of their phenology may be synchronised in their efforts, likewise species synchronous in their onset need not be synchronous in their peaks.

Consistency

Trees in general showed more consistency than shrubs for both vegetative and reproductive phenophases. Plants in general use photoperiod as their primary cue for their phenological response. Moisture availability may however constrain this response. The consistent trees are probably less moisture stressed and less sensitive to yearly variation in weather as compared to the inconsistent shrubs which are moisture sensitive. Although different species have different consistencies and possibly combination of triggering cues, their fruiting and flowering phenologies are similarly timed. Different species therefore maybe utilising different environmental factors to initiate the same response at similar times.

Shrubs have shallow roots are highly stressed for water. Their leaf flush and flowering may therefore be dependent on moisture availability through early showers, so as to utilise the high irradiance. Trees however may not be so water limited and can faithfully flush and flower every year at the same time utilising the increasing photoperiod. Thus, though the ultimate factors for phenological timing are the same, plants have evolved varied proximate cues.

Individual Consistency

Most species showed some level of consistency at the individual level, except the *Ficus* species in leaf flush and one shrub in flowering. *Ficus* showed little seasonality in their phenologies and is not surprising that individuals were inconsistent. The consistency of individuals may likely reflect the genetic variation in the population or their microhabitats. Genetic variation may lead to a consistent difference among individuals to the same cues. Microhabitats could also shape availability of resources for plants. Individuals surrounded by other plants may get access to less moisture for example as opposed to individuals which are isolated. Individuals on slopes may receive less soil moisture as opposed to individuals in valleys. Similarly, individuals in the shade may experience different levels of irradiance in comparison to individuals in the open. Multiple factors both biotic and abiotic, could explain the differences in timing of individuals. Reasons for inconsistency in individuals is unclear but may have advantages such as increased outcrossing. Changing their timing of flowering would alter the genetic diversity available for them across years. Inherent stochastic processes could possibly cause such variation and may have been selected for considering the advantages it provides. Reasons as to why some individuals are consistent while others are not is also unclear. It may be due to genetic differences, factors that are temporally inconsistent or possibly poor resolution.

Lack of resolution was a major hindrance to this analysis. Large number of ties reduced the sensitivity of the results, decreasing the confidence in them. While data from following years could help staggering the ties, closer monitoring of the phenophases during the critical periods may be more insightful.

Correlation to Rainfall

Species with inconsistent populations in leaf flush phenology showed high correlation to rainfall as predicted. 5 of the 7 species showed strong correlation ($r > 0.95$, $p < 0.05$) for a threshold rainfall of 1cm, suggesting that little quantities of moisture provided could trigger phenological response. Of these 5, 4 species responded immediately while the other showed a considerable time lag between the rainfall event and the response. The time lag could be because of the time spent in physiological processes between the triggering of the phenology and the flushing itself.

Of the slightly weaker correlated species, *S. nux-vomica* showed immediate response to certain rainfall events, while not for others, suggesting that while rainfall might be the proximate cue, its threshold of response might be different. *R. dumetorum* on the other hand showed a weak correlation and a delayed response. While the delay and the correlation might be due to different threshold and physiological lag, the correlation may also have occurred just by chance.

Despite being water limiting, populations did not show increase in vegetative or reproductive efforts in years with increased water availability. This could possibly be because, the total rainfall in a year may not be a faithful representation of the moisture made available for plants. A heavy downpour may cause high amounts of runoff that drain out of the valley as opposed to a slower rainfall of the same quantity which could percolate into the ground. Similarly soil moisture from discrete rainfall events may be lost at a greater quantities due to evaporation as opposed to replenished soil moisture from continuous rainfall. A year with excessive or extremely poor rainfall however may reveal if there may be a correlation or if plants are independent of it. Phenology data is also qualitative which may not reflect the true efforts of populations.

Irrigation experiment

Even though leaf flush of *F. sepiaria* and *R. dumetorum* was correlated to rainfall, they did not show any response to artificial irrigation of either the 2cm or 4cm treatment of water. Profuse flushing by *F. sepiaria* and signs of leaf buds by *R. dumetorum* after a 2cm rainfall during the course of the experiment suggests that the event of a rainfall, rather than just moisture, triggers phenological response in the plants. A reason as to why no response was seen, could be that soil moisture may not have been sufficiently replenished. Flushing of *L. camara* adjacent to certain irrigated individuals however suggested otherwise. previously leafless *L. camara* individuals were observed flushing next to two 4cm treatment plants in less than a week of the irrigation. Only the two that flushed were noted and no other note was taken of individuals of the species to verify the effect of irrigation on them.

The experiment tried to recreate the amount of water made available by rainfall events. Individual plant watering may not have adequately recreated moisture from rain, as dry soil may be highly hydrophilic causing high subsoil spread decreasing the effective water poured for a half a meter radius. Conclusions about soil moisture could not be made due to lack of quantitative soil moisture readings. Assessing soil moisture drainage after irrigation in the subsequent dry period as opposed to how long moisture lasts in the soil after a rain may reveal the validity of the experiment.

It could also be possible that plants respond to other cues that co-vary with the event of a rainfall apart from moisture, such as increase in humidity, change in irradiance due to cloud cover or a combination of the factors. Rainfall also causes runoff and transfer of nutrients, whose presence may lead to flushing. Rainfall also leads to dropping of a large number of senescent leaves, that fall as a result of force from the rain drops. Fallen leaves could create mulch, that cover the top soil to reduce evaporation.

A similar experiment in Mexico that shares very similar abiotic conditions as this field site produced varying responses in plants depending on the amount of water provided (Hayden et al., 2010). The key difference was that irrigation was done on larger plots and conducted on trees. Another experiment however, that recreated moisture and humidity by using sprinklers for irrigation did not report a response to irrigation (Wright and Cornejo, 1990). The above results reiterate the need for establishing causality rather than just covariance with experiments conducted on field and the complexity of phenological processes.

Manual weather data has limited analysis in correlating weather data to the wide spectrum of weather variables. Data now available from the automated station may provide more seasonal abiotic factors that plant phenology track. Qualitative data of the monitoring, also primarily yields qualitative analysis that could point towards further investigation. The analysis is also restricted by the temporal resolution of the data. A 15 day resolution may be too coarse for more sensitive responses (Miller-Rushing et al., 2008). The lack of resolution from the sampling frequency however becomes less significant for every additional year monitored.

Conclusion

Phenology monitoring revealed the capacity of the landscape to support diversity despite being severely moisture limited and having erratic monsoons. Understanding the underlying drivers of plant behaviour is essential for efforts in ecosystem conservation and management. Rishi Valley itself has undertaken a large scale restoration effort. Knowledge of plant phenology would be essential in assessing an adequate species composition to sustain the ecosystem. They also engage in watering plants in the dry season during acute water shortages, which may not be advisable from our analysis of the limited species in the irrigation experiment, as they do not seem to respond.

Phenology work has been given more and more attention as phenology has been recognised as an ecological phenomenon that is particularly sensitive to climate change. In the tropics, in particular, further work is needed on both the drivers of phenology, and also the downstream effects of changing phenology – on frugivores, pollinators, and herbivores.

Most phenological work conclude with correlation with abiotic factors. Very few test the causality behind these correlations and even lesser have linked field observations to upstream physiological mechanisms driving these processes. Similarly downstream consequences of phenology is speculated but also poorly understood. True understanding of plant responses and its implications will not be achieved unless it is studied at all three links of the causal chain and interactions with downstream animals are also clear.

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