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Research Paper

Does seasonal flowering and fruiting patterns of cacao only depend on climatic factors? The case study of mixed genotype populations in Côte d'Ivoire

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ABSTRACT

Theobroma cacao, a tropical cauliflorous fruit tree, typically produces flowers and fruits twice a year and exhibits alternate harvesting patterns over consecutive six-monthly seasons in regions with bi-modal rainfall distribution, such as Côte d'Ivoire. This study investigated seasonal variations in flowering and fruiting among trees in populations of mixed cacao genotypes. The intensities of crown and trunk flowering and pod production were monitored for eight consecutive six-monthly seasons on 114 adult cacao trees grown from seedlings. We investigated distributions of seasonal flowering and fruiting values, relationships between flowering and pod production, and the effects of seasonal cumulative rainfall. The patterns of seasonal flowering and fruiting series were analyzed using two descriptors: the first distinguishing between regular and variable patterns, and the second analyzing the structure of such variability, classifying it as either irregular or alternating. Despite being subjected to similar climate and agronomic management, individual trees exhibited highly variable flowering and fruiting behaviors within each season, as well as variable patterns of flowering and fruiting across seasons. Seasonal alternate fruiting on a population scale masked highly variable patterns among trees, and only 19 % of the trees exhibited marked alternate fruiting patterns. Variations in pod production on a tree scale were mainly related to variations in trunk flowering. Endogenous factors seemed to control seasonal variations in flowering and fruiting, even though exogenous factors, both climatic and agronomic, could structure flowering and fruiting patterns at the orchard scale.

1. Introduction

Cacao (*Theobroma cacao)* is a tropical tree cultivated for its fruits, called pods, and its seeds are used in the chocolate and cosmetics industries. The species is native to the Amazonian rainforest and displays cauliflory and ramiflory reproductive development, which results in a scattered distribution of flowers on the tree trunk and branches (Bell and Bryan, 1991). Inflorescences develop at the leaf or leaf scar axil on a persistent bud complex commonly called "flower cushions" (Alvim, 1984; Bell and Bryan, 1991). Each inflorescence bears several flower buds and a single tree can produce up to 100 000 flowers annually (Alvim, 1984; Lachenaud, 1991). The number of flowers produced by a tree, flower fertility, fruit set rate and length and periodicity of flowering events are highly variable between cultivars (Alvim, 1984; Lachenaud, 1991). These variations in flowering features are usually attributed to the degree of sexual self-compatibility, which is under genetic control (Boyer, 1970; Mossu et al., 1981; Omolaja et al., 2009; Restrepo et al., 2017). Variations in reproductive traits within trees have also been

Abbreviations: NA

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reported. Pollination rate, fruit set, fruit survival rate and fruit weight are greater on trunks than on branches (Cortez, 2009; Melnick, 2016; Warren et al., 1997). It is also common to observe asynchronous flowering and fruiting events on cacao trees, whether between trunk and branches, or between flower cushions (Adjaloo et al., 2012; Claus et al., 2018).

Literature on the flowering phenology of cacao trees is scarce, and most studies have focused on the effects of climatic factors. Strong correlations between flowering phenology and annual distributions of rainfall, temperature and radiation have been reported in various climates and for different cultivars (Adjaloo et al., 2012; Alvim, 1984; Owusu et al., 1978; Sale, 1970, 1969). Rainfall, or soil moisture, are often presented as the most critical factors controlling the timing and intensity of flowering (Adjaloo et al., 2012; Almeida and Valle, 2007; Alvim, 1993). In regions subjected to seasonal drought, flowering is usually inhibited during drought, and rainfall following the dry period triggers intense flowering episodes. In this case, rainfall distribution determines the onset and distribution of flowering episodes throughout the year (Bridgemohan et al., 2017; Restrepo et al., 2017). However, in tropical regions with well-distributed rainfall and low variations in temperature, a cacao orchard can flower and produce throughout the year, though it is established that individual trees usually maintain a rhythmic and alternate vegetative and reproductive phenology (Alvim, 1966; Sale, 1970). As a result, standard phenological models are often calibrated for each cacao producing region, based on the specific climate and the behavior of cacao cultivars grown in the area. In Côte d'Ivoire, where almost half of the world's cocoa is produced, production follows a biannual distribution model, which consists of two distinct and uneven harvesting seasons, known as "main-crop" and "mid-crop" harvests ("*Grande et Petite Traites*"). This pattern follows the bimodal rainfall climate found in the southern part of the country, where most of the cocoa is produced (Brou et al., 2003; Coulibaly et al., 2019). In this model, flowering peaks in the wettest months and subsequent fruiting fluctuates accordingly, i.e., the major flowering season and "mid-crop" harvest happen during the main rainy season, whereas the minor flowering season and "main-crop" harvest happen during the minor rainy season. This pattern constitutes a case of irregular bearing, structured in marked alternation between high and low reproductive seasons, under the control of climate.

Irregular bearing, i.e., irregular fruiting between consecutive reproductive events, is a frequent feature of fruit tree species. An inclination towards irregular bearing is partly controlled by genetics, and cultivars of species subjected to irregular bearing can exhibit various patterns of irregularity (Lauri et al., 1995). As a result, bearing patterns are essential criteria for varietal selection and are often studied in fruit tree breeding programs for either temperate (Laurens et al., 2000) or tropical species (Cilas et al., 2011). However, the bearing pattern of a specific cultivar is not absolute. It may differ or fluctuate depending on environmental conditions, tree management practices and individual tree features, such as age or health status (Lauri et al., 1997, 1995; Monselise and Goldschmidt, 1982). Abiotic factors are usually involved in the reproductive phenology of perennial fruit species, such as temperature, photoperiod, or water stress (Smith and Samach, 2013). However, endogenous factors such as carbon status, carbon to nitrogen ratio and hormonal balance also seem to be involved in irregular bearing (Capelli et al., 2021). Competition between vegetative and reproductive tree compartments is especially involved in alternate bearing, the specific case of irregular bearing with an alternation of heavy and low yields in consecutive reproductive events, be it on an annual scale or not (Monselise and Goldschmidt, 1982).

In cacao, the role of endogenous factors in controlling flowering phenology is often overlooked, as climate and rainfall patterns are presumed to be the main driving factors (Boyer, 1970). However, reports of endogenously controlled cacao flowering and fruiting rhythmicity exist. Cacao exhibits rhythmic flowering phenology under constant climatic conditions, suggesting an endogenous control of flowering (Sale, 1970, 1969), with the duration of the flowering episode and the duration between consecutive flowering episodes depending on the genotype (Sale, 1970; Valle et al., 1990). Hutcheon (1981) demonstrate a strong inhibitory effect of fruit load on cacao tree flowering in the same cycle, leading to alternate patterns of high and low production between consecutive reproductive cycles. Girdling and fruit thinning induce recurrent flowering (Alvim, 1984). Vegetative events, such as flushing or root and cambial growth, also negatively impact cacao tree flowering (Almeida and Valle, 2007; Alvim, 1984; Glendinning, 1966; Hutcheon, 1981; Valle et al., 1990). It can thus be presumed that seasonal flowering and fruiting irregularity of cacao might be under the control of both exogenous (climatic and/or cultural practices) and endogenous factors.

In West Africa, cacao orchards are almost exclusively grown from seedlings of either a mix of selected hybrids, or germplasm of unknown parentage, i.e., mixed genotypes, and several studies have reported high levels of tree-to-tree variability in reproductive behavior (Adjaloo et al., 2012; Boyer, 1970; Mossu et al., 1981; Sounigo et al., 2005; Wibaux et al., 2018). We put forward the hypothesis that seasonal reproductive patterns may vary between trees in a given orchard of mixed genotypes. In order to investigate this hypothesis, we analyzed series of seasonal flowering and pod production data across four consecutive years, i.e., eight reproductive events, on a sample of cacao trees from an industrial cacao orchard in Côte d'Ivoire. Our objectives were to (1) investigate the variation in seasonal flowering and fruiting at the scale of a population of mixed genotypes and examine the possible link with seasonal cumulative rainfall, (2) determine the patterns of seasonal flowering and fruiting at the scale of individual trees from the population, and (3) investigate the relationships between trunk and crown seasonal flowering and fruiting patterns. Our discussion focuses on the respective roles of endogenous and exogenous controls of flowering and fruiting patterns at tree and orchard scales, and the consequences for crop management.

2. Material and methods

2.1. Plant material

The study took place in a commercial cacao plantation located in the region of Gagnoa (Centre-West of Côte d'Ivoire). The plantation comprised various cacao orchards of different ages and cropping systems. The orchard selected for the study was composed of cacao trees planted in 2010 under full sun, in lines and rows at a regular spacing of 3 m x 3 m. Individual trees were grown from seedlings of unclear parentage, provided by a technical institute at the time of planting. The population was supposedly composed of a mix of hybrids between Upper Amazon and Lower Amazon or African Trinitario parental genotypes, as usually found in the region (Pokou et al., 2006). Each tree was therefore genetically unique, and we refer hereafter to the population as "mixed genotypes". In the following we refer to individual cacao trees from our sample as "trees" or "individuals". Trees were over 7 years old at the beginning of the study and had already achieved a well-established flowering and fruiting behavior. Agronomic management followed recommended practices. Each tree was fertilized once a year in April with 150 g of 0–23–18 NPK fertilizer complemented with micronutrients. Trees were heavily pruned every year during February-March, after the return of precipitation following the dry season, to reduce foliage density and avoid excessive competition with neighboring trees. Maintenance pruning and sanitary operations on the trees were performed once every month to maintain a single trunk and a single crown of 2 to 5 healthy scaffold branches. Sanitary treatments with insecticides were usually performed in June-July and again in December-January, and fungicides were applied in September-October. The timing, dosage, and recurrence of sanitary treatments were rationalized depending on pest dynamics and could vary between seasons, but all management operations were applied synchronously and homogeneously at the orchard scale.

One hundred and twenty trees were sampled in a continuous 5 ha plot. A rational sampling strategy was chosen in order to avoid sampling bias while limiting the effects of biological constraints. Six areas with a low incidence of pests and diseases and tree mortality were identified in the plot. Twenty neighboring trees were selected in each area. Six trees died during the study and were removed from the sample, leaving 114 trees for data analysis. Considering the small size of the selected plot, climatic differences between the sample areas, such as rainfall, temperature and irradiance dynamics, were considered negligible.

2.2. Data collection

Flowering intensity and pod production were observed weekly on the trees from 1 December 2017 to 31 December 2021. Cacao flowering is usually monitored by either counting flowers on sections of trunk and/or branches, or by collecting fallen flowers in traps before weighing or counting them. However, these standard methods are partial and catch only a share of the flowering of a tree, overlooking flowering events outside the monitored areas or traps. Considering our objective of surveying the dynamics of flowering on the whole crown and trunk of each tree, as well as the high frequency of data collection, we chose to adopt a method to score flowering intensity. Flowering intensity was monitored by weekly rating visual observations of mature flowers, i.e., at anthesis or close to anthesis, on trunk and crown separately. The visual scoring method was calibrated between successive observers over the 4-year period of the study. The rating of flowering intensity ranged from 0 (no mature flowers) to 5 (high frequency of active flower cushions, all bearing high numbers of open flowers). It is common in cacao to observe a few scattered flowers throughout the year, and studies usually distinguish between the continuous presence of a few flowers, and the noticeable flowering event resulting in intense development of flower cushions on sections of the branches or stem (Alvim, 1993). To differentiate between flowering episodes and continuous flowering, a rating of 1 was given when flowering was scarce, usually with a few scattered flowers, and a rating of 2 or higher was given when conspicuous flowering episodes were observed. A rating of 2 was given for observations of low frequency of active flower cushions with low numbers of open flowers; a rating of 3 was given for higher frequency of active flower cushions but with low numbers of open flowers; a rating of 4 was given for medium to high frequency of active flower cushions with both high and low numbers of open flowers; and a rating of 5 was given for high frequency of active flower cushions, all with high numbers of open flowers (Fig. 1).

The production data consisted of weekly counting of harvested pods at least 15 cm long, i.e., excluding wilted young pods ('cherelles'). Pods harvested from both trunk and crown were counted together in a single measurement of "pod production". Harvested pods included either ripe or damaged pods and their number represented the reproductive investment of the whole tree in pods. Although the sizes of harvested pods were monitored during data collection, we lacked information on the size of pods lost because of pests and diseases, which accounted for about 15 % of total pod production. As a result, we chose to focus on the number of pods produced by the plant, as a function of reproductive investment, rather than yield descriptors that would account for the size or weight of the pods.

The delineation of seasons was made according to the reproductive cycling of the cacao trees in the study area (Brou et al., 2003; Coulibaly et al., 2019; Kassin et al., 2008). The first season of each year, or "Season A" (odd numbers in the results), ran from January to the end of June. It starts with a dry period (January-March), followed by the major rainy period (April-June), during which the "mid-crop" harvest and the main flowering peak of the cacao trees are usually observed. The second season of each year, or "Season B" (even numbers in the results), ran from July to the end of December. It usually starts with the minor dry period (July-August), followed by the minor rainy period (September--November). It is usually the "main-crop" cacao harvesting period and it includes the second flowering peak of the year. In the study, each 6-month season was considered as a functional phase of cacao flowering and fruiting, and consecutive seasons were considered without reference to the year.

Time series of weekly flowering intensity ratings showed very heterogeneous patterns among the trees. Depending on the tree, the floral episodes could be more or less intense and/or could be concentrated into a short timespan or spread over long periods (see appendices: Figs. A1 and A2). In order to combine both intensity and length of the flowering episodes in a single "seasonal flowering index" on a trunk and crown scale, we calculated the area under the flowering curve of each tree for each season n ($Surf\_Flo_n$) as:

$$Sur\_Flo_n = \sum_{t=1}^{T} \frac{N\_Flo_t + N\_Flo_{t+1}}{2} \quad (1)$$

where T is the total number of weeks in season n, and N_Flo_t and N_Flo_{t+1} are the rating of trunk or crown flowering intensity for weeks t and $t+1$, respectively. With a maximum of 26 weeks in a season and a maximum flowering score of 5, $Surf\_Flo_n$ values can range between 0 and 130.

For each tree and each season, we computed the sum of pods harvested throughout the season. The sum of all the pods produced per tree over the course of the study, i.e., total production over the eight seasons, was also calculated. Daily rainfall was monitored with a rain gauge located close to the cacao orchard. Seasonal cumulative rainfall was computed from this data.

2.3. Analysis of seasonal flowering and fruiting patterns

The seasonal flowering and fruiting patterns of each cacao tree were calculated around their linear trend over the eight seasons studied. The individual patterns could be either regular, alternating, or irregular. A pattern was considered regular when the variability around the trend was low. In this case, it was pointless determining the structure of the variability. Conversely, the pattern was variable when the variability

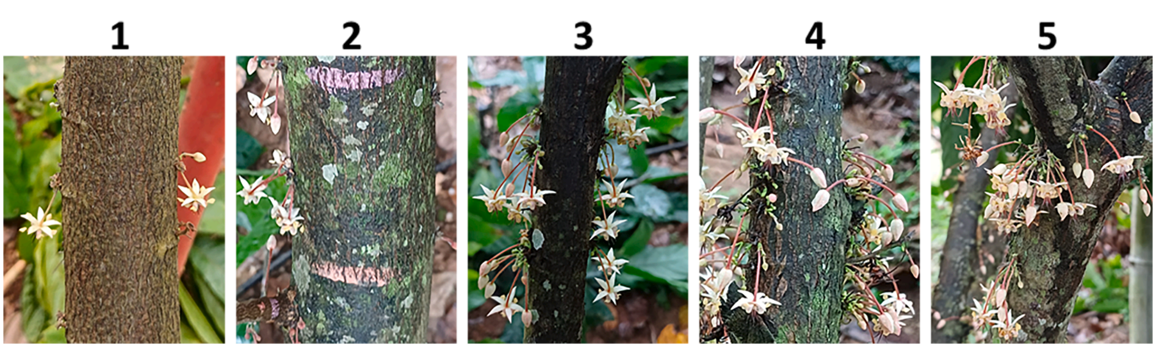

Fig. 1. Photos of cacao axis bearing flowers and associated visual rating of flowering intensity from 1 to 5.

around the trend was high. If the variability showed alternation between successive seasons, the pattern was alternating. If the variability had no regular structure, the pattern was irregular. We therefore needed two descriptors to characterize seasonal flowering and fruiting patterns, with one descriptor quantifying variability of the data around the linear trend, and the other characterizing the structure of that variability. The two descriptors were calculated for seasonal trunk and crown flowering indices, and for the seasonal pod production of each tree.

The first descriptor was derived from a classical "biennial bearing index" (BBI) that quantifies the variability of a variable (fruit number or weight) around the mean of a series of consecutive values (Wilcox, 1944). BBI has been adapted to quantify the variability of the residuals around the linear trend of a series of consecutive values of yield or flowering intensity, normalized by average yield or flowering intensity (Durand et al., 2013). The descriptor, called BBI_res_norm, was calculated in our study as:

$$\text{BBI\_res\_norm} = \frac{\sum_{t=2}^{T} |\varepsilon_t - \varepsilon_{t-1}| / (T-1)}{\sum_{t=1}^{T} Y_t \ / T} \quad (2)$$

where Y_t and ε_t correspond to the value of the studied variable Y and the Gaussian residual from the linear trend in season t, respectively, and T is the total number of measurements (here $T = 8$ seasons).

This descriptor was used to discriminate between regular (values close to 0) and variable (higher values) patterns for the variable Y (Durand et al., 2013). Based on empirical observations of each individual series of data and in order to help in interpreting the results, BBI_res_norm value of 1 was set as an informative threshold to distinguish trees with significant variation around the trends (BBI_res_norm > 1). Calculation of the descriptor depended on the range of values achieved by the individual over the series of data, independently from the range of values observed in the rest of the population. BBI_res_norm was normalized by the average flowering index or pod production of the tree over the eight seasons, possibly leading to high BBI_res_norm values for trees that flowered or produced little, whereas the amplitude of variation around their trend was low in comparison with trees that displayed higher flowering or production. Thus, we need to also consider the average value of the variable when interpreting the calculated BBI_res_norm values. In the following we refer to this descriptor as "BBI_res_norm" or "variability descriptor".

The second descriptor was computed from the seasonal residuals ε_t around the linear trend for each tree, to detect any alternating structure in the series. This corresponded to a negative correlation between consecutive residuals. This descriptor was calculated through a first-order autoregressive model performed on residuals ε_t:

$$\varepsilon_t = \gamma \times \varepsilon_{t-1} + u_t \quad (3)$$

Where u_t is the residual from the autoregressive model in season t. The autoregressive coefficient γ, called "Auto.cov" in our study, illustrated the dependency between consecutive residuals. Auto.cov values around 0 indicated the absence of autocorrelation between consecutive values of the series, and corresponded to an irregular structure of the variability around the trend. Values close to – 1 indicated an alternating structure of the variability around the trend (Durand et al., 2013). Based on empirical observations of individual series, – 0.7 was set as an informative Auto.cov threshold to distinguish trees with marked alternate patterns (Auto.cov < – 0.7). In the following, we refer to this descriptor as "Auto.cov", or "alternation descriptor".

2.4. Data analysis

Graphics of data dispersion and dispersion statistics were used to describe the average trends and seasonal variability of trunk and crown flowering indices and pod production values over the eight seasons of the study. Considering the asymmetry of data distributions, non-parametric Friedman and Nemenyi post-hoc tests were used to analyze the differences between the eight seasons for each variable. A Wilcoxon signed rank test was used to analyze differences between pairs of variables and btween the A and B seasons for each variable.

Individual series of eight seasonal trunk flowering index, crown flowering index and pod production values were standardized using the z-score method, in order to correct the effects of individual variations in the analysis of relationships between variables. Linear regression models were used to analyze the effects of seasonal cumulative rainfall values on the flowering indices and pod production variables. Both visual representations of linear trends and interpretation of R^2 were used to comment on the relationships.

Pearson correlation tests were used to analyze the pairwise relationships between seasonal values of flowering indices on trunk and crown, and pod production over the same season and over the following season. Pearson correlation tests were also used to test the pairwise relationships between individual total pod production values over the eight seasons and BBI_res_norm and Auto.cov values calculated from pod production and flowering indices.

The various patterns of seasonal flowering and fruiting observed within the population were illustrated by the projection of each tree on the Auto.cov (y-axis) vs. BBI_res_norm (x-axis) plane. This graphical representation allowed differentiation between trees with (1) a regular pattern around the linear trend, i.e., BBI_res_norm values close to 0, in the left-hand part of the plane; (2) a variable and irregular pattern around the linear trend, i.e., high BBI_res_norm values (>1) and Auto.cov values over −0.7, located in the center-right part of the plane; and (3) a marked alternating pattern around the linear trend, i.e., high BBI_res_norm values (>1) and Auto.cov values lower than −0.7, in the bottom right-hand corner of the plane (see Fig. 5-C; Durand et al., 2013). Examples of trees with regular, irregular and alternating series of pod production are presented in Supplementary Materials (Fig. A3).

All statistical tests and graphic outputs were obtained using R software (R Core Team, 2022), with the R packages "stats" (version 4.2.0), "beanplot" (version 1.3.1), "graphics" (version 4.2.0), "ggplot2" (version 3.4.1) and "lmerTest" (version 3.1–3). The threshold for statistical significance for all mean comparisons was set at $P < 0.05$.

3. Results

3.1. Seasonal variability of cumulative rainfall, flowering, and pod production

Seasonal cumulative rainfall ranged from 575 to 843 mm during the study. The average values for the A seasons (January - June) and B seasons (July - December) were 702 mm and 694 mm, respectively, and were not significantly different (Table 1).

Individual values for the crown and trunk flowering indices ranged from 0 to 68.5 and 108 respectively (Fig. 2-A, 2-B and Table 1). The values of both indices were highly variable within each season, with coefficients of variation (CV) within seasons ranging from 48 % to 60 % for crown flowering, and from 52 % to 114 % for trunk flowering. There were significant differences between the eight seasons for both crown and trunk flowering. Average trunk flowering was significantly higher in the A season than in the B season, but there was no significant difference between A and B seasons for average crown flowering. Over the eight seasons, average crown flowering was significantly higher than average trunk flowering (Table 1).

Seasonal pod production values (Fig. 2-C) ranged from 0 to 183 pods per tree, with an average of 21.9 pods per tree over the eight seasons. Intra-seasonal variability was high, with CV between 75 % and 120 %, and distributions of values within each season were positively skewed. There were significant differences between seasons for pod production. There were significant differences between the average pod production in the A and B seasons, with average values of 14.6 and 29.2 pods per tree, respectively (Table 1).

Table 1

Range (Min-Max), mean and coefficient of variation (CV) for the crown flowering index, trunk flowering index and pods production for each season (1 to 8), for seasons A and B and for the 4 years of study (TOTAL). Cumul. rainfall = cumulative rainfall measured during the season. *Av.* = average value of cumulative rainfall over seasons A or B. Mean values among the eight seasons followed by the same lower-case letter are not significantly different (Nemenyi test). Mean values among seasons A and B followed by the same capital letters are not significantly different (T-test for Cumul. rainfall; Wilcoxon signed-rank test for the other variables).

	Cumul. rainfall (mm)	n	Crown flowering			Trunk flowering			Pod production		
			Min - Max	Mean	CV	Min - Max	Mean	CV	Min - Max	Mean	CV
Season 1	718	114	7.5 - 85.5	36.8 ^{a}	48 %	2 - 58.5	22.2 ^{a}	53 %	0 - 95	16.8 ^{bc}	120 %
Season 2	781	114	0 - 83.5	26.2 ^{d}	60 %	0 - 40	11.4 ^{c}	74 %	0 - 183	35.2 ^{a}	88 %
Season 3	656	114	2.5 - 74.5	22.8 ^{e}	51 %	0 - 46	13.1 ^{c}	56 %	0 - 111	17.8 ^{b}	103 %
Season 4	765	114	8 - 93.5	28.4 ^{cd}	52 %	0.5 - 52	13.3 ^{c}	81 %	1 - 95	27.2 ^{a}	75 %
Season 5	843	114	8.5 - 80.5	30.9 ^{bc}	45 %	6 - 58.5	23.5 ^{a}	52 %	0 - 51	10.3 ^{c}	99 %
Season 6	575	114	2 - 98	32.3 ^{ab}	50 %	0 - 62.5	12.9 ^{c}	114 %	0 - 167	30.9 ^{a}	83 %
Season 7	594	114	0 - 100.5	35.3 ^{a}	51 %	0 - 68.5	18.5 ^{b}	74 %	0 - 72	13.4 ^{bc}	106 %
Season 8	653	114	0 - 108	33.8 ^{ab}	57 %	0 - 62.5	13.4 ^{c}	107 %	0 - 133	23.5 ^{a}	84 %
A seasons (odd)	*Av.* 702 ^{A}	456	0 - 100.5	31.4 ^{A}	52 %	0 - 68.5	19.3 ^{A}	63 %	0 - 111	14.6 ^{B}	112 %
B seasons (even)	*Av.* 694 ^{A}	456	0 - 108	30.2 ^{A}	56 %	0 - 62.5	12.7 ^{B}	97 %	0 - 183	29.2 ^{A}	86 %
Total	–	912	0 - 108	30.8	54 %	0 - 68.5	16.0	79 %	0 - 183	21.9	102 %

3.2. Effect of rainfall on crown and trunk flowering and on subsequent pod production

Average values were calculated for each season on standardized crown flowering, trunk flowering and pod production data. The linear regression analysis between seasonal values of cumulative rainfall and average standardized values of crown flowering, trunk flowering and pod production yielded non-significant relationships (Fig. 3). In all cases, cumulative rainfall in the range of values recorded over our 4-year study did not explain the variations in seasonal average standardized values for the flowering indices and pod production. Data dispersion of each variable was high for each season, regardless of the value of cumulative rainfall. Both positive and negative standardized values were observed for each season, as illustrated by the dispersion of values above and below the dashed horizontal line set at $y = 0$. This indicates that trees responded both positively and negatively to every season, regardless of the level of rainfall recorded during the season, for both flowering on the trunk and crown, as well as pod production.

3.3. Relationships between flowering indices and pod production

Pairwise relationships between variables were tested on standardized data (7 seasons x 114 trees = 798 values) for crown and trunk flowering indices, pod production in the same season 'n' and pod production in following season '$n + 1$' (Fig. 4). Trunk and crown flowering indices were positively correlated. Trunk and crown flowering indices were negatively correlated to pod production in the same seasons, and positively correlated to pod production in the following seasons. A negative correlation was observed between successive pod productions. The low but significant values of Pearson's correlation coefficient were probably related to the substantial dispersion of the data and the large sample ($N = 798$), increasing the statistical power of the test.

3.4. Joint distributions of BBI_res_norm and auto.cov–

The distributions of BBI_res_norm and Auto.cov calculated for the 114 cacao trees differed between the three studied variables (Kruskal-Wallis test, $P < 0.001$).

For crown flowering (Fig. 5-A), data distribution along the BBI_res_norm x-axis was grouped around a median value of 0.26, with values ranging from 0.10 to 1.04. The low values of BBI_res_norm indicated that crown flowering was rather regular over the eight seasons for all trees. Only one tree displayed a BBI_res_norm value over 1, and this tree also had the lowest value of crown flowering indices (see dot area on Fig. 5-A). BBI_res_norm is a normalized descriptor (Eq. (2)), which makes it very sensitive to low values. As a result, the calculation of BBI_res_norm for this individual yielded a high value, even though its crown flowering indices were consistently low across the eight seasons, with low absolute variations between seasons. The distribution of data along the Auto.cov y-axis (Fig. 5-A) spread from -0.84 to 0.41, with a median value of -0.12. Trees displaying the lowest Auto.cov values also displayed low values for BBI_res_norm, corresponding to alternate patterns with low amplitudes of variations around the trend. Thus, these situations still corresponded to regular patterns.

For trunk flowering (Fig. 5-B), data distribution along the BBI_res_norm x-axis was more scattered than for crown flowering. The values ranged from 0.18 to 1.63, with a median of 0.64. Data distribution along the Auto.cov y-axis was also more scattered and displayed lower values than for crown flowering, ranging from – 0.96 to 0.46, and a median of – 0.39. Dispersion of individuals on the graph showed substantial variability in patterns of trunk flowering, with trees displaying regular, irregular and alternate patterns. Twenty-eight trees (25 %) displayed values over the empirical threshold of BBI_res_norm values > 1. Among them, nine trees (8 %) were characterized by Auto.cov < – 0.7, corresponding to marked alternating individuals. Eighty-six trees (75%) were considered as regular for trunk-flowering, with BBI_res_norm < 1.

For pod production (Fig. 5-C), data distribution along the BBI_res_norm x-axis was more scattered than for trunk flowering. Values ranged from 0.24 to 2.11, with a median of 0.95, illustrating less frequent regular patterns of pod production over the eight seasons. Auto.cov values varied in a range similar to trunk flowering, from – 0.98 to 0.36, but low Auto.cov values were more frequent, with a median of – 0.57. Fifty-two trees (46 %) displayed BBI_res_norm values > 1. Among them, twenty-two trees (19 %) were characterized by Auto.cov < – 0.7, corresponding to marked alternating individuals. Sixty-two (54 %) trees were considered as regular producers with BBI_res_norm < 1.

For each variable, the distribution of individuals along the BBI_res_norm vs Auto.cov plane followed a negative linear trend (Pearson's correlation tests, $P < 0.001$). Pearson's coefficients of correlation between BBI_res_norm and Auto.cov were – 0.51, – 0.56 and – 0.55 and the slopes of the linear regressions were – 0.94, – 0.51 and – 0.42 for crown flowering, trunk flowering and pod production, respectively (Fig. 5). These results indicated higher regularity of flowering on the crown as compared to flowering on the trunk, and more variable pod production on a whole-tree scale with, in the latter case, more individuals displaying alternate bearing.

3.5. Relationships between cumulative pod production over eight seasons and BBI_res_norm and Auto.cov values

A negative linear trend was found between the total pod production of trees over the eight seasons and BBI_res_norm for pod production (Fig. 6-A3), but the correlation was quite weak. In contrast, the correlations between the total pod production of trees over the eight seasons

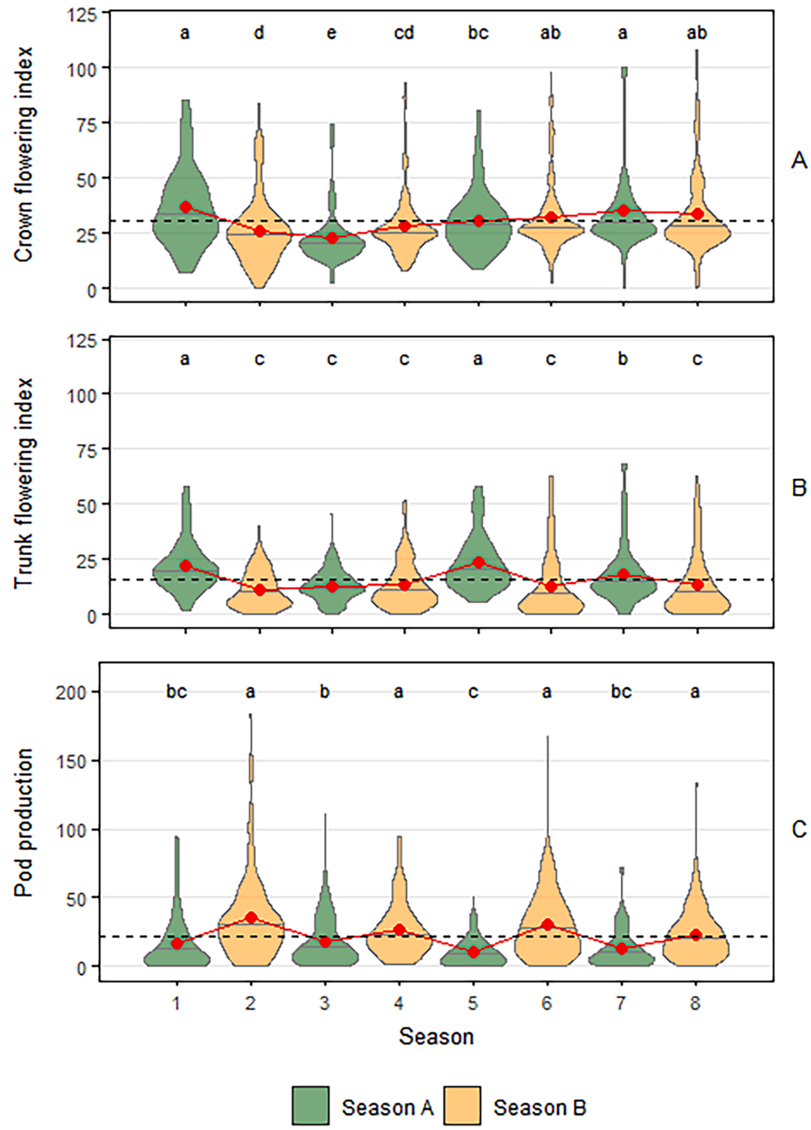

Fig. 2. Seasonal distributions of values for (A) crown flowering index, (B) trunk flowering index and (C) pod production among a mixed-genotype cacao trees population. From season 1 (January-June 2018) to season 8 (July-December 2021). $N = 114$ trees. Green and orange colors = Seasons A and B, respectively. Dashed black lines = average value over the eight seasons. Red dots and red curves = changes in seasonal average. Seasons with the same letter above the distribution do not differ in mean values (Nemenyi test).

and Auto.cov for pod production, or BBI_res_norm and Auto.cov for crown and trunk flowering, were not significant (Fig. 6).

3.6. *Correlations between BBI_res_norm or Auto.cov values for pod production, crown and trunk flowering*

Weak but significant positive correlations were observed between BBI_res_norm values for crown flowering and for trunk flowering (Fig. 7-A3), and between BBI_res_norm values for crown flowering and for pod production (Fig. 7-A1). However, for both cases, the correlations were stretched by the two individuals with the highest BBI_res_norm values for crown flowering indices. These two trees had the lowest values for total crown flowering indices within the population, indicating that they displayed very low flowering ability over the eight seasons. As a result, their high BBI_res_norm value resulted from the normalized calculation of BBI_res_norm (Eq. (2)). When these two individuals were removed from the sample, the correlation between BBI_res_norm values for crown flowering and trunk flowering was not significant and the correlation between BBI_res_norm values for crown flowering and pod production yielded poorer results, although still significant (Fig. 7-A1 and A3).

Significant correlations were found between both BBI_res_norm and Auto.cov values for trunk flowering and pod production, although individuals were scattered around the trends (Fig. 7-A2 and B2). No significant correlation was found between Auto.cov values for crown flowering and pod production (Fig. 7-B1), nor between Auto.cov values for crown and trunk flowering (Fig. 7-B3).

4. Discussion

In this study, we investigated the seasonal variations of flowering on trunk and crown and pod production of a cacao population of mixed genotype, and the patterns of seasonal variations of flowering and fruiting of individual trees. Our results showed high variability in flowering and fruiting of trees within each season, and significant differences between seasons. Variations in seasonal mean flowering and fruiting values were not related to seasonal cumulative rainfall values. Analysis of the two descriptors of variability and structure of seasonal series of flowering and fruiting at the tree scale, BBI_res_norm and Auto.cov, respectively, showed regular patterns of crown flowering for every tree over eight consecutive seasons. 25 % and 46 % of trees showed

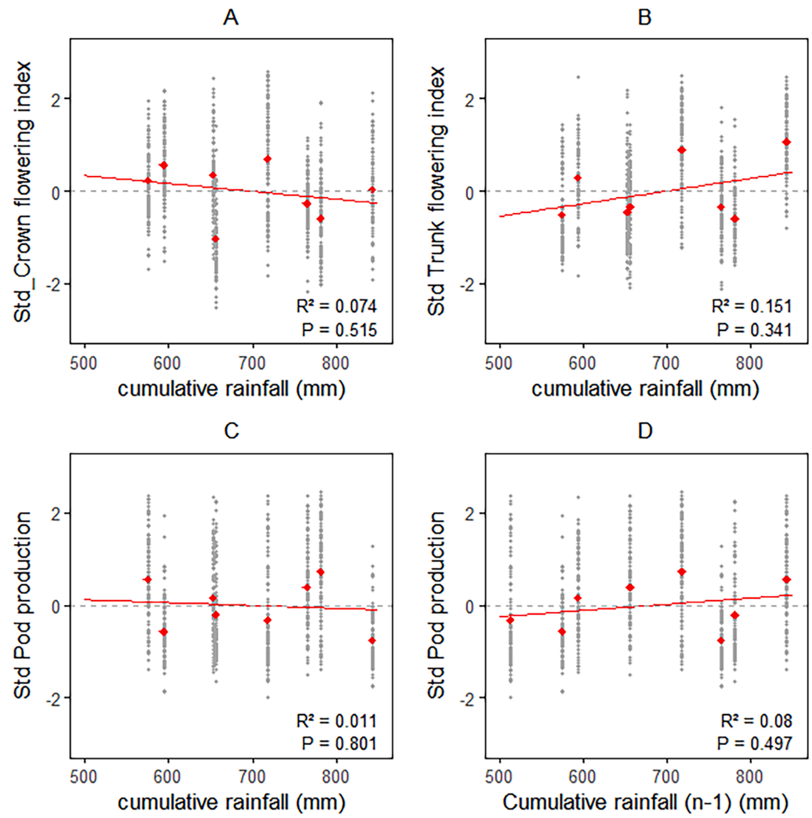

Fig. 3. Values of standardized data (grey dots, $N = 912$ [8 seasons x 114 trees]), seasonal averages (red dots, $n = 8$) and linear regressions of seasonal averages on seasonal values of cumulative rainfall (red line) for (A) crown flowering, (B) trunk flowering and (C) pod production, and (D) values of standardized data of pod production and linear regressions of seasonal averages on cumulative rainfall during the previous season ('cumulative rainfall (n-1)'). R^2= coefficient of determination.

irregular patterns for trunk flowering and pod production, respectively, with only 8 % and 19 % of trees showing marked alternating patterns for trunk flowering and pod production, respectively. Significant correlations were found between both BBI_res_norm and Auto.cov values for trunk flowering and pod production, suggesting a relationship between the patterns of seasonal flowering on the trunk and pod production. In the following section, we discuss the roles of exogenous and endogenous factors in controlling individual patterns of flowering and fruiting, and comment on the implications of these findings for crop performance.

4.1. Seasonal alternation of orchard production hid different individual patterns of seasonal fruiting, related to trunk flowering and independent of cumulative rainfall

An analysis of data dispersion exhibited high levels of tree-to-tree variability in terms of flowering indices and pod production, not only over the whole study but also within each season. These differences reflected the various flowering strategies, i.e., more or less intense and/or prolonged flowering episodes (supplementary material, Figs. A1 and A2), and production levels showed by trees of mixed genotypes as found in a standard Ivorian orchard (Boyer, 1970; Mossu et al., 1981; Omolaja et al., 2009; Restrepo et al., 2017; Wibaux et al., 2018). Trunk flowering indices were on average significantly lower in the B seasons (July – December) than in the A seasons (January – June) (Table 1), with also more frequent null values. This result is consistent with observations made by Adjaloo et al. (2012), who reported low to null flowering on cacao trees during the minor rainy seasons in Ghana. Conversely, lower pod production was observed on cacao trees in the A seasons, in relation to the lower trunk flowering observed in the B seasons (Table 1, Fig. 2C).

The differences in trunk flowering and pod production between the A and B seasons corresponded to the expected seasonal variations in flowering and fruiting, assumed to follow the bimodal annual climate, as described by Boyer (1970), Mossu et al. (1981) and Adjaloo et al. (2012). Differences in pod production between the A and B seasons corresponded to the "mid" and "main" crop harvesting patterns in Côte d'Ivoire. However, cumulative rainfall values recorded during our study differed from the expected pattern of high and low rainy seasons usually observed in the study area (Kassin et al., 2008) and showed no significant differences between the A and B seasons. As a result, cumulative rainfall in the range recorded during our study explained neither the average variations in flowering on either trunks or crowns, nor pod production (Fig. 3). Although this lack of relationships between reproductive pattern and variations of seasonal cumulative rainfall suggests an apparent independence between the two, other climatic factors should also be considered when studying seasonal variations in flowering and pod production, such as intra-seasonal dynamics of rainfall or soil water content, temperature, humidity and radiations (Adjaloo et al., 2012; Almeida and Valle, 2007; Alvim, 1984; Minimol et al., 2019). However, the remaining high variability of standardized values observed for each variable in each season, as illustrated by the dispersion of individual values around seasonal averages in Fig. 3, showed that, although all the trees were subjected to the same climatic conditions in each season, they displayed contrasting patterns of flowering and fruiting.

Crown and trunk flowering indices were correlated and both flowering indices were correlated to subsequent pod production (Fig. 4). However, there was a stronger effect of the trunk flowering index than the crown flowering index on subsequent pod production (Fig. 4), and a marked relationship between patterns of seasonal variations in trunk flowering and pod production (Fig. 7). Higher rates of fruit setting of flowers located on the trunk have been reported in cacao and other cauliflorous species (Cortez, 2009; Warren et al., 1997), supporting the

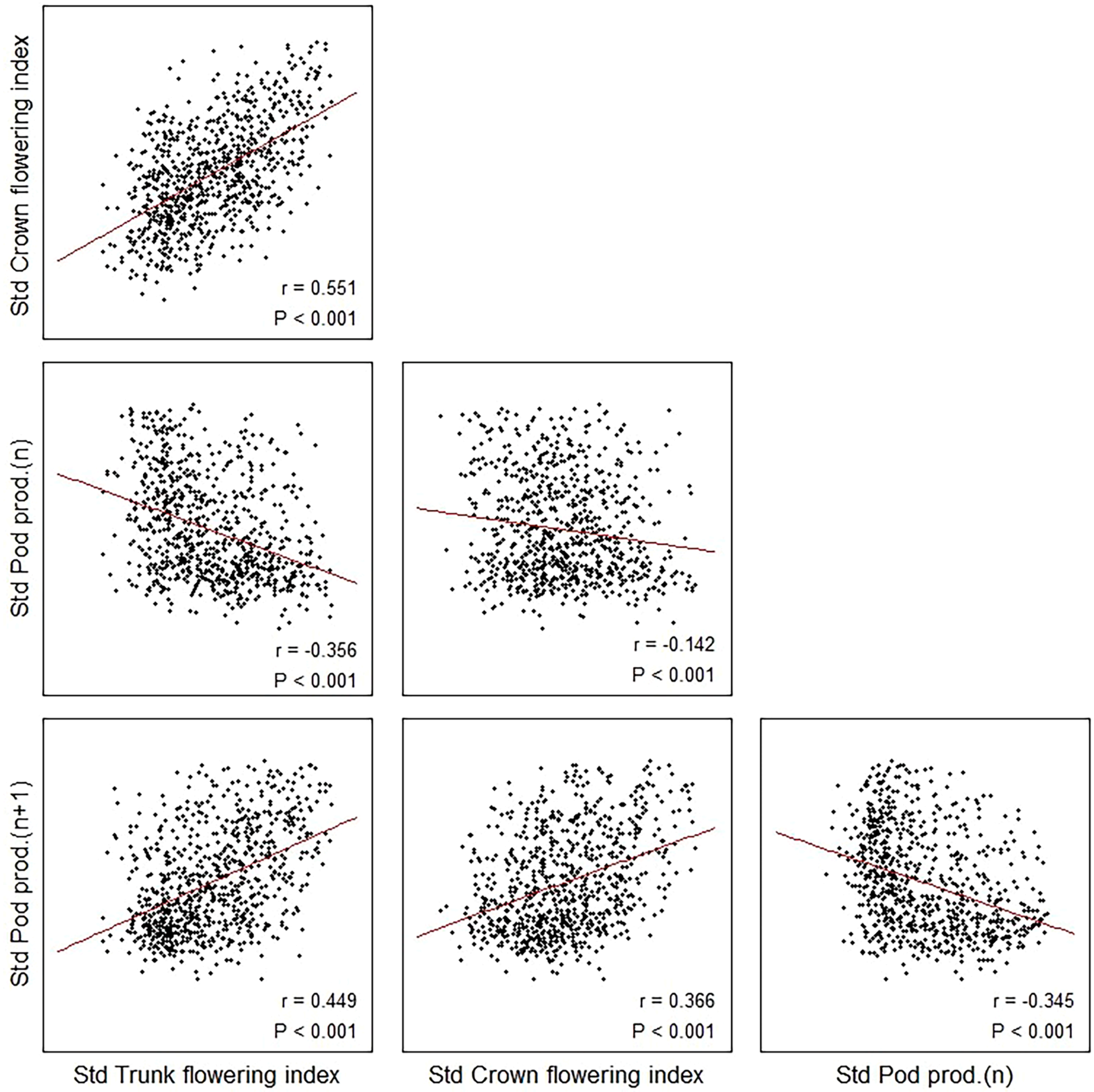

Fig. 4. Correlation matrix of standardized data for the seasonal trunk flowering index, crown flowering index and pod production during the flowering season (n) and during the consecutive season ($n + 1$). r and p-values are calculated from Pearson's correlation test. The red line is the linear trend. $N = 798$ (7 seasons [1 to 7] x 114 trees).

hypothesis of a marked and positive effect of trunk flowering on pod production. These results suggest that trunk flowering has a stronger impact on pod production on tree scale than crown flowering, and seasonal variations in trunk flowering could be responsible for seasonal variations in pod production.

An analysis of the two descriptors for the variation and structure of seasonal series showed that most of the trees displayed irregular patterns of seasonal pod production, i.e., unstructured patterns of variation around their trends over the course of our study. Only 19 % of trees actually exhibited marked alternating patterns of pod production between consecutive seasons. Thus, seasonal alternate bearing of cacao trees should not be considered as a predominant feature of the species in this orchard and presumably in Côte d'Ivoire. The alternation between seasons for "mid-crop" and "main-crop" harvests observed on a population scale (Fig. 2) did not reflect these individual habits. However, all trees that showed an alternating pattern of seasonal pod production were synchronized during our study, with lower production in the A seasons and higher production in the B seasons (data not shown). Similarly, average values of trunk flowering index and pod production in seasons A and B were significantly different between seasons (Table 1). This observation suggests that common exogenous factors influenced the rhythmicity of trunk flowering and pod production, even though trees exhibited various patterns of regular, irregular, and alternating production between consecutive seasons. It is likely that small differences at the scale of individual trees were amplified at the scale of a larger population. The effect of exogenous factors may thus be undetectable at the tree scale but would appear when a larger number of trees are observed, revealing the structuring effect of exogenous factors on patterns of flowering and production at the orchard scale. Our two descriptors, BBI_res_norm and Auto.cov, were not suited to quantify this phenomenon, and further research should address it.

As for the exogenous factors that may have contributed to the structuration of seasonal patterns at the orchard scale, the literature offers many references on abiotic factors, especially climatic, that influence the seasonality and intensity of flowering and pod production. Sale (1970) and Alvim (1993) demonstrate that the return of rain after a long dry period triggered intense flowering episodes. Sale (1969), Boyer (1970), and Owusu et al. (1978) show the combined effects of radiation,

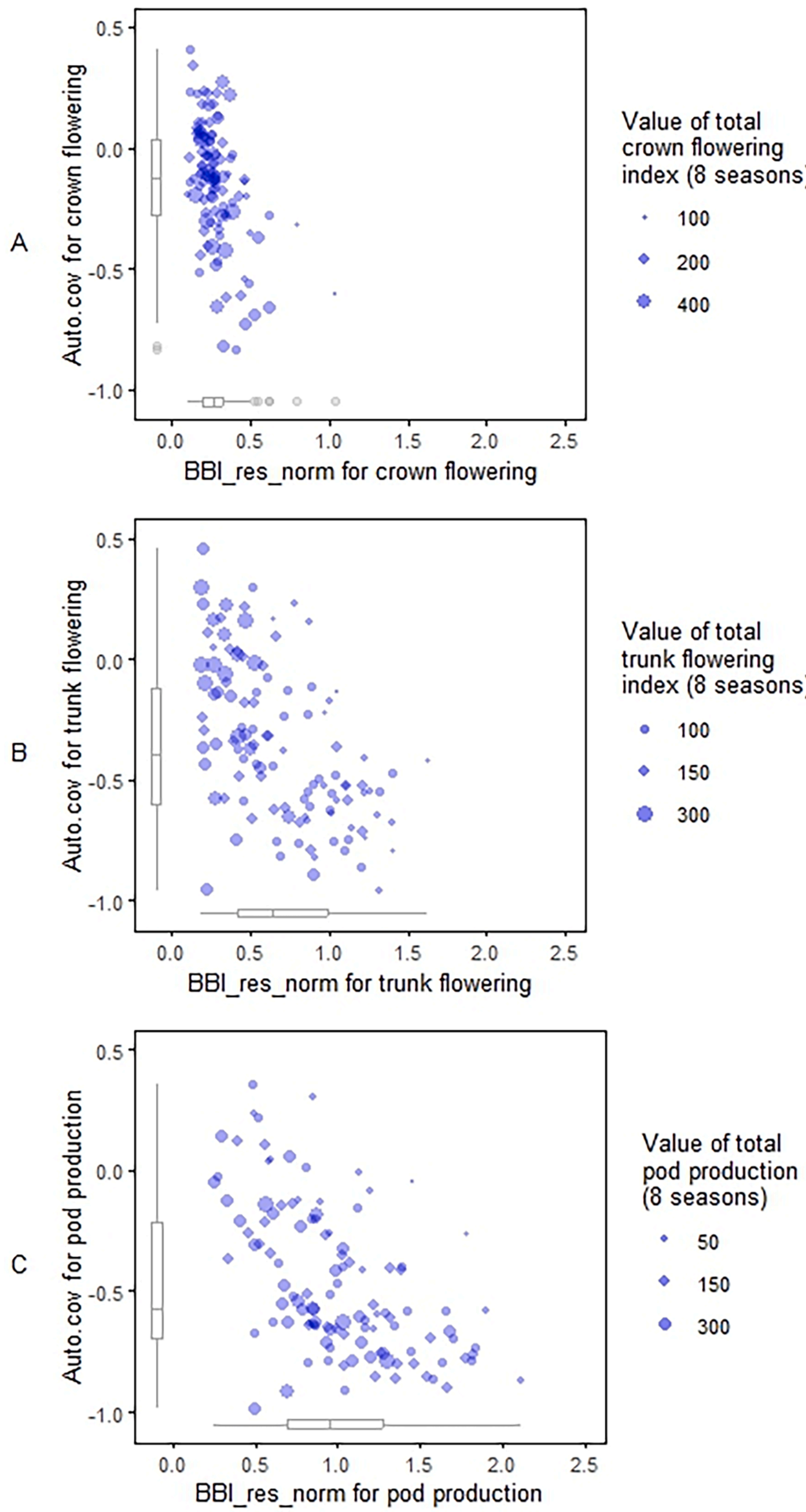

Fig. 5. Relationships between descriptors BBI_res_norm (x-axis) and Auto.cov (y-axis) for (A) crown flowering, (B) trunk flowering and (C) pod production, calculated for each tree over eight successive seasons. $N = 114$ trees. Dots area is proportional to the sum of individual values of the variable observed per tree over the 8 seasons. Horizontal and vertical boxplots located along the x-axis and the y-axis represent the distributions of BBI_res_norm and Auto.cov values, respectively.

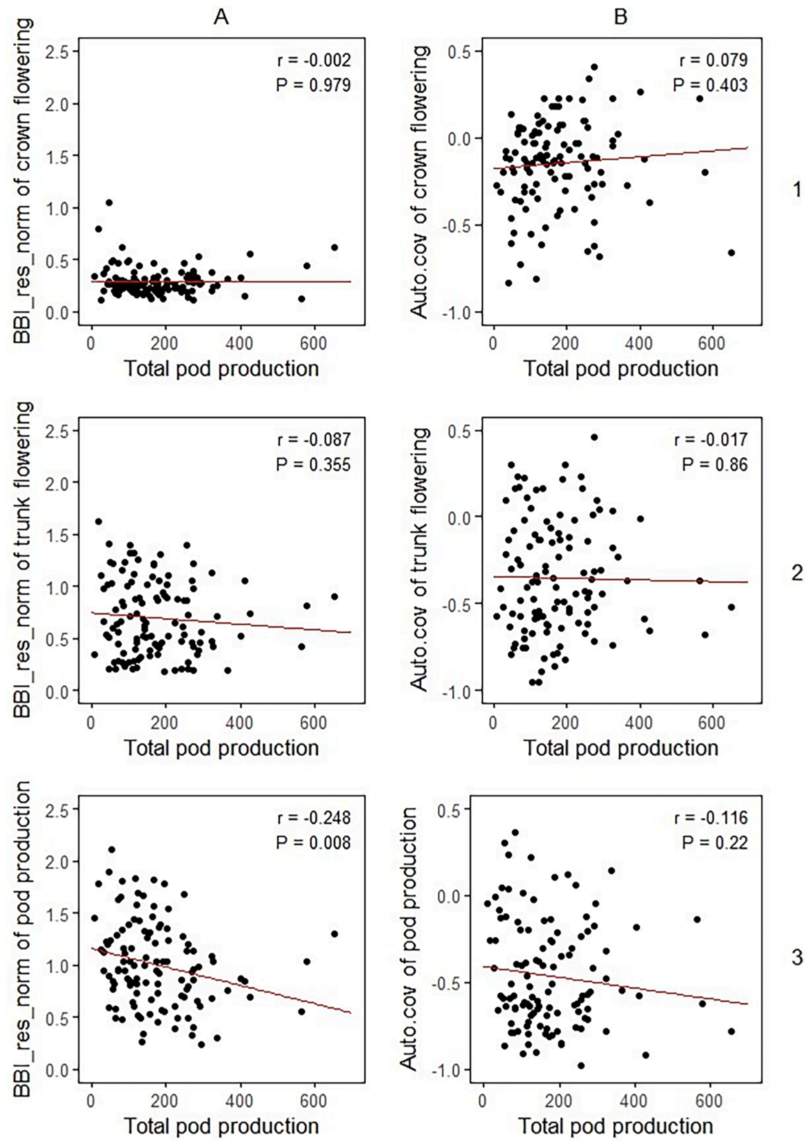

Fig. 6. Correlations between total pod production over the eight seasons and (A) variability descriptor (BBI_res_norm) or (B) alternation descriptor (Auto.cov) calculated for the variables (1) crown flowering index, (2) trunk flowering index and (3) pod production. The r and p-values are calculated from Pearson's correlation test. The red line is the linear trend. $N = 114$ trees.

temperature, and soil moisture on flowering. Biotic factors may also influence reproductive dynamics of cacao. Mossu et al. (1981), Lachenaud (1991), Omolaja et al. (2009), and Claus et al. (2018) demonstrate the effect of climate on dynamics of pollinators and successful pollination and fruit set, which impact seasonal variations in pod production. Almeida and Valle (2007) report that cultural practices also affect tree phenology and reproductive cycles. In our study, heavy pruning and the application of fertilizers once a year, during the first season, may have contributed to the significant differences in trunk flowering and subsequent pod production recorded between seasons A and B. Variations in both biotic and abiotic exogenous factors should thus be considered when studying cacao phenology at orchard or individual tree scales.

4.2. Our findings call for new hypotheses of endogenous control of flowering and fruiting in cacao trees

As observed in the literature, micro-environmental variations due to soil and competition between trees may be sources of reproductive variations among cacao trees within orchards (Lachenaud, 2005; Wibaux et al., 2018). However, when considering the existing knowledge of bearing control in other fruit tree species, be they tropical or temperate, genetic variability and other endogenous factors should be considered as primary factors controlling an individual propensity to irregular and alternate patterns of flowering and fruiting in cacao (Monselise and Goldschmidt, 1982).

A distinctive feature of our study, when compared to related research conducted on other fruit tree species, is that it was conducted on a population of mixed genotypes. This situation corresponds to the standard practice in western Africa, and the aim of our study was to analyze the variability of seasonal reproductive patterns generated by this specific context, on an individual tree scale and on a population scale. On the other hand, the lack of genotype replications prevented an analysis of potential genetic determinisms for flowering and fruiting variability.

A second distinctive feature of our experiment is that the cacao tree is a cauliflorous species. Literature on fruit tree species usually points out the importance of both spatial and temporal relationships between vegetative and reproductive meristems. The vegetative or reproductive fate of a meristem is partly related to its architectural position, and decisive relationships between the growth status of a shoot and its ability to bear flowers and fruits have been demonstrated on various

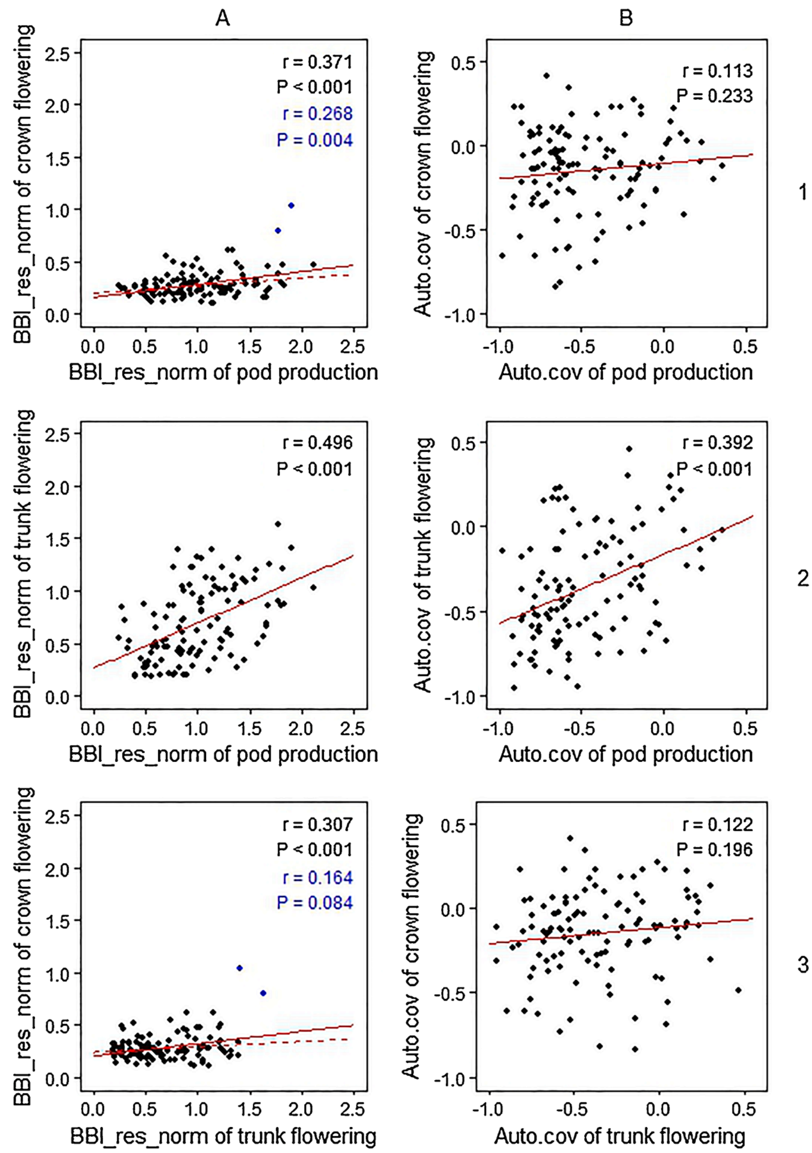

Fig. 7. Correlations between (A) the variability descriptor (BBI_res_norm) and (B) the alternation descriptor (Auto.cov) for (1) crown flowering and pod production, (2) trunk flowering and pod production, and (3) crown and trunk flowering. The r and p-values are calculated from Pearson's correlation test. The red line is the linear trend. $N = 114$ trees. Blue dots are trees with excessive BBI_res_norm values for crown flowering resulting from normalized calculation of the indices. Dashed red line and blue annotations are the linear trends and results from Pearson's correlation test obtained on samples without the blue dots.

fruit tree species (Génard et al., 2008; Julian et al., 2010; Lauri and Trottier, 2004; Puntieri et al., 2018). In these situations, irregular bearing may be attributed to the delay of vegetative growth and/or to poor vegetative growth in response to high fruit load, which in turn may limit flower induction or the number of potential flowering sites (Capelli et al., 2021; Dambreville et al., 2014; Normand et al., 2009; Wilkie et al., 2008). Due to its cauliflorous nature, the flower cushions of the cacao tree have potentially life-long return-bloom, with repeated development of inflorescences on the same persistent bud complex. This characteristic leads to a spatial disjunction between vegetative growth, which develops upwards, and reproductive sites, which remain largely on the trunk and oldest parts of branches, suppressing the topological proximity between vegetative growth and reproduction. This situation suggests that the flowering of cacao trees ought to be under the control of other endogenous factors regulating inflorescence emergence and return-bloom, as investigated in other species, such as the position of the flowering site on the growth unit (e.g., apple; Lauri et al. 1995, 1997), age of the growth unit, competition for resources and hormonal control (e.g., apple and mango; Wilkie et al. 2008, Normand et al. 2009).

Given the agronomic interest of controlling the regularity or alternation of cacao tree production, as well as the physiological interest of studying reproductive mechanisms in cauliflorous species, we recommend conducting further studies on the relationships between reproductive patterns and trophic or hormonal factors in cacao. We suggest that further studies should be conducted under experimental conditions, to control the effect of climate on the reproductive and vegetative phenology of the species, with controlled and replicated genotypes, or considering the genotypic and phenotypic variability found in cultivated populations. In view of the heterogeneity of reproductive sites in cauliflorous species, these studies should also further explore the possible architectural (e.g., trunk vs. branch as done here) and morphological (e.g., shoot orientation and circumference, position of the node along the growth unit, leaf size) determinants of flower cushion development, fruit-set ability and fruit life span, and the link with the regularity vs. alternating patterns.

4.3. The diversity of seasonal reproduction patterns impacts crop performance

Crop management and calendar of management practices of cacao are usually established based on average phenology and requirements of a crop, considering the agronomical objectives of the farmer and the contextual features of the farm and plot. As a result, most of the operations, such as fertilizer applications, phytosanitary treatments, pruning or sanitary harvests, are implemented synchronously and uniformly at the scale of the orchard. In this case, the efficiency of the crop management relies on the assumption that trees within the orchard exhibit a certain level of homogeneity in their phenology, as well as in the intensity of their vegetative and reproductive growth phases. As demonstrated in our study of a cacao orchard of mixed genotypes, trees composing the sample population displayed high levels of tree-to-tree variability regarding both flowering intensity and production during each of the eight seasons that we recorded. Individual trees also exhibited important variations in patterns of seasonal trunk flowering intensity and pod production, as compared to the expected average alternating rhythm of flowering and pod production observed at the orchard scale. As a result, we can assume that the management practices established from average behavior of the orchard is unfit to most of the trees, resulting in poor performance of the crop management. Adapting crop management to tree phenology, flowering and fruit load could be an important lever in improving crop performance (Wibaux et al., 2018). In addition, this study took place in an industrial plantation, planted at regular spacing with trees of the same age, grown under full sun and subjected to rational crop management, thus limiting micro-environment variability between trees. In Côte d'Ivoire, most cacao orchards managed by smallholders exhibit more heterogenous spatial design, with frequent associations with shade tree species and uneven competition for resources between trees of various ages, planted at uneven distances (Assiri et al., 2009; Lachenaud, 2005). We can only assume that this enhanced heterogeneity in growth conditions found within typical smallholder cacao orchards would foster even more the variability in flowering and fruiting behavior of individual trees, with possible consequences on orchard management efficiency.

Our results indicated that there is no relationship between the pod production pattern over 8 seasons and the number of pods produced by trees (Fig. 6-B3). However, based on knowledge of other fruit tree species, we can expect irregular bearing trees to produce smaller or lighter fruits in seasons of high fruit production, in comparison with trees with regular seasonal production (Monselise and Goldschmidt, 1982). Alternate patterns may also affect the quality and quantity of harvested cacao beans. In order to assess the extent of this probable consequence of irregular seasonal fruiting patterns, data on fruit size, weight or other quality traits should be collected in further studies.

5. Conclusions

In this study, we investigated the variations in seasonal flowering and fruiting at the scale of a population of mixed genotypes of cacao and analyzed the patterns of seasonal flowering and fruiting of individual trees over eight consecutive seasons. The apparent alternation between "main-crop" and "mid-crop" harvests observed on an orchard scale did not reflect individual habits, and trees with marked alternate patterns of seasonal pod production actually represented only 19 % of the population. It was shown here that irregular or alternate patterns of seasonal pod production on a tree were related to variations in seasonal flowering on the trunk, whereas flowering in the crown was rather regular between successive seasons. Exogenous factors, other than the cumulative amount of rainfall and common to all trees in the same orchard, structured the seasonal variations in flowering and pod production, resulting in apparent alternate patterns of pod production at the orchard scale. Given the various spatial, geometrical, and structural characteristics of axes bearing active flowering sites, as well as the potential rhythm of flowering on the scale of a persistent bud complex, we advise that further investigations into the flowering phenology of the cacao tree should include architectural and physiological (carbon allocation, hormones) approaches on various spatial and temporal scales.

CRediT authorship contribution statement

Thomas Wibaux: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Frédéric Normand:** Writing – review & editing, Methodology. **Rémi Vezy:** Writing – review & editing, Methodology. **Jean-Baptiste Durand:** Methodology. **Pierre-Éric Lauri:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2024.113529.

Appendices

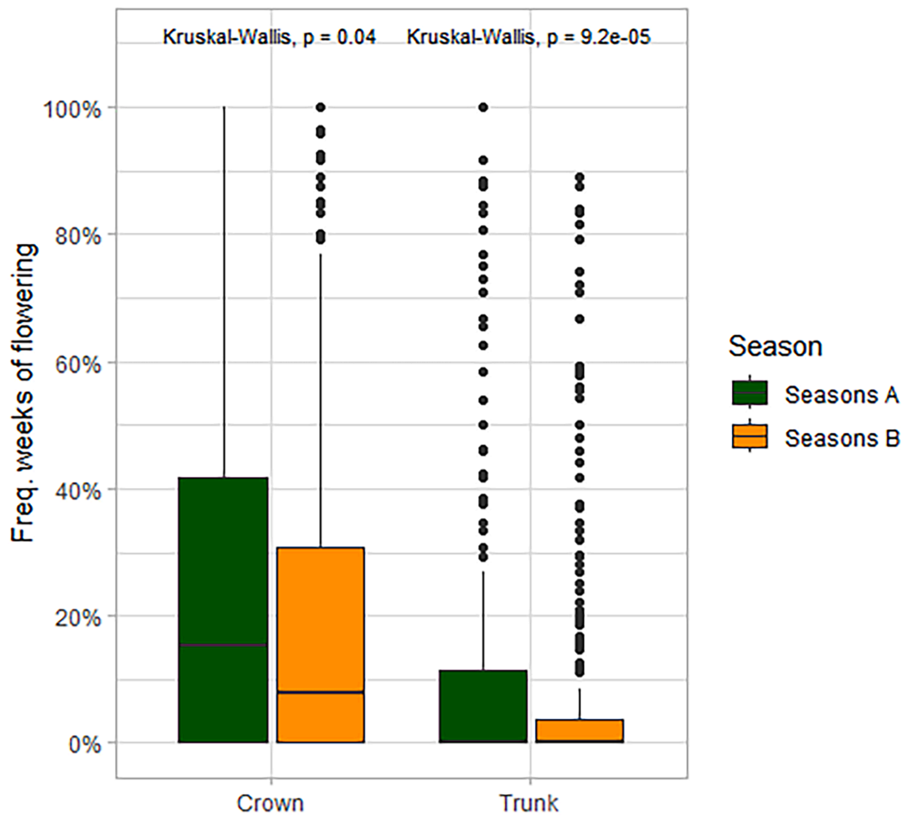

Fig. A1. Boxplots of seasonal frequencies of weeks spent in "flowering episodes", i.e. observations of flowering intensity of grade >2, in the A and B seasons.

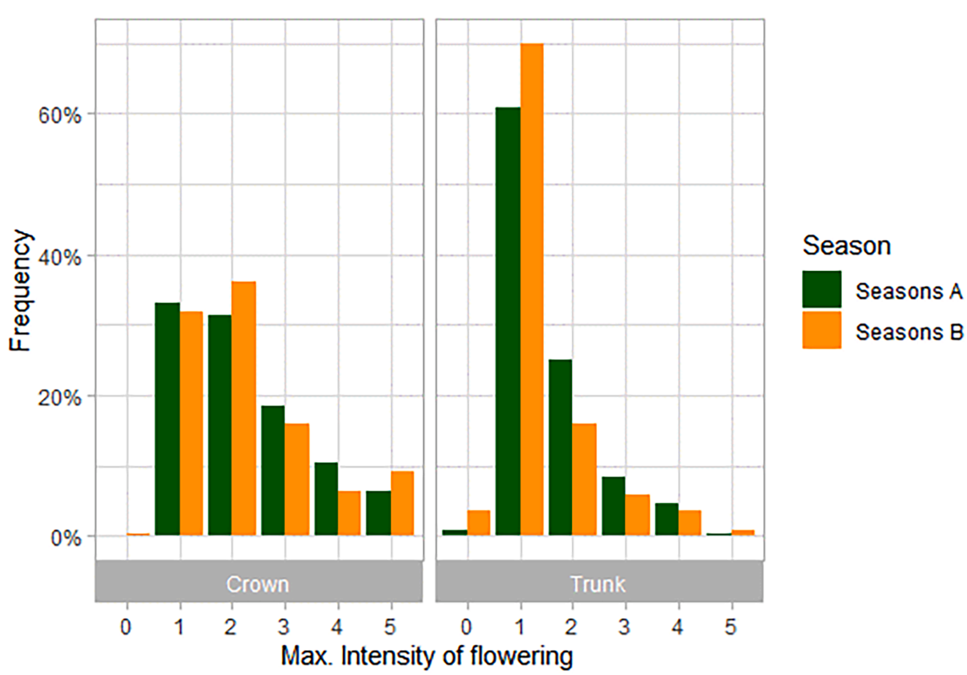

Fig. A2. Barplots of frequencies of maximum flowering grade observed during a season, from observations on crown and trunk and in the A and B seasons.

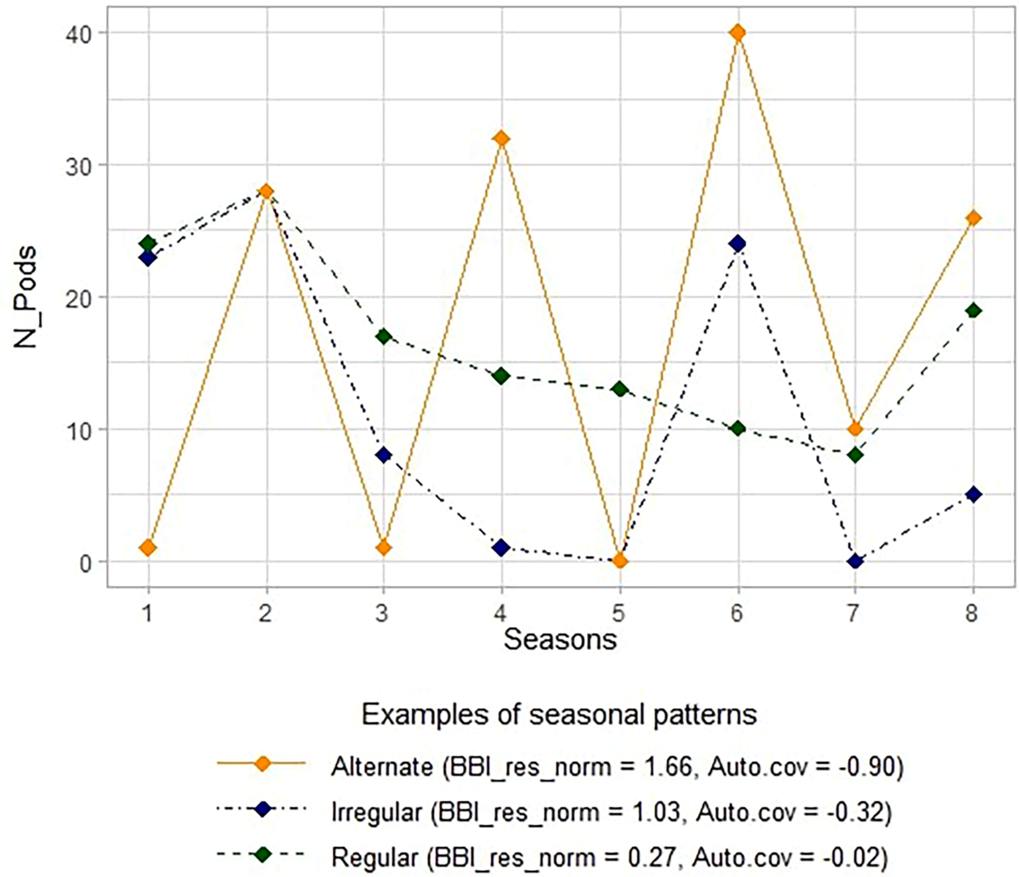

Fig. A3. Examples of series of seasonal pod production for three trees with regular, variable and alternate patterns.

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