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Geographic variation in shea (*Vitellaria paradoxa* subsp. *paradoxa*) floral phenology and morphology in the Guinea savanna zone of Ghana

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ABSTRACT

Vitellaria paradoxa is a multipurpose tree endemic to the Sudano-Sahelian zone of Africa. The edible fat extracted from shea kernel is of cultural, nutritional and industrial significance. Floral phenology and morphology do not only influence pollinator attraction but also serve as indicators of genetic diversity in tree improvement programmes. Understanding shea floral phenology is essential to unveiling phenological responses to climate change. The study investigated the relationship between floral phenology and climatic variables, and examined spatial variation in floral traits across six sites in three regions (Upper West, Upper East, and Northeast) of Ghana. Twenty focal trees were tagged for observation of phenological parameters and measurement of floral traits in each site. We found a variation in the date of flowering onset between regions. Flowering commenced in Upper West over a month earlier than Upper East and Northeast regions. The weekly number of trees commencing flowering was found to be significantly associated with soil moisture and soil temperature. Shea floral traits (pedicel diameter, pedicel length, petal length, filament length and style length) also differed significantly between regions. Although the study recommends multiple years of phenological observations on the impact of climatic conditions, the geographic variation in floral morphology should be considered in germplasm collection for tree improvement and domestication.

Key Words: Flowers; floral phenology; floral traits; climatic factors; shea parkland; *Vitellaria paradoxa*

INTRODUCTION

Environmental conditions and biotic interactions act as evolutionary drivers of phenological and morphological traits (Miller-Rushing, Høye, Inouye, & Post,

2010). Plants have evolved to avoid flowering during adverse environmental conditions, and to match their flowering time with favourable conditions for fruiting and seedling establishment (Fogelström,

2019; Miller-Rushing et al., 2010). Similarly, plant reproductive success can be enhanced if flowering, fruiting and seed production are asynchronous with antagonists (competitors, herbivores and seed-predators), but synchronised with mutualists (pollinators and seed dispersers) (Ehrlén, 2015). The timing of flowering is genetically controlled (Craine et al. 2012), but can be influenced by climatic factors (Chauhan et al. 2019; Jarrod et al. 2021; Kubov et al. 2022). Thus, short term climatic variability can influence the timing of flowering (Anderson et al. 2005; Barrett and Brown 2021). This can shift flowering phenology, potentially resulting in a mismatch between flowering period and pollinator activity (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007; Forrest & Miller-rushing, 2010). Phenological mismatches are being exacerbated by climate change, with studies showing early flowering in a range of species in response to increasing mean annual air temperature (Kubov et al., 2022). However, evidence for complete temporal mismatches between plants and their pollinators is scarce, as often the factors influencing the timing of flowering also influence pollinator activity and behaviour (Renner and Zohner 2018).

In addition to timing of flowering, floral morphology and rewards influence pollinator activity and behaviour, thereby affecting pollination efficiency (Martins, Gabriela, & Camargo, 2021; Rossi, Fisogni, Nepi, Quaranta, & Galloni, 2014). Floral traits such as colour, size, shape and scent, together with the quantity and quality of nectar and pollen rewards, influence the foraging behaviour of floral visitors (Proctor et al. 1996; Parachnowitsch & Caruso 2008). Floral traits also influence the duration that floral visitors spend searching for and handling floral rewards, which in turn can influence pollination success (Fisogni et al. 2011; Rossi et al., 2014). Aside from floral rewards, the density of flowers produced at the community or individual level influences

pollinator attraction (Lázaro, Jakobsson, & Totland, 2013). Rathcke and Lacey (1985) theorised that a functional relationship exists between flower density and insect visitation, where floral density increases with increasing insect visits until a maximum is attained, then declines at saturation of pollinators. Primarily, a larger number of flowers increases the visual conspicuousness of the flower, thereby increasing its attractiveness to insects. Flower number was found to be significantly associated with pollinator visitation rate, with plants bearing more flowers attracting higher number of pollinators (Eckhart, 1991).

Although there have been many studies on floral phenology and morphology, these have focused extensively on temperate herbaceous plants (Horbach, Rauschkolb, & Römermann, 2023; Kubov et al., 2022), whilst less is known about woody tropical plants. Phenological studies are particularly important for plants in the arid and semi-arid regions of Sub-Saharan Africa, as savanna biomes are known to be sensitive to climatic changes (Bond, Midgley, & Woodward, 2003; Sala et al., 2000). *Vitellaria paradoxa* (shea) is endemic to arid and semi-arid regions of Sub-Saharan Africa (Hall et al. 1996). The species is generally undomesticated but retained and managed on farmlands for multiple reasons, including its contribution to carbon sequestration and soil rejuvenation (Chimsah, Nyarko, & Abubakari, 2013), medicinal use of its leaves and stem bark (Gwali et al., 2012), the local and international use of the fat extracted from shea kernel (Glew and Lovett, 2014; Lovett, 2005), and because the edible fruits are rich in vitamins and sugars (Nguekeng, Hendre, Tchoundjeu, & Kalousová, 2021). Owing to the high value of the fruits, shea research has been focused on fruiting, with limited knowledge on floral phenology, morphology, and interactions with pollinators (Nasare, Stout, Lovett, & Kwapong, 2022).

Existing data indicate that floral phenology is influenced by land use and parkland management practices (Kelly, Gourellet-Fleury, & Bouvet, 2007; Kelly, Poudyal, & Bouvet, 2018; Okullo, Hall, & Obua, 2004). There is also a variation in the timing of shea flowering across agro-ecological zones of the shea belt (Kelly et al., 2018; Nguemo, Mapongmetsem, Tchuenguem, Gounhagou, & Yougouda, 2014). Despite this variability, less is known about the specific climatic factors influencing flowering, except Okullo (2004) and Nguemo et al. (2014), who examined the effect of climatic factors (relative humidity, temperature and precipitation) on flowering in Uganda and Cameroon. Identifying the proximate environmental cues to floral phenology is a fundamental step to predicting the effect of climate change on shea productivity. Moreso, existing literature revealed a variability in the shea floral density (Okullo, 2004; Stout et al., 2018) but differences in study years do not permit fair comparison of floral density between ecological zones or sites. The floral morphology of *V. paradoxa* subsp. *nilotica*, endemic to East Africa, has been documented (Okullo 2004), whilst less is still known about the morphometric traits of *V. paradoxa* subsp. *paradoxa* of West Africa.

Understanding the floral phenology and morphology of shea is essential to domestication and stand management for optimum fruit yield, as it influences plant pollinator interactions and fruit set (Okullo et al., 2004). Moreso, domestication and tree improvement would require a detailed understanding of the variability in morphological traits in developing ideotypes for specific regions. We hypothesised a geographic variability in the floral phenology and morphology of shea. The study specifically aimed to: i) examine the geographic differentiation in the onset of shea flowering, ii) identify the climatic variables related to shea flowering, and iii) examine the geographic differentiation in floral density and morphometric traits.

Materials and Methods

Study Area

The study was conducted in the Guinea savanna zone of Ghana for a 12-month period from August 2020 to July 2021. The Guinea savanna zone of Ghana covers the entire Northern, North East, Savanna, Upper West and Upper East regions, as well as the northern parts of Oti and Bono East regions of Ghana (Adjei and Odai, 2020).

The area records a mono-modal rainfall pattern, which varies significantly in amount and the onset of rains between years (Incoom et al., 2020). The wet season commences in April and ends in October with a mean annual rainfall of 1,034 mm (Savanna Agriculture Research Institute, 2015). Maximum mean monthly temperatures are recorded in March/April whilst the lowest temperatures are recorded in December. Mean monthly temperatures range between 27 and 36 °C (Darko et al. 2019; Ghansah et al. 2018).

The vegetation density is shaped by the land use and land management. The area is dominated by cultivated landscapes but periods of cultivation alternates with bush fallows creating mosaics of semi natural vegetation patches in some areas. However, the natural vegetation of the area is composed of grasses dotted with indigenous woody species (Darko et al., 2018). The most frequently occurring woody plants of the zone include shea (*Vitellaria paradoxa*), baobab (*Adansonia digitata*), dawadawa (*Parkia biglobosa*), African mahogany (*Azizelia africana*), ebony (*Diospyros mespiliformis*), Linnea (*Lannea acida*), acacia (*Faidherbia albida*), among others (Tom-Dery, Hinneh, & Asante, 2013). These economic trees are equally retained and managed in farmlands for multiple uses.

Selection of study sites

The study was conducted in six shea parkland sites, two in each of three political regions (Upper West, Upper East and North East) of Ghana (Figure 1). In each region,

the two sites were located 4 – 25 km apart, to minimize potential variability in climatic conditions within the region. Study sites were located in young fallows (lands that were uncultivated for 2-5 years), which were identified based on land use history obtained from farmers.

Tree selection

A random point was located in each site, and all trees of a predetermined size class (DBH: 25-30 cm, Height ≥ 10 m and crown area ≥ 20 m²) within a 500 m radius of the focal point were identified and coded to

constitute a population. This size class was used because it is reported to be the most abundant in the Guinea savanna zone (Tom-Dery, Sakyi, & Bayor, 2015), and was used to standardise sampling while minimizing the effects of tree age and size on flowering. Twenty focal trees were randomly selected per study site using a random number generator and each tree was sequentially numbered and tagged. Twenty trees were selected based on the mean tree density previously recorded by Tom-Dery et al. (2015) in the Guinea savanna.

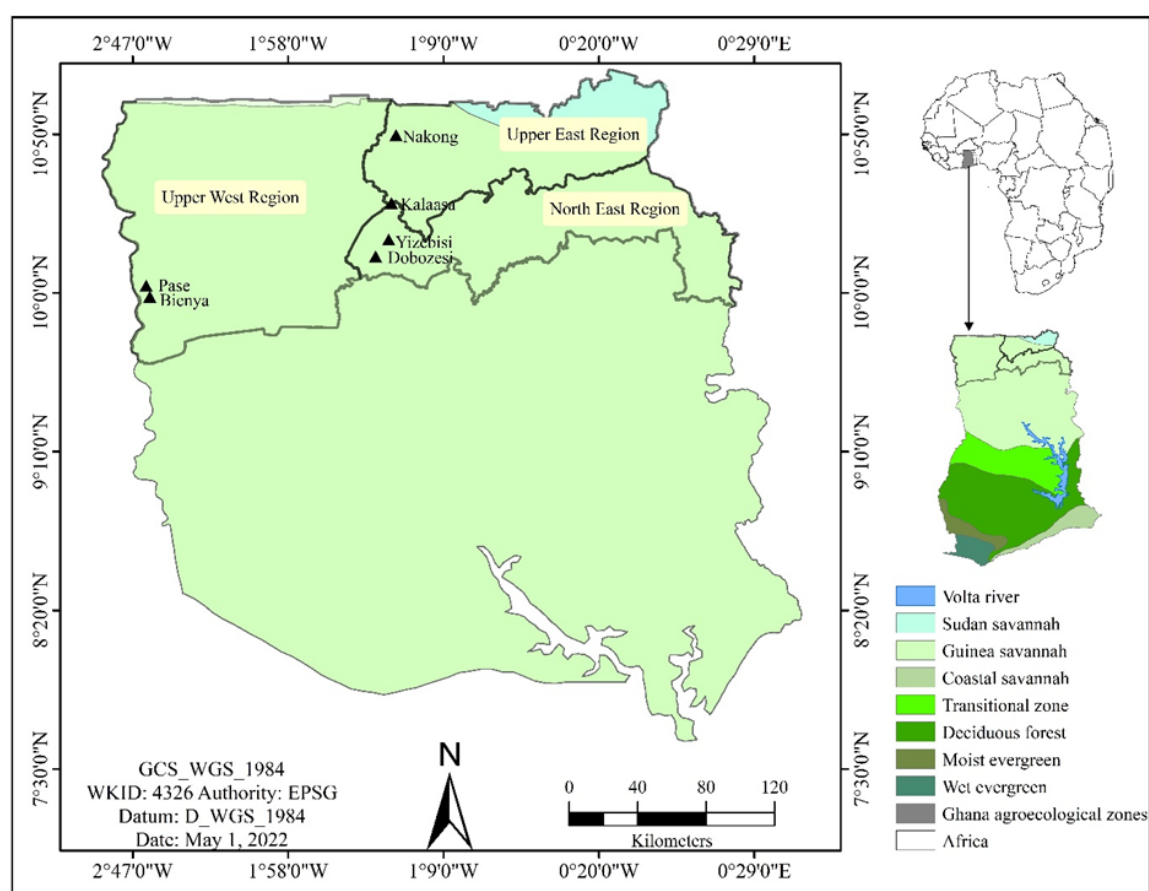


Figure 1: Geographical locations of study sites in three regions of Ghana

Phenological parameters recorded

Weekly observations of focal trees were conducted from October 2020 to May 2021. During observations the following phenological parameters were recorded:

1. **Onset of flowering:** the date on which the first open flower(s) were recorded on a focal tree.
2. **Weekly number of trees in flower:** the number of focal trees that have commenced flowering per site

3. **Days to 50% flowering:** The number of days taken to have 50% of the focal trees commence flowering in a site.
4. **Flowering ability:** measured on a binary scale either as 0 (if the individual tree did not produce any flower) or 1 (if the individual tree produced flowers) as used in Kelly et al. (2007).
5. **Number of flowers/flower buds per inflorescence:** the number of flowers/flower buds initiated per inflorescence was counted in three randomly selected inflorescences during peak flowering of each focal tree.

Morphometric traits of floral parts

Three inflorescences were randomly sampled from independent branches of each

focal tree in peak flowering and transported in an ice-chest to the Laboratory for the measurement of floral traits. Following Guitián et al. (1997), three flowers were sampled from each inflorescence at three distinct lateral positions along the inflorescence axis. Thus, measurements were made on three inflorescences and nine flowers per tree. For each flower, the morphometric traits of floral parts (pedicel length, pedicel diameter, petal-limb length, filament length, and style length) were measured with callipers (Figure 2a). For filament length, three independent filaments were measured per flower and averaged. Also, pedicel diameter was measured on the lower and upper ends of the pedicel and averaged (Figure 2. b and c).

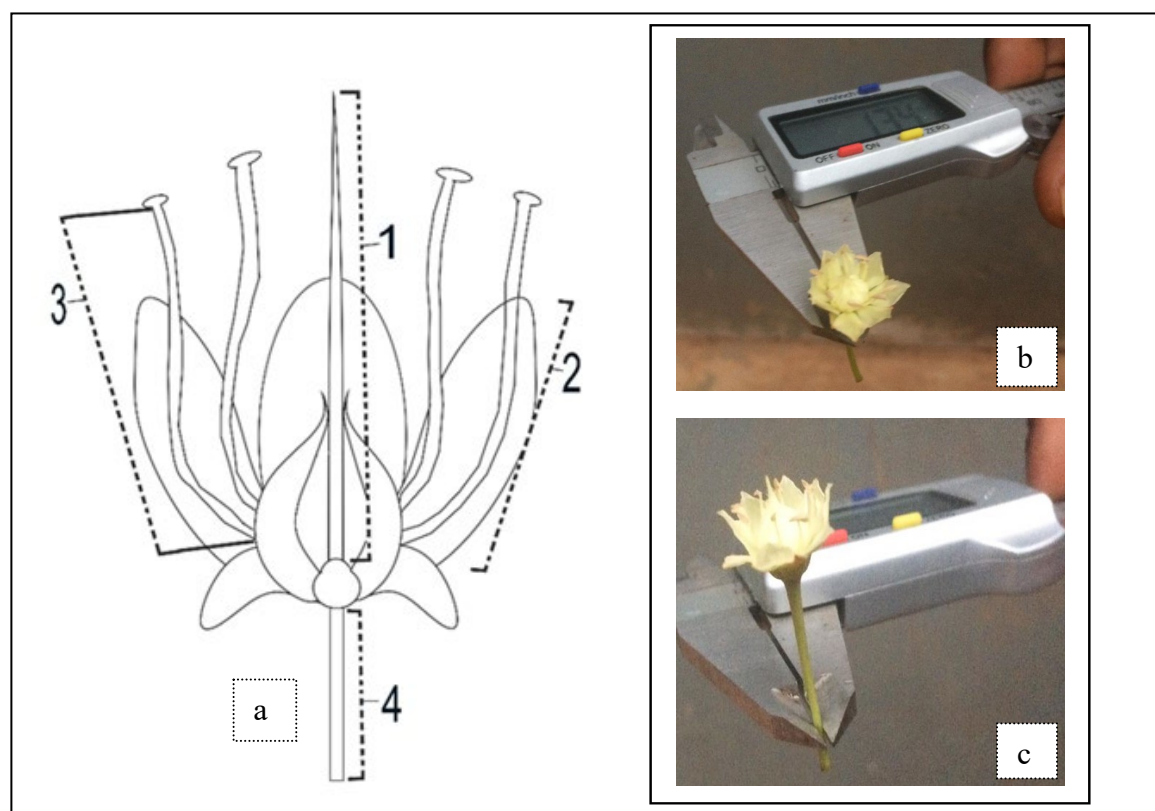


Figure 2. Morphometric traits of *V. paradoxa* floral parts. The numerals/alphabets correspond to measured floral parts: (a.1) style length, (a. 2) Petal length, (a. 3) Filament length, (a. 4) Pedicel length, (b) pedicel diameter at the upper end, (c) pedicel diameter at the lower end.

Climatic variables

Daily weather data of each region was collected from the nearest weather station to the study sites from the Trans-African Hydrometeorological Observatory (TAHMO). All weather stations were located within a 30 km radius of the study site. The climatic variables examined included air temperature, soil moisture, soil temperature, relative humidity and wind speed. The weekly and monthly means were calculated for each climatic variable.

Data analysis

Generalised Linear Mixed-effect Models (GLMMs) were used to model the weekly number of trees initiating flowers as a function of climatic parameters. GLMMs were used based on the multilevel structure of the data (climate being nested in the region), having repeated measures of a dependent variable (weekly number of trees in flower) on a discrete scale. A stepwise regression with backwards elimination procedure was used in identifying the most relevant predictors of flowering. The initial model was fitted by inserting all predictor variables (atmospheric temperature, minimum soil moisture, relative humidity, wind speed, maximum atmospheric temperature, and minimum atmospheric temperature) as fixed effects and site as a random factor using a Poisson distribution. Thereafter, each insignificant factor was eliminated, and Akaike's Information Criteria (AIC) and Bayesian Information Criteria (BIC) were used in assessing the model performance of each set of variables in a stepwise procedure. All models were fitted using the lme4 and glmmTMB packages in R (Bates, Mächler, Bolker, & Walker, 2015; Brooks et al., 2017).

Multicollinearity was checked with the Variance Inflation Factor estimates before models were fitted. Climatic factors with VIF greater than 5 were tested for collinearity. Predictors that were correlated at Pearson $r \geq 0.7$ (level of collinearity that can bias regression) were not combined in the same model based on Dormann et al. (2013) and Kath et al. (2021).

A Kruskal-Wallis test was used to compare the mean flowering ability of trees and branches between regions, as these measurements were categorical. Post hoc comparisons were performed to separate significant means using Bonferroni corrections. Morphometric traits (pedicel length, pedicel diameter, petal-limb length, filament length and style length) were analysed by comparing the means between regions with a one-way ANOVA ($\alpha=0.005$). A Tukey test was used for post hoc multiple comparisons of significant means. All analyses were done using the R Core Team (2021).

Results and Discussion

Geographic differentiation in floral phenology of *V. paradoxa*

Onset and rate of flowering

The onset of shea flowering varied among regions, where first flowering was recorded in late November in the Upper West (UW) region, and in January and February in the North East (NE) and Upper East (UE) regions, respectively. However, the shea parklands in UW took the longest duration (21 days) to attain 50% flowering where as those in UE and NE attained this in 14 days (Table 1).

Table 1: Onset of flowering and number of days taken to attain 50% flowering

Region	Site	First flower set		≥ 50% of trees flowering		Days to 50% flowering
		Month	Week	Month	Week	
UW	Pase	Nov. 2020	3	December	2	21
	Bienya	Nov. 2020	3	December	2	21
UE	Kalaasa	Feb. 2021	1	February	3	14
	Nakong	Feb. 2021	3	March	1	14
NE	Yizibisi	Jan. 2021	4	February	2	14
	Dobozisi	Feb. 2021	1	February	3	14

Variation in the date of flowering onset between regions mirrors previous phenological studies in which shea flowering varied between study sites (Kelly et al., 2007, 2018; Okullo et al., 2004). However, differences recorded in previous studies were marked by agro-ecological zones; this study observed a variability in the onset of flowering within the same agro-ecological zone. This seems to suggest flowering is not an outcome of the wider agro-ecological zone's climatic conditions, but rather influenced by local microclimatic conditions. The commencement of flowering in November in UW is similar to the onset of flowering in the Guinean zone of Cameroun, whereas the February onset in UE resembles that of the Sudanian zone of Cameroon (Nguemo et al., 2014).

Shea flowering is known to occur along a South-North gradient, where flowering commences in relatively humid agro-ecological zones prior to less humid zones of most countries (Kelly et al., 2007, 2018; Nguemo et al., 2014). Although the current study was limited to one agro-ecological zone, the early flowering recorded in UW, followed by NE and UE, depicts this South-North gradient of flowering, considering the geographical locations of study sites (Figure 1). The South-North gradient effect extends beyond floral phenology; this has been observed for fruit productivity (Romain et al., 2011), as well as fruit pulp and kernel fat composition (Allal et al. 2013; Maranz and Wiesman 2003; Maranz

et al. 2004). A similar gradient effect on phenological events has been reported for *Adansonia digitata* (Oni et al. 2016) and *Parkia biglobosa* (Oni, 2001) across Sub-Saharan Africa.

Although our findings portray the South-North gradient of flowering, there might also be a West-East gradient of flowering in the Guinea savanna zone of Ghana. This is supported by the fact that the study sites in UE and NE regions are geographically closer to the Sudan savanna zone (the driest agro-ecological zone) of Ghana. Consequently, flowering commenced in the relatively humid parts (UW) of the ecological zone before the less humid areas (UE). Lovett and Haq (2000) also reported an increasing trend of shea seed characteristics along a North-East gradient in Ghana.

The commencement of flowering in the early dry season (November) of the Guinea savanna, is inconsistent with Okullo (2004) who indicated shea flowering in Uganda occurs in the late dry season as an adaptation to avoid fire-related disruption of flowering and fruit development. Flowering in UW commenced in the peak fire season, a period that poses a high risk of floral parts been damaged or destroyed by fires. The dry season flowering of *V. paradoxa* confirms Oni et al. (2014), assertion that most tropical plants flower in the dry season prior to the onset of rains. Notwithstanding, dry-season flowering of shea is most likely an adaptation for

optimum pollination services. Shea flower development and arrangement of floral structures indicate a high dependence on insects for pollen transfer (Nasare, Kwapong, & Doke, 2019; Nasare, Stout, & Kwapong, 2024; Okullo, 2004; Yidana, 2004). However, rainfall is known to have both direct and indirect impacts on plant-pollinator interactions (Lawson and Rands 2019). For instance, flowers produced in the raining season risks nectar dilution, and loss of volatiles needed in pollinator attraction (Cnaani, Thomson, & Papaj, 2006). Loss of pollen viability, and reduced pollen adhesion to stigma surfaces are also associated with wet season flowering(Fan et al. 2012).

As a mitigation strategy, plants flowering in the rainy season position their flowers to be downward-facing to reduce nectar dilution and pollen degradation (Whitney et al. 2011). Considering the upward-facing position of the shea flower, flowering in the raining season would be a great disadvantage to pollination. Thus, flowering in the early dry season in northern Ghana prevents overlap of flowering with the raining season and aligns with the peak activity periods of bee pollinators. Unlike shea, cocoa flowers in the raining season as an adaptation to synchronise flowering with pollinator activity since its primary pollinators (biting midges and gall midges) are most abundant during that period (Adjaloo, Oduro, & Banful, 2012). The timing of flowering is a co-evolutionary process for enhanced

reproductive success (Van Schaik, Terborgh, & Wright, 1993).

Climatic factors associated with the rate of flowering

The analysis was aimed at predicting the weekly number of trees in flower based on weekly means of climatic variables. Air temperature was autocorrelated with soil temperature (Supplementary Tab. S1.). Therefore, no model was fitted combining these two climatic variables in the same model. The first model fitted had relative humidity, soil moisture, atmospheric temperature and wind speed as predictors of number of trees in flower, with AIC and BIC of 205 and 214 respectively (Supplementary Tab. S2). In the second model, relative humidity, soil moisture, soil temperature and wind speed were fitted as predictors of number of trees flowering, resulting in AIC and BIC of 202 and 210 respectively (Supplementary Tab. S3). In the third model, relative humidity, soil moisture and atmospheric temperature were fitted as predictors of number of trees flowering with AIC and BIC of 205 and 212 respectively (Supplementary Tab. S4). Therefore, the best fitting-model was the one in which relative humidity, soil moisture, soil temperature and wind speed were fitted as predictors of flowering (Table 2). Among these predictors, soil moisture ($\beta = -58.558 \pm 18.463$, $p = 0.0015$), and soil temperature ($\beta = 0.262 \pm 0.098$, $p = 0.0073$) were significantly associated with weekly number of trees in flower (Table 2).

Table 2: Relationship between climatic factors and shea flowering

Climatic factors	β	$SE\beta$	Wald Chi-square	95% C. I		P value
				Lower	Upper	
(Intercept)	-2.438	2.835	-0.86	-8.00	3.12	0.389
Relative Humidity	1.473	1.616	0.91	-1.69	4.64	0.362
Soil moisture	-58.558	18.463	-3.17	-94.74	-22.37	0.0015 **
Soil temperature	0.262	0.098	2.68	0.07	0.45	0.0073 **
Wind Speed	0.125	0.701	0.18	-1.25	1.50	0.859

β = Beta, $SE\beta$ = standard error of Beta, ** = significance at 1%.

The climatic factors (Soil moisture and temperature) that significantly predicted flowering in the GLMM were different from those reported to be significantly correlated with flowering in previous studies. In Cameroun, relative humidity and air temperature were identified as the climatic factors associated with flowering (Nguemo et al. 2014). Also, in Uganda maximum air temperature and relative humidity significantly correlated with flowering (Okullo et al., 2004). In this study neither relative humidity nor air temperature predicted flowering significantly but rather soil temperature and soil moisture. The reliability of soil moisture in predicting flowering was demonstrated in other plants. Models that included soil moisture as a predictor of flowering were able to explain 66 % of the variation in flowering compared to 24% when soil moisture was excluded (Chauhan et al., 2019).

Despite the accuracy of soil conditions in predicting shea flowering, none of the previous phenological studies included soil moisture nor soil temperature in phenological observations. Air temperature and relative humidity were the most used predictors perhaps owing to easy availability of data compared to soil temperature and moisture data that sometime requires cumbersome and expensive procedures in measurements (McMaster & Wilhelm, 1998). Significant relationships observed between air temperature and flowering in the previous studies were likely due to autocorrelation between air and soil temperatures. Therefore, air temperature served as proxy for soil temperature. However, it is evident in this study that, soil temperature enhances model performance more effectively than air temperature.

The climatic factors associated with flowering are unique to each plant species, in central Himalayas, increasing soil moisture was found to be associated with flowering of *Rhododendron arboreum*

(Tewari, Bhatt, & Mittal, 2016). Likewise, precipitation was found to be the most perfect external factor influencing early flowering of cocoa (Adjaloo et al. 2012). For winter oilseed rape (*Brassica napus*), air temperature was the most accurate predictor of flowering onset (Hájková et al., 2021). Soil moisture stress seems to be the most significant trigger of shea flowering in northern Ghana. However, the interpretation of our results is limited by the short duration (one year) of phenological observations. Observation of flowering patterns for longer periods are needed to gain a better understanding of the factors underlying the observed flowering trends. Notwithstanding, climatic factors identified to be associated with flowering in this study would guide future phenological studies to include soil moisture and temperature as predictors of flowering.

Geographic variation in the floral density of *V. paradoxa*

Flowering ability of trees

The flowering ability of trees (number of trees that initiated flowers) varied significantly between regions ($H(2) = 5.3041$, $p < 0.05$). The UE recorded a significantly lower percentage (80%) flowering compared to other regions (Figure 3). Pairwise comparisons revealed a statistically significant difference between UE and NE ($P < 0.05$). The percentage of trees that flowered in all sites was within the flowering range (80 - 100 %) previously observed in northern Mali (Kelly et al. 2018). Significant differences in the flowering ability of trees between regions can be attributed to land use history. Land use and stand age were previously reported to have a significant effect on the percentage of trees that flower (Kelly et al., 2007, 2018; Okullo et al., 2004).

Moreover, significant differences in flowering could also be influenced by biotic factors, particularly mistletoe infestation. Over 50% of the shea trees in Northern Ghana are known to be infested with

mistletoe (Asare et al. 2019). The severity of infestation varies between trees, and this could have contributed to the variability in flowering. Mistletoes are xylem-tapping, and evergreen for most parts of the year, with higher transpiration rates. This lowers the water use efficiency of the host, with

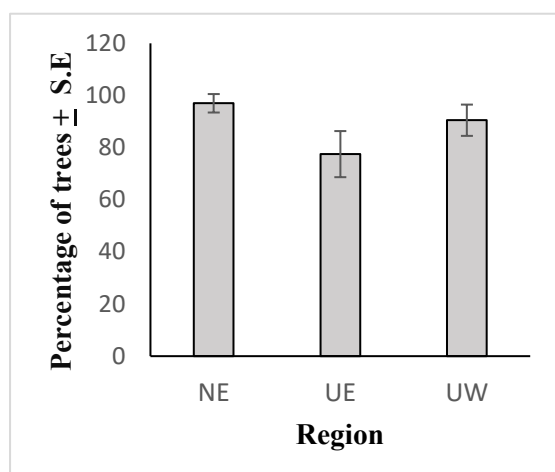


Figure 3. Percentage of trees that flowered

Number of buds/flowers initiated

The mean number of flowers initiated per inflorescence differed significantly among regions ($H(2) = 19.93, p < 0.05$). Pairwise comparisons showed a significantly higher mean number of flowers (41.10) in UW compared to UE ($p < 0.05$) and NE ($p \leq 0.05$), which recorded mean counts of 31.88 and 30.93 flowers, respectively. However, there was no statistically significant difference observed between UE and NE (Figure 4).

The mean number of flowers per inflorescence recorded in this study is consistent with Okullo (2004), who indicated shea produces 20 to 100 flowers in a fascicle. Also, the mean number of flowers recorded in UE and NE was similar to Stout et al. (2018), who previously reported an average count of 31 flowers per inflorescence in northern Ghana. The significantly higher number of flowers produced per inflorescence in the UW

immediate impacts being felt in reduced growth vigour of branches above the point of attachment (Broshot and Tinnin, 1986). This can retard the production of reproductive structures, contributing to the variability in flowering.

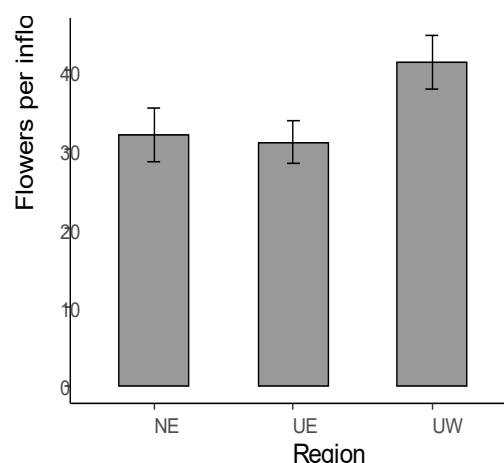


Figure 4: Mean number of flowers per inflorescence $\pm$ S.E

region can be attributed to high soil fertility in the area. The soils in UW were reported to contain higher amounts of organic matter due to long fallow periods compared to other parts of northern Ghana (Tetteh et al., 2016). Also, the western highlands near Bole and Wa were identified among the most favourable areas for yam cultivation, especially newly cleared farmlands (Lovett & Haq, 2000). The suitability of this area for yams is an indication of high soil fertility since yam has high soil nutrient demands. A comparison of soil physical and chemical properties reveals some variability among the three regions (Tetteh et al., 2016). Soils in the UW region are generally richer in organic matter and nutrients than those in UE and NE. Soils deficient in essential nutrients required for flowering, particularly phosphorus, can limit flower production in plants. The soil properties play a significant role in plant growth and reproduction; therefore, the variability in flowering could be explained by soil properties. Similarly, Kelly et al.

(2007) detected a significant influence of soil conditions on the flowering of tree stands in Mali.

Geographic variation in morphometric traits of shea flowers

The one-way ANOVA revealed a statistically significant difference in mean pedicel diameter among regions ($F_{2, 536} = 5.22$, $p < 0.001$). Tukey's HSD Test for multiple comparison of means showed a significantly ($p < 0.001$, 95% C.I. = 0.0258, 0.157) larger mean pedicel diameter in UW (1.29 mm) compared to UE (1.21 mm). Pedicel diameter of UW was also marginally larger than NE ($p > 0.05$, 95% C.I. = -0.025, 0.106). No statistically significant differences were recorded between NE (1.26 mm) and UE ($p > 0.05$, 95% C.I. = -0.116, 0.015) (Figure 5.a). The mean length of the pedicel also differed significantly among regions ($F_{2, 536} = 323.5$, $p = 0.001$). The Tukey's HSD Test for multiple comparison of means showed a significantly higher pedicel length (20.1 mm) in UW compared to NE ($p < 0.001$, 95% C.I. = 1.252, 2.964) and UE ($p < 0.001$, 95% C.I. = 8.026, 9.743), which

recorded 18 and 11.5 mm, respectively. On the other hand, flower pedicels in NE were significantly longer than those in UE flowers ($p < 0.001$, 95% C.I. = -7.63, -5.919) (Figure 5.b).

The mean petal length also varied significantly among regions ($F_{2, 536} = 58.63$, $p = 0.001$). Petals from UW were substantially longer (9.00 mm) than NE ($p < 0.001$, 95% C.I. = 0.712, 1.276) and UE ($p < 0.001$, 95% C.I. = 0.935, 1.497) that recorded 8.02 and 7.79 mm respectively. However, no statistically significant difference was observed in petal length between UE and NE ($p > 0.05$, 95% C.I. = -0.505, 0.058) (Figure 5.c). The mean filament length varied significantly between the three regions ($F_{2, 536} = 173.2$, $p < 0.001$). Multiple comparison of means showed a significantly longer filament (8.76 mm) in UW compared to NE ($p < 0.001$, 95% C.I. = 0.358, 0.902) and UE ($p < 0.001$, 95% C.I. = 1.829, 2.374) that had 8.12 and 6.65 mm respectively. However, filament length in NE was significantly greater than UE ($p < 0.001$, 95% C.I. = 1.744, -1.199) (Figure 5.d).

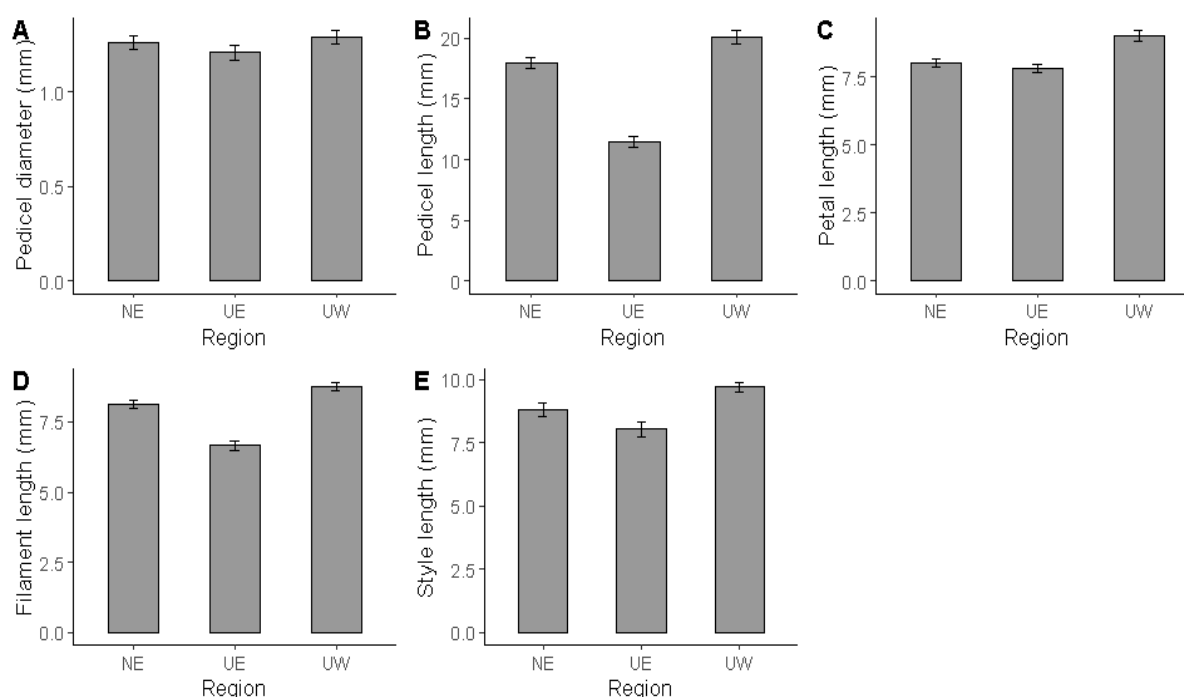


Figure 5. Morphometric traits of *V. paradoxa* flowers

Region had a statistically significant effect on style length of a flower ($F_{2,536}=38.67$, $p < 0.001$). Tukey's HSD test for multiple comparison of means revealed a significantly longer style in UW (9.71 mm) compared to NE ($p < 0.001$, 95% C.I. 0.475, 1.342) and UE ($p = 0.001$, 95% C.I. = 1.619, 1.185) with 8.05 and 8.88 mm, respectively. Meanwhile, the mean style length in NE was also significantly longer than UE ($P < 0.001$, 95% C.I.= -1.144, -0.277) (Figure 5.e).

The morphometric traits of all floral parts recorded in this study were smaller than those reported in Uganda, except the mean pedicel length (20.1mm) recorded in UW, which was slightly longer than the Ugandan mean (19.7mm) (Okullo 2004). This confirms Hall et al.'s (1996) assertion that flowers of *paradoxa* sub-species tend to be smaller than those of *nilotica* in terms of petal length, sepal length and style length. The longest mean style (9.71 mm) recorded in this study exceeds the mean style length (2.89 mm) reported in Cameroun by Nguemo et al. (2014). Apart from difference observed across studies, there was also a significant variation in morphometric traits among the three regions of northern Ghana. Generally, the UW region recorded higher values for all floral traits measured.

Although flower development is known to be influenced by environmental factors, other studies have shown a large influence of selected genotypes on flowering (Craine et al. 2012). There is a high DNA polymorphism in shea (Abdulai, Krutovsky, & Finkeldey, 2017), which could have accounted for this variability in floral traits. Just like many other ecological phenomena, phenology is known to be under strong genetic control (Craine et al. 2012), therefore the internal reproductive capacity of each plant may significantly affect floral traits expressed.

Conclusion

Although one year of data was insufficient to draw definitive conclusions on shea flowering phenology, the present study provides some insights into the geographic variation in shea flowering within the Guinea savanna zone. Flowering commenced in the Upper West region about 4-6 weeks earlier than the North East and Upper East regions. The weekly number of trees commencing flowering was found to be significantly associated with soil temperature and soil moisture. The mean number of flowers initiated per inflorescence was found to be significantly higher in Upper West (41.10) compared to Upper East (30.93) and North East (31.88) regions. Morphometric traits of shea flowers also differed significantly between the three regions. For most morphometric traits (pedicel diameter, pedicel length and petal length), Upper West recorded a significantly higher mean than the other regions, although no statistically significant differences were observed between the Upper East and North East regions.

This study highlights the need for further research spanning multiple flowering seasons to examine the impact of climatic conditions on the phenology of shea. However, the morphological variations in floral traits should be considered in germplasm collection for domestication and tree improvement. Incorporating these differences will support the development of ideotypes that are better adapted to specific geographical areas rather than generalized across broad agro-ecological zones.

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Conflict of Interest Statement: The authors declare that there is no conflict of interest

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Supplementary information

Tab. S1: Correlation Matrix for climatic factors

Correlation matrix

	(Intr)	RH	Soil Moisture	Soil Temp	Mean Air Temp.	Max. Air Temp.	Min. Air Temp.
RH	0.183	-					
Soil Moisture	0.694	0.242	-				
Soil Temp.	0.647	0.098	0.383	-			
Mean Air Temp.	0.266	0.473	-0.158	0.627	-		
Max. Air Temp.	0.527	0.38	0.285	0.612	-0.917	-	
Min. Air Temp.	0.124	0.462	-0.099	0.22	-0.839	0.652	-
Wind Speed	-0.39	0.225	0.256	0.032	-0.144	0.304	-0.01