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# Phenology and early growth performance assessment of the endangered Afromosia (*Pericopsis elata*) of the high forest zones in Ghana

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*Pericopsis elata* is a tall tree of high commercial value within moist and dry semi-deciduous West African forests. It is threatened with extinction, mainly due to overexploitation. Information on the reproductive phenology of such threatened but highly demanded trees remains crucial for taking conservation measures. This study examined the reproductive phenology of 50 individual trees relative to climatic variables, within three selected forests in Ghana. Period and intensity of the various phenophases of trees under study were monitored and scored. The effects of planting distance on early growth performance in plantation were also evaluated. Leaf flushing in the species across all sites occurred at the onset of the wet season (April-July). This was closely followed by flowering between August - September. Fruiting and seed dispersal occurred between October - February. Seed dispersion across all sites was observed for approximately 3 months (November-January), when mean monthly maximum temperatures exceeded 30°C. It was concluded that it is the ideal season for seed collection. The findings further suggest that although increasing in the species reduced survival in the first two years, planting distance of 4mx4m will result in a higher periodic annual height increment, indicating faster primary growth of seedlings.

Key words: Pericopsis elata, reproductive phenology, leaf flushing, flowering, fruiting and planting distance.

# INTRODUCTION

Phenological monitoring involves the careful observation and documentation of the timing of recurring biological events in plant and animals, the causes of their timing, regarding biotic and abiotic forces, and the interrelation among phases of the same or different species (Leith, 1974; Badeck et al., 2004; Zhang et al., 2006). Plant phenology, the seasonal growth cycle of plant developmental stages, is sensitive to climatic changes (IPCC, 2007), and strongly influenced by the terrestrial carbon and water balance (Richardson et al., 2013; Piao et al., 2019a). Phenological information has been a reliable data in predicting how species respond to

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Table 1. Study sites location and vegetation types.

Study site	Latitude	Longitude	Forest type
Amantia	06°15'6.14"N	01° 7'48.79"W	Moist semi- deciduous
Bobiri	6°41'45.78"N	01°21'41.18"W	Moist semi-deciduous
Abofour	07°10'46.10"N	01°43'26.76"W	Dry semi-deciduous

weather variations or climatic changes (Archeti et al., 2013; Fitchett et al., 2015). Small variations in climate could have significant influence over vegetation. Pattern of phonological events is variously used for characterization of vegetation type (Jadeja, 2010). Phenological patterns in plants may have direct implication for their survival, reproduction and subsequent fitness of a population (Gezon et al., 2016). Some studies have correlated phenological events such as flowering, leaf flushing and seed dispersal to subsequent survival of seedlings, and predation rate in plant communities (Borchert et al., 2005). Phenological studies can inform us about the timing and duration of resource availability in ecological communities. For instance, through phenology observation, we can predict when pollen and nectar are available to pollinators, when fruits are available to fruit eating animals, when leaves are available for herbivory and whether plants must compete for the services of pollinators and seed dispersers (Lechowicz, 2001).

Pericopsis elata (Harms) Meeuwen is tall tree timber tree species of high commercial value belonging to family Fabaceae. It occurs mostly in moist and dry semideciduous tropical west-African forests (Hawthorne and Gyakari, 2006). The tree has a cylindrical bole often identified with large reddish patches on the bark. P. elata is currently classified as "endangered with declining population" by the International Union for the conservation of Nature (IUCN). This is due to decades of unsustainable exploitation for its precious wood (Dickson et al., 2005; Hills, 2020). Wood from this species is highly valued on the international market, not only for furniture and as decorative veneer, but also for interior and exterior joinery, stairs, flooring and boat building. It is considered a substitute for teak and suitable for heavy and light construction (NDF, 2017). P. elata is also listed on CITES Appendix I, and therefore subject to stricter controls in harvesting and international trade to prevent possible future extinction (Betti, 2008; CITES, 2016).

Clearly, understanding the phenology and early growth performance of endangered tree species such as *Pericopsis elata*, is a key requirement for their conservation and use in reforestation activities. At the moment, there is scanty information on improving propagation success, ex-*situ* conservation techniques and protocols for plantation establishment for this important but threatened tree. To ensure sustainability, there is the need to generate reliable data on phenology and early growth performance within range countries. Such information will guide the timely collection of highquality germplasm from the field for raising seedlings or foe seed banking purposes (Amponsah et al., 2018).

While a host of literature exists on international trade and industrial uses of the wood of *P. elata*, there seems to be little known about the essential biological parameters controlling population dynamics, reproduction, and its phenological patterns (Doucet, 2003; Bourland et al., 2012). This study aimed to contribute to existing useful scientific information required for P. elata conservation. The specific objectives were to: (1) Observe and document the timing of the recurring reproductive life cycle of the species across the moist and dry semi deciduous forest ecological zones in Ghana. (2) Determine the relationship between the various phenological phases and local weather variables including temperature and rainfall. (3) Assess the early growth performance of *P*. elata in plantation establishments at varying seedling spacing or planting distances.

### MATERIALS AND METHODS

## Study sites

Phenological monitoring was undertaken across selected forest reserves within three ecological zones for a two year reproductive cycle. These forest reserves were located in Amantia (AM) within the moist semi deciduous Pranum forest reserve, Bobiri (BO) forest reserve in the moist semi-deciduous ecozone and Abofour (AB) located in the dry semi deciduous Afram Headwaters Forest reserve in Ghana (Table 1). These sites were selected based on the natural distribution range of the target species, and also to ensure a wider coverage of the high forests and forest-savannah transitional ecological zones of Ghana (Hawthoerne).

## Phenological survey

A total of fifty matured individuals of P. *elata* were selected and tagged with laminated labels across all sites (Figure 1). Geographical position system (GPS) coordinates of sampled individuals were recorded to facilitate easy access to the trees. Individual trees were selected if they appeared to be healthy, had a crown easily observed from the route and were of reproductively matured size of at least 20 cm diameter at breast height (DBH; 1.3m above ground) following Amponsah et al. (2018).

The sampled trees were monitored fortnightly, from January 2019-December 2021. Tree crown assessment was carried out visually with the use of binoculars, digital cameras, and with the assistance of tree climbers. The various phonological phases were scored using the widely adopted Biologische Bundesanstalt, and



Figure 1. Map of the three study locations.

Chemical Industry (BBCH) system of coding plant phenology (Borchet et al., 2005; Schwartz, 2003). An image analysis computer software (*Image J* version 10.12) was used in transforming digital images of tree crowns phenophases into nominal percentages. A species was considered to be passing through the peak of a phenophase when more than 50% of the individuals of that species under observation were found to be in that same phase. As no observations were made during the interval between two sampling dates (approximately 15 days), a standardised protocol established by Singh and Kushwaha, (2006) was adopted. This protocol, assumes that in a tree, a particular phenophase began before, or continued beyond, the date of first/last record by one half of a sampling interval.

Weather data on rainfall as well as minimum and maximum daily temperatures of the study site were recorded, and their monthly means calculated. The weather data was further validated using the nearest computerized weather stations or data from the Ghana Meteorological Department located near the three study sites. The duration of a phenological event in the species was computed by obtaining the number of days required for the completion of an event from the first observation date of that event (Borchet, 2005; Amponsah et al., 2018). Pearson correlation analysis was carried out between the mean days of phenological events and weather data variables, mostly temperature and rainfall.

#### Early growth performance assessment

Early growth performance assessment was carried in the Asenanyo

Forest Reserve near Akota in the Ashanti Region of Ghana (GPS). *P. elata* seedlings raised at the same time and under similar growth conditions at the Nursery, were transplanted using various planting distances (3 x 3m, 4 x 4m and 5 x 5m) as treatments. At the experimental site, three replicates of 20 m<sup>2</sup> <sup>P</sup>. *elata* plots were demarcated for each treatment, where data were recorded on seedling survival rate, seedling height, collar diameter, and number of leaves. These variables were defined as follows (equations 1 and 2):

Survival rate (%) =  $\frac{\text{Number of seedlings surviving}}{\text{Number of seedlings planted}} X 100$  (1)

Seedling volume index 
$$(cm^3)$$
: =  $Cd^2(h)$ 

where, Cd is the collar diameter of the seedling measured using a digital Vernier calliper placed at the base of the seedling just above the soil surface, and H is the total height (m) of the seedling measured from base to the tip of the leading stem. Also, Periodic Annual Diameter Increment (PAId) and the Periodic Annual Height Increment (PAIh) were calculated using the following equations as proposed by Yahya et al. (2020) for the first two years of seedling growth (equations 3 and 4).

PAId = [(dt + k - dt) / k] * t	(3)	)
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PAlh =  $[(ht + k - ht) / k]^* t$  (4)

Where ht + k = total seedling height at the end of the early growth period (cm), dt = diameter at the beginning of early growth period

(cm), ht = total height at the beginning of growth period (cm), k = length of the growth period in (days) and t = 365 x 2 days.

To enable measurement on leaf area, high resolution images of sampled leaves within each plot were taken and analysed using the *Image J* computer software.

## RESULTS

Results of the weather data across all three study sites are presented as Ombrothermic diagrams (Figure 2). Also, a summary of flowering/fruiting, seed maturity/ dispersal and leaf flushing phenology is presented as a colour-coded Phenological chart for the species (Figure 3).

Across all three locations, a bi-modal climatic pattern was observed. A dry period spanning mid to late November - through April with high maximum temperatures and a major wet seasons from May - June and September - October. Leaf flushing in *P. elata* generally began in early April through May and June for all three sites; although leaf flushing in Amantia seems to have been somehow delayed during the same period.

# Leaf flushing

For *P. elata* populations observed in the Pranum Forest Reserve in Amantia, leaf flushing began in early May to late July with 30% of individuals under observation initiating intensive leafing for Year 1 (Y1). Similarly, 43% of sampled populations-initiated leaf flushing earlier (in mid-April) of Year 2 (Y2) at this same location. This period also coincided with end of the dry season from November- March for each year, and the onset of rains in late April for Y1 and Y2.

There were records of low mean monthly maximum temperatures with relatively increased rainfall for this period. Leaf flushing in the species at the other two locations followed a similar pattern and weather conditions with the exception of leaf flushing of *P. elata* in Abofour that lasted until September in Year 2.

# Flowering and fruiting

Flowering and fruiting in the species covered the months of June to late October across all the three study locations for the two-year period. Remarkably *P. elata* populations in both Pranum and Bobiri extended their fruiting season to November, which slightly overlapped with seed maturity and dispersal. It was also observed that flowering and fruiting phenological phases overlapped with leaf flushing for all two years, but this trend was much more pronounced in Abofour and Bobiri for Y1 and Y2 respectively. Peak flowering of the species occurred in the months of October for all sites (>83% and >85% for Y1 and Y2, respectively). No flowering activity was observed in December for both years, when rainfall was lowest (>1cm for Y1 and Y2). This occurred at the onset of the dry season with high mean monthly maximum temperatures of 31.6 °C.

# Seed maturity and dispersion

Closely following flowering and fruiting for the species across all three locations were seed maturity and subsequent dispersion. The peak period of seed dispersion was recorded in mid-to-late. December, where >75 and >83% of P. elata individuals under observation across all sites dispersed their seeds. Seed dispersal occurred alongside leaf fall in the dry cool season when deciduous species within the various ecological zones were shedding leaves. Periods of complete leaflessness was observed in some individuals during the drier months of December-February for both years. P. elata individuals under observation in Pranum forest reserve (Amantia) recorded the longest seed dispersion period in Y1 from late November to early March. This was during a period of low rainfall (1.3 mm on average) and high maximum temperatures (>31°C). Markedly, seed dispersion in the P. elata stands that were observed in Abofour started earlier (as early as October), but did not go beyond January for all the two years, compared to all the other sites.

# Phenology weather variable correlation

The duration of a phenological event in the species was computed by obtaining the number of days required for the completion of an event from the first observation date of that event (Borchet, 2005; Amponsah et al., 2018). Pearson correlation analysis was carried out between the mean days of phenological events and weather data variables, mostly temperature and rainfall. Summary of the results of this analysis is presented in Table 2. There was a strong positive correlation (0.934) between Leaf flushing in the species across all sites and rainfall. Similarly, the data indicated a strong positive correlation between seed maturity/dispersion and temperature

# Early growth performance

Mean seedling height and root collar diameter of *P. elata* seedlings did not show significant differences as a result of planting distance (F= 0.096 and 0.036, respectively). Figure 4 presents a boxplot of the mean seedling height and root collar diameter as influenced by planting distance after 2 years of seedling establishment.

Also, Figure 5 presents the summary of survival rate as calculated from 3 replicated plots under the various planting distances. It is evident that 3x3m planting distance treatment showed a slightly higher survival rate







Figure 2. Ombrothermic diagrams for the three research locations during a two-year period.

compared to the rest of the treatments. Comparatively, the highest seedling survival rate (92.5%) was recorded in the first plot of the 3m planting distance treatment, whiles plot 3 of the 5m planting distance treatment

showed the lowest survival. Generally, the data seem to suggest that increasing planting distances across the treatment resulted in higher seedling mortality.

Similarly, volume index of seedlings across the various



Figure 3. A Phenological Chart of P. elata across the 3 forest ecological zones in Ghana for a two-year reproductive cycle.

 
 Table 2. Pearson correlation coefficients of weather variables and mean days of phenological events.

Phenophase	Temperature	Rainfall
Flowering/fruiting	-0.741	0.312
Leaf flushing	0.633	0.934
Seed maturity/dispersion	0.872	-0.314



Figure 4. P. elata seedling height and collar diameter with planting distance after 2 years of establishment.



Figure 5. P. elata seedling survival in the 3 replicated plots at the various planting distances.

Planting distance	Volume index (cm <sup>3</sup> )	Leaf area (cm <sup>3</sup> )	PAId (cm year <sup>-1</sup> )	PAIh (m year <sup>-1</sup> )
3 m x 3 m	96.327 <sup>a</sup>	35.22 <sup>a</sup>	0.872 <sup>a</sup>	0.124 <sup>a</sup>
4 m x 4 m	112.28 <sup>a</sup>	53.322 <sup>b</sup>	0.524 <sup>b</sup>	0.923 <sup>a</sup>
5m x 5 m	126.56 <sup>b</sup>	31.23 <sup>a</sup>	0.476 <sup>b</sup>	0.635 <sup>a</sup>
SEM (±)	9.06	12.42	0.02	0.96

**Table 3.** Summary of the mean values of the various parameters for early growth performance assessment in *P. elata* seedlings.

PAId is the periodic annual diameter increment (cm year<sup>-1</sup>)

PAIh is the periodic annual height increment (m year<sup>-1</sup>)

Values with the same alphabet letters were not statistically significant at the 5% probability level.

treatments declined with seedling spacing. For instance, the 5 m x 5 m spacing recorded the highest seedling volume index of 112.28 cm<sup>3</sup>; while the 3 m x 3 m planting space recorded the lowest volume index of 96.32 cm<sup>3</sup> (Table 3). Again, periodic annual increment in height as well as the periodic annual increment in diameter were identified to be highest in 3mx3m planting distance treatment closely followed the 4mx4m planting spacing (0.923).

# DISCUSSION

The timing of the reproductive life cycle in *P. elata*, like other tree species, is affected by seasonal peaks and depressions common in tropical rainforests with pronounced dry periods (Borchert et al., 2005; Forrest and Miller, 2010; Sonnentag et al., 2012). Leaf flushing and flowering occurred mostly in the wet season, but were virtually absent in the dry cool months of November-March. This trend in *P. elata* was also observed by Dean et al. (2005), who worked on closely related species in the lvory Coast. The response of the species to rains indicated that *P. elata* floral phenology was largely driven by water availability than photoperiod.

Intense flushing and flowering of *P. elata* across all study sites at the onset of the rains in May indicated intensive use of stored resources. Moreover, van Schaick et al. (1993) observed that in moist semi-deciduous tropical forests, community wide leaf flushing peaks tend to occur during the time of the year with high temperatures, rainfall and longer hours of sunshine. This is an adaptive strategy that enabled the species to use the favourable wet season for leafing and flowering. It is essential in order to accumulate sufficient photosynthate, and initiate reproduction prior to the steep fall in soil water reserve during the drier periods in the annual cycle.

A relatively extended flowering phenophase (June to mid-November) was observed in *P. elata* stands under monitoring in Pranum for both Y1 and Y2. This phenomenon observed in other tropical trees is believed to aid in the attraction of insect pollinators since their activity is greater in the months with warm and dry days (Augspurger, 1982).

Bhat (1992) argues that an advantage of dry season flowering enhanced visibility of flowers to pollinators since neighbouring trees may lack leaves and other floral parts. At all study sites, periods of complete leaflessness were observed in some individuals under observation during the drier months of December-February for both years. This leafless period is an adaptation to avoid water stress which affects flowering time of tropical forest trees (Bullock et al., 1995).

An increase in the period of leaflessness in deciduous species also causes a reduction in vegetative growth to avoid water loss through excessive evapotranspiration.

Dispersal of matured seeds across all three sites occurred in the dry-cool months of November - January with the exception of individual *P. elata* stands in Abofour, which seems to have initiated dispersal as early as October of Y1. Dispersal seems to have occurred in the dry-cool months when average monthly maximum temperatures were above 30°C.

For seedling early growth experiment, the differences in mean seedling height was not statistically significant. This indicates that seedling planting spacing within the first two years of *P. elata* likely has no influence on height and root collar diameter. However, there were significant differences in volume index, leaf area and periodic annual height increment. This indicates that although planting *P. elata* seedlings in 5 m x 5 m spacing will increase seedling volume index during early stages of growth, a planting distance of 4 m x 4 m results in higher periodic annual height increments, indicating possible faster primary growth of the seedling.

# Conclusions

*Pericopsis elata* stands within the selected ecological zones of Ghana tend to undergo consistent and synchronized annual reproductive cycles, influenced by temperature and rainfall. Leaf flushing in the species across is triggered by the onset of the wet season in April – July or August. Leaf flushing is closely followed by an extended flowering and fruiting phenophase from August to mid-November. Seed dispersion in *P. elata* across the various forests takes place for approximately 3 months in

the year (November-January); where average monthly maximum temperatures are high (>30°C). This period, therefore, is an ideal season for seed collection towards propagation and germplasm conservation.

For early growth performance assessment, a planting distance of 4mx4m will result in a higher periodic annual height increment, indicating faster primary growth of the seedling. Thus, 4m seedling planting spacing is highly recommended to attain relatively better primary growth.

## **CONFLICT OF INTERESTS**

The authors have not declared any conflict of interests.

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#### REFERENCES

- Amponsah JO, Maaleku BK, Djagbletey GD, Asomaning JM, Debrah DK, Kumah P, Tandoh PK (2018). Phenology and seed germination improvement of Terminalia superba And Terminalia ivorensis in a moist semi-deciduous forest in Ghana. Ghana Journal of Forestry 34(1):1-14.
- Archeti M, Richardson AD, O'Keefe J, Delpierre N (2013). Predicting climate change impacts on the amount and duration of autumn colours in a New England Forest. PLoS ONE 8(3):1-8e57373. https://doi.org/10.1371/journal.pone.0057373.
- Augspurger CK (1982). Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinator and seed predators on Hybanthus prunifolius (Vioraceae). Ecology 62:775-788.
- Badeck FW, Bondeau A, Bottcher K (2004). Responses of spring phenology to climate change. New Phytologist 162(2): 295 -209.
- Betti JL (2008). Non-detriment Findings Report on Pericopsis elata (Fabaceae) In Cameroon. NDF Workshop Case Studies WG 1 – Trees, Case Study 2:59.
- Bhat DM (1992). Phenology of tree species of tropical moist forest of Uttara Kannada district, Karnataka. Indian Journal of Biosciences 17(3):325-352.
- Borchert P, Robertson MK, Schwartz MD, Williams-Linera G (2005). Phenology of temperate trees in tropical climates. International Journal of Biometeorology 50:57-65.
- Bourland N, Kouadio YL, Leguene P, Doucet J (2012). Ecology of *Pericopsis elata* (Fabaceae), an Endangered Timber Species in Southeastern Cameroon. Biotropica 44(6):840-847.
- Bullock SH, Mooney HA, Medina E (Eds.) (1995). Seasonally dry tropical forests. Cambridge University Press.
- Convention on International Trade in Endangered Species (CITES) (2016). SC66 Com. 14. Sixty-sixth meeting of the Standing Committee Geneva (Switzerland), 11-15 January 2016. https://cites.org/sites/default/files/eng/com/sc/66/Com/E-SC66-Com-14%28RevbySec%29.pdf
- Dickson BP, Mathew S, Mickleburgh S, Oldfields D, Pouakouyou D, Suter J (2005). An assessment of the conservation status, man agement and regulation of the trade in *Pericopsis elata*. Fauna & Flora International, Cambridge, UK.

- Fitchett JM, Grab SW, Thompson DI (2015). Plant phenology and climate change: Progress in methodological approaches and application. Progress in Physical Geography 39(4):460-482.
- Forrest J, Miller-Rushing AJ (2010). Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical Transactions of the Royal Society B 365:3101-3112.
- Gezon Z, Inouye D, Irwin R (2016). Phenological change in a spring ephemeral: implications for pollination and plant reproduction. Global Change Biology 22(5):1779-1793.
- Hills R (2020). Pericopsis elata (Harms) van Meeuwen. The IUCN Red List of Threatened Species https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T33191A67802601.en
- Intergovernmental Panel on Climate Change (IPCC) (2007). Climate Change 2007: the physical science basis. Contribution of the WG 1 to the fourth assessment report of the Intergovernmental Panel on Climate Change, Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds.), Cambridge University Press, ISBN 978 0521 88009-1, Cambridge.
- Jadeja BA, Nakar RN (2010). Phenological studies of some tree species from Girnar Reserve Forest, Gujarat. India Plant Archives 10(2):825-828.
- Lechowicz MJ (2001). Phenology. In the Encyclopedia of Global Environmental Change, Volume 2. The Earth System: biological and ecological dimensions of global environmental change. Wiley, London.
- Leith H (1974). Phenology and seasonality modelling. New York, Springer Verlag 41:6-8.
- Nature and Development Foundation (NDF) (2017). Conservation of *Pericopsis elata* (Afromosia) in Ghana: Evidence from the Field Centre for African Wetlands Building, University of Ghana, Legon, Accra, Ghana.
- Piao S, Fang J, Zhou LG (2019a). Variations in satellite-derived phenology in China's temperate vegetation. Global Change Biology 12:672-685.
- Schwartz MD (2003). Phenology: an integrative environmental science. Dordrecht. Netherlands: Kluwer Academic Publishers
- Singh KP, Kushwaha CP (2006). Emerging paradigms of tree phenology in the dry tropics. Current Science 89:964-975.
- Sonnentag O, Hufkens K, Teshera-Sterne C (2012). Digital repeat photography for phenological research in forest ecosystems. Journal of Forest Meteorology 152:159-177.
- Van Schaik CP, Terborgh JW, Wright SJ (1993). The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annual Review of Ecology and Systematics 24:353-377.
- Zhang GQ, Song P, Yang D (2006). Phenology of Ficus racemosa in Xishuangbanna, Southwest China. Biotropica 38:334-341.