



## Variation in phenology of *Acacia senegal* (L.) Wild. in relation to origin and ploidy level: Implications for climatic adaptation

Oulimata Diatta<sup>a,b,\*</sup>, Adja Madjiguene Diallo<sup>b</sup>, Diaminatou Sanogo<sup>b</sup>,  
Lene Rostgaard Nielsen<sup>a</sup>, Anders Ræbild<sup>a</sup>, Erik Dahl Kjær<sup>a</sup>, Jon Kehlet Hansen<sup>a</sup>

<sup>a</sup> Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvej 23, 1958 Frederiksberg C, Denmark

<sup>b</sup> Institut Sénégalais de Recherches Agricoles/Centre National de Recherches Forestières (CNR/ISRA), Route des Pères Maristes, BP 2312, Dakar, Senegal

### ARTICLE INFO

#### Keywords:

Flowering  
Fruiting  
Genetic variation  
Leafing  
Sahel  
*Senegalia senegal*

### ABSTRACT

Correct timing of phenology is crucial for the survival and growth of species in arid areas with long dry seasons. Nevertheless, knowledge on genetic variation and adaptive patterns in phenology in deciduous African dryland species is limited. Here we study the variation in phenology of diploid and polyploid *A. senegal* trees from rangewide populations growing in a common garden trial in Senegal and test correlations between population phenology and climate at the site of origin. The leafing, flowering and fruiting phenology was monitored during 17 months and compared to detailed observations of the rainfall in the common garden during the period. We found that *A. senegal* trees in general started development of leaves prior to the beginning of the rainy season with flowering and fruiting initiation occurring during the rainy season. The results lead us to conclude that it was not the rain per se that initiated leaf development. We also conclude that phenology in *A. senegal* is under genetic control, because significant differences could be observed among populations and ploidy levels when grown at the same site. In general, early leaf flushing trees had a longer growing period and performed better in terms of growth at the tested site and the results thus support that leaf phenology influence fitness. We further found that differences among trees in phenology seem to be associated with differences in climate at their site of origin, because the timing of leaf development in the common garden and the timing of the rainy season at the site of origin was significantly correlated for the diploid trees (not for tetraploids). However, it was diploid trees from sites with a late arriving rainy season that developed leaves *earliest* in the year. The environmental cues that control leafing phenology and the associated physiological mechanisms therefore still need to be identified in order to understand how the variation among populations has evolved, its relationship to local adaptation and the implication for smart transfer of seed sources as mean to mitigate changing growing conditions related to global warming.

\* Corresponding author at: Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvej 23, 1958 Frederiksberg C, Denmark.

E-mail addresses: [diatta\\_oulimata2@yahoo.com](mailto:diatta_oulimata2@yahoo.com), [dou@ign.ku.dk](mailto:dou@ign.ku.dk) (O. Diatta), [madjiguene.diallo@isra.sn](mailto:madjiguene.diallo@isra.sn) (A.M. Diallo), [diaminatou.sanogo@isra.sn](mailto:diaminatou.sanogo@isra.sn) (D. Sanogo), [jkh@ign.ku.dk](mailto:jkh@ign.ku.dk) (J.K. Hansen).

<https://doi.org/10.1016/j.gecco.2021.e01957>

Received 29 September 2021; Received in revised form 6 December 2021; Accepted 6 December 2021

Available online 9 December 2021

2351-9894/© 2021 The Author(s).

Published by Elsevier B.V. This is an open access article under the CC BY license

(<http://creativecommons.org/licenses/by/4.0/>).

## 1. Introduction

Phenology refers to the timing of plant growth and reproduction (Rathcke and Lacey, 1985), and is an important component of plant fitness in seasonal climates. Phenology is generally controlled by environmental cues such as temperature, photoperiod and water availability (Polgar et al., 2014; Omondi et al., 2016; Di Lucchio et al., 2018), and is therefore also a biological indicator of climate change (Parmesan, 2006; Cleland et al., 2007; Nicotra et al., 2010). The acclimation of plant phenology to prevailing climatic seasonality enables plants to grow and reproduce under the climatic conditions at the given site and in the given year (Lim et al., 2007; Omondi et al., 2016).

Seasonal variation in temperature, humidity, rainfall, wind speed and even day length can control phenology in tropical plants, although tropical ecosystems are not characterized by strong differences between summers and winters in photoperiod as seen at higher latitudes (Lieberman, 1982). In tropical drylands, water availability is generally the main environmental factor controlling phenology (Borchert, 1994; Eamus and Prior, 2001; Do et al., 2005). However, some dryland species produce leaves and flowers before the onset of the rainy season while others do so after the onset of the season (Lieberman, 1982; Tybirk, 1993). Observations made by satellite imagery of population stands have revealed that leafing phenology of tropical dryland species may be triggered by other environmental cues than water availability (Ryan et al., 2017; Tian et al., 2018).

Perennial plants must time their growth to match the annual variation in temperature and water availability. The length of the growing season (time of leaf appearance to leaf senescence) defines the window for photosynthetic activity and therefore affects water, carbon and nutrient cycling and the net ecosystem production (Wu et al., 2013; Panchen et al., 2015), and too late or early leaf flushing or too late or early senescence will therefore reduce growth. The timing of flowering and fruiting can be similarly important for successful plant reproduction (Milla et al., 2005), because plants that flower too early, before having accumulated enough resources, can have a limited capacity for seed production. On the other hand, plants that delay flowering might gain higher capacity for seed production or risk lacking time to produce mature fruits before the end of the season (Omondi et al., 2016). Besides adaptation to prevailing seasonality, differences among species in phenology can also facilitate coexistence of species in diverse plant communities by reducing competition for pollinators and other resources (Rathcke and Lacey, 1985; Khanduri, 2014).

Studies of variation within and among tree populations in their phenology can reveal the degree of adaptive potential, local adaptation and phenotypic plasticity in response to variation in climate, and therefore shed important light on wise management of genetic resources in the face of climate change. There is limited knowledge of genetic variation in phenology of African dryland species (Ræbild et al., 2010). However, recent analyses of provenance trials (common garden trials) have revealed clear differentiation among populations of species covering areas with substantial ecological variation. Genetic variation in phenological traits has thus been reported in *Adansonia digitata* (Di Lucchio et al., 2018; Bamba et al., 2019) and *Parkia biglobosa* (Ouedraogo, 2015). In a greenhouse trial, Di Lucchio et al. (2018) exposed *A. digitata* seedlings of different origins to water and day length treatments, and found that the leaf phenology depends on both day-length and water regimes, but also that the response varied among geographic origins. Bamba et al. (2019) reinforced the findings by exploring a provenance trial in Mali, and showed that *A. digitata* populations differed in their senescence, and that these differences could be partly explained by climate of the site of their origins as an indication of adaptation. In a provenance trial in Burkina Faso, Ouedraogo (2015) explored different populations of *P. biglobosa* and found that leaf phenology was correlated with the latitude and temperature of the origins with provenances from cooler areas reaching their leaf flushing peak earlier than provenances from hotter areas.

*Acacia senegal* is a multipurpose tree species that is widely distributed across Africa from the Sahelian belt to southern Africa (Fagg and Allison, 2004), and is also found in India and Pakistan. The species was recently conferred to the new name *Senegalia senegal* (L.) Britton (Kyalangalilwa et al., 2013), but here we maintain the rule of first priority and the name *A. senegal* is used in the present publication. *Acacia senegal* is well adapted to arid zones with low soil fertility and a seasonal rainfall varying between 200 and 800 mm (Fagg and Allison, 2004). Gum Arabic is collected from the tree (Fagg and Allison, 2004; Raddad and Luukkanen, 2006; Diallo et al., 2015), and provides an important source of income for rural populations that also use the species for other products. The ability to fix nitrogen and tolerate drought impacts makes *A. senegal* an essential component of dryland agroforestry systems (Fagg and Allison, 2004; Raddad et al., 2006) and the species is therefore widely recommended in reforestation programs in Sahel. A number of studies have investigated the phenological events of *A. senegal* (Tandon et al., 2001; Seghieri et al., 2012b; Omondi et al., 2016), but the genetic variation among origins that can reflect adaptation to the climate conditions has to our knowledge not been described up to now.

Genetic differentiation among origins of *A. senegal* has been found in growth (Ræbild et al., 2003a, 2003b, 2003c; Raddad and Luukkanen, 2006; Raddad, 2007; Larwanou et al., 2010; Diatta et al., 2021a) and when investigating molecular markers (Assoumane et al., 2013; Odee et al., 2015; Diallo et al., 2015). The studies have revealed patterns of adaptation to local climatic conditions, and also that the species can co-occur in different levels of ploidy (different numbers of sets of chromosomes), where the level of ploidy influences the species' performance and response to drought stress (Diallo et al., 2015, 2016). It is therefore important to take the level of ploidy into account when studying the genetic variability in phenological traits of *A. senegal*.

The present study aims to investigate variation in phenology among different origins (populations) of *A. senegal*, and the hypothesis is that these differences are related to the climate at the origin of the population and to the ploidy level. It also addresses whether differences in flower phenology limits crossings between diploid and tetraploid individuals.

## 2. Material and methods

The present study was conducted in a common garden trial established in August 1994 in Dahra (15° 20'N, 15° 28' W, elevation 45

**Table 1**Origins and environmental characteristics of *A. senegal* populations used in the study. Populations are arranged according to WAI0<sub>i</sub>.

Populations	Country	Latitude	Longitude	Altitude (masl)	Mean annual Temperature (°C)	Mean annual rainfall (mm)	WAI0 <sub>i</sub> (MOY)	WAI0 <sub>f</sub> (MOY)	#WAI0 (mm)	No. diploid (2 n) trees	No. Tetraploid (4 n) trees
Sodera	Ethiopia	08°24' N	39°23' E	1500	21.4	762	4.9	9.0	292	0	5
India60	India	26°19' N	79°31' E	120	25.9	867	7.0	8.7	80	0	9
Somo	Mali	13°17' N	04°54' W	40	27.5	627	7.1	8.7	187	5	0
Di	Burkina Faso	13°10' N	03°25' W	260	28.0	637	7.3	8.2	121	3	0
Bissiga	Burkina Faso	12°26' N	00°32' W	280	28.3	696	7.3	8.4	128	5	0
Kidira	Senegal	14°28' N	12°13' W	39	28.9	611	7.3	8.9	184	14	1
Sudan	Sudan	12°44' N	29°35' E	620	26.8	408	7.4	7.8	56	9	0
Ngane	Senegal	14°08' N	16°12' W	2	27.9	570	7.6	8.8	194	7	7
Karofane	Niger	14°18' N	06°11' E	280	28.4	366	7.7	7.8	51	14	1
Chad	Chad	12°49' N	15°18' E	280	29.0	349	7.8	7.9	64	9	0
Kirane	Mali	15°23' N	10°15' W	140	29.3	380	7.8	8.2	59	7	4
Aite	Mali	15°05' N	11°39' W	80	29.7	449	7.9	8.2	75	13	2
Kankoussa	Mauritania	15°56' N	11°27' W	80	29.7	294	7.9	8.2	60	27	0
Daiba	Senegal	15°22' N	13°08' W	28	29.6	437	8.1	8.5	65	13	0
Djiguéri	Mauritania	15°44' N	08°40' W	226	28.9	309	8.1	8.1	45	26	0
Diamenar	Senegal	16°00' N	15°54' W	20	27.1	288	8.4	8.4	28	25	0

masl: meters above sea level. #Water availability index calculated as the yearly sum of monthly rainfall minus potential evapotranspiration estimates which are positive and for the period 1961–1990. Estimates of rainfall and evapotranspiration are from the Climate Research Unit, East Anglia University (Harris et al., 2014). WAI0<sub>i</sub>: initial WAI0 defined as the first month of year (MOY) with WAI > 0; WAI0<sub>f</sub>: final WAI0 defined as the last MOY with WAI > 0. Reference period 1961–1990.

m), Senegal. The trial site is characterized by very dry growing conditions with an annual rainfall that ranged between 169 mm in 2002 and 650 mm in 2010 and a daily mean temperature ranging between 15.9 and 39.9 °C (Tagesson et al., 2015). The rainy season is in general relatively short from July to October, with August being the wettest month (Tagesson et al., 2015). The soil is sandy, and the natural vegetation consists mainly of grass and sparse trees such as *Acacia tortilis* subsp. *radiata*, *A. senegal* and *Balanites aegyptiaca* (Göttsche et al., 2016).

## 2.1. Experimental design and climatic conditions of the site

The trial was established from seeds collected from 18 populations (origins, referred to as provenances) across the distribution area of *A. senegal* in Africa and Asia using standard protocols. The design was a randomized complete block design with four blocks. Each block is divided into 18 plots, representing the 18 populations originally with 25 trees each and a spacing of 5 × 5 m, i.e. 1800 trees at the time of establishment. The survival rate at the time of assessment was 12% with 225 trees and with only 16 populations left out of the 18 populations (Table 1). The ploidy level was determined for all the 225 living trees in October 2018 by flow cytometry analysis (Diatta et al., 2021b). This present study only concerns 177 diploid and 29 tetraploid trees that were still alive at the end of the assessment in 2019, i.e. 206 trees. Daily observations of rainfall and temperature were available from a local climate station (15°24'10"N, 15°25'56"W) (Tagesson et al., 2015).

The first day with precipitation in 2018 was registered day 157 (6th June) with 0.05 mm while rain > 2 mm occurred at day 178 (27th June). More continuous rain was registered from day 236 (24th August) in 2018. In 2019, the first day with rain was registered day 181 (30th June) with 0.6 mm while rain > 2 mm occurred at day 205 (24th July), i.e. a month later compared to the previous year. More continuous rain was registered from day 228 (16th August). The last day with rain > 2 mm was day 272 (29th September) and day 298 (25th October) in 2018 and 2019, respectively (Fig. 1). The total annual rainfall recorded in 2018 and 2019 was 295 mm and 355 mm, respectively.

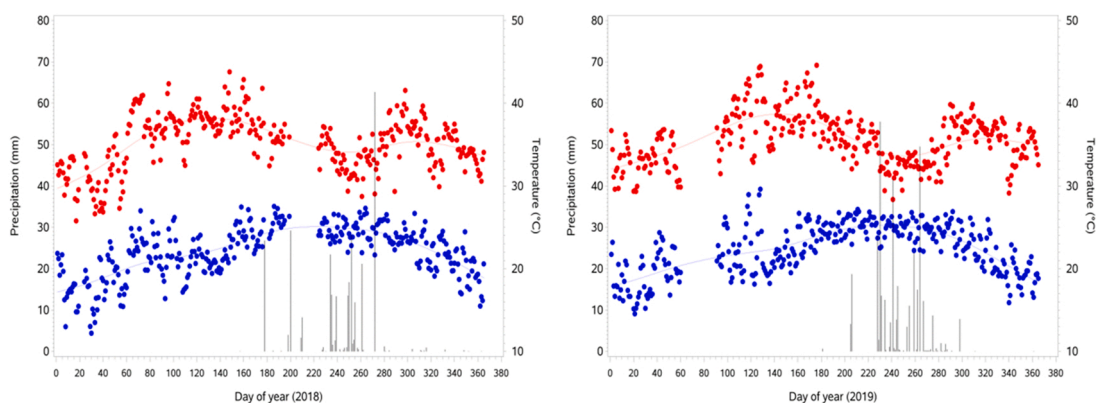
The daily maximum temperature varied between 25°C and 44°C in 2018, and between 28°C and 45°C in 2019, with two peaks (inflection) corresponding to days 120 (30th April) and 300 (27th October) in 2018, and days 140 (20th May) and 320 (16th November) in 2019. The daily minimum temperature varied between 12°C and 28°C in 2018, and between 14°C and 30°C in 2019 (Fig. 1).

For each site of population origin, monthly water availability indices (WAI) were estimated as the differences between estimates of rainfall and potential evapotranspiration and these were used to estimate a cumulated WAI (WAI0) for the months of each year where WAI was above 0. The estimated WAI0 ranged from 28 mm to 292 mm (Table 1). The estimates of annual precipitation, potential evapotranspiration and mean annual temperatures were from the Climate Research Unit at East Anglia University (Harris et al., 2014) and for the period of 1961–1990. The above estimates were also used to estimate the first month of the year (MOY) with WAI > 0 (WAI0<sub>i</sub>), and the last MOY with WAI > 0 (WAI0<sub>f</sub>) for the period 1961–1990 as estimates of the start and the end of the rainy season respectively.

## 2.2. Phenology assessments

The phenology was assessed every week from August 2nd, 2018 (day 214 of 2018) to December 26th, 2019 (day 360 of 2019). At each assessment, the phenological stages of leaves, flowers, and fruits of all trees were recorded (Table 2).

As different parts of the trees could be in different phases of phenology, the dominant phase of the tree was recorded. The day of change from one dominant phase to another was estimated as the day between two assessments with different phenology phases. Two measures for the start of leaf senescence were estimated as respectively (i) day of change from a phase before 7 to phase 7 with “10–50% brown and shed leaves”, and (ii) day of change from a phase before 8 to phase 8 with “> 50% brown and shed leaves”. The



**Fig. 1.** Daily measures of precipitation (bars), maximum temperature (red dots) and minimum temperatures (blue dots) at 10 km (15°24'10"N, 15°25'56"W) from the Dahra field site in 2018 and 2019. Please note that some temperature data points are missing because of incomplete data.

**Table 2**  
Phenological dominating phases of leaves, flowers and fruits recorded for each tree.

	Scores	Phases
Leafing	0	No buds
	1	Buds visible
	2	Buds developed
	3	Signs of leaves
	4	Leaflets visible
	5	Leaf expansion
	6	Leaf complete
	7	10–50% brown or shed leaves (senescence i)
	8	> 50% brown or shed leaves (senescence ii)
Leaf development (i)	Days between leafing score 1 ("buds visible") and 3 ("signs of leaves") (LD (i))	
Leaf development (ii)	Days between leafing score 3 ("signs of leaves") to 6 ("leaf complete") (LD (ii))	
Growing period (i)	Days between leafing score 3 ("signs of leaves") and 7 ("10–50% brown or shed leaves") (GP (i))	
Growing period (ii)	Days between leafing score 3 ("signs of leaves") and 8 ("> 50% brown or shed leaves") (GP (ii))	
Flowering	0	No flower buds
	1	Flower buds
	2	Fully developed flowers
	3	Withered flowers
Flowering period	Length from occurrence of "Flower buds" to "Withered flowers"	
Fruiting	0	No fruits
	1	Fruit initiation
	2	10–50% fruits developed
	3	> 50% fruits developed
	4	10–50% fruits ripe
	5	All fruits ripe

growing period (GP) with assumed photosynthetic activity of the leaves of a tree was defined and estimated as respectively (i) the number of days between the first day with registration of "signs of leaves" and the first day with registration of "10–50% brown and shed leaves" (GP (i)), and (ii) the number of days between the first day with registration of "signs of leaves" and first day with registration of "> 50% brown and shed leaves (GP (ii))". The leaf development speed (LD) was estimated as (i) the number of days between the first registration of "buds visible" and first registration of "leaf complete" (LD (i)), and (ii) the number of days between the first registration of "signs of leaves" and first registration of "leaf complete" (LD (ii)).

The length of flowering period (FP) was estimated for each tree as the number of days between the first day with registration of "flower buds" and the first day with registration of "withered flowers". The frequency of diploid and tetraploid trees that reached "fully developed flowers" was plotted (heatmap) to reveal a potential difference in flowering phenology between cytotypes in *A. senegal* that could limit or prevent pollination between cytotypes. The two populations, Kirane (Mali) and Ngane (Senegal), that had mixed ploidy levels (diploid and tetraploid individuals growing at the same site), and with a fair number of each cytotype was chosen to test this hypothesis.

The frequency of trees that developed ripened fruits was calculated by block and population to test for population differences in the years 2018 and 2019.

### 2.3. Statistical analysis

The phenological development of leaves, flowers and fruits for diploid and tetraploid populations were analyzed using the R statistical software (R Core Team, 2020). The R package *ggplot2* (Wickham, 2016) was used to illustrate the phenological patterns.

As the frequency of polyploid individuals differed highly among populations, effects of geographic origin and ploidy level were confounded. We therefore used a two steps approach for the analyses. First, we analyzed the effect of ploidy for only the five populations (Kidira, Ngane, Karofane, Kirane, Aite, Table 1) where both diploid (total: 55 trees) and tetraploid trees (total: 15 trees) were present, based on the general linear model (model 1):

$$Y_{ijk} = \mu + B_i + G_j + P_k + \varepsilon_{ijk}, \quad (1)$$

where  $Y_{ijk}$  is the mean estimated day for a change in phenological phase by block  $i$  and population  $j$ , and ploidy  $k$ ,  $\mu$  is the general mean,  $B_i$  is the random effect of block  $i$ ,  $G_j$  is the fixed effect of geographic origin  $j$ ,  $P_k$  is the fixed effect of ploidy level  $k$  and  $\varepsilon_{ijk}$  represent the residual errors assumed to be independent and normal distributed (0,  $\sigma^2$ ). This model was applied to test the effect of ploidy.

The second step was to analyze the variation among origins. Here, we made the analysis separately for diploid (total: 177 trees) and tetraploid trees (total: 29 trees, Table 1) based on the following model to avoid confounding effects of origin and ploidy (model 2):

$$Y_{ij} = \mu + B_i + G_j + \varepsilon_{ij}, \quad (2)$$

with abbreviation of effects as above. Here, we thus made two analyses for each trait, one for the diploid trees and one for the tetraploid trees.

The function *lmer* (Linear Mixed-Effect Models) in the package *lme4* (Bates et al., 2015) for R (R Core Team, 2020) was applied and using the Kenward-Roger adjusted degrees of freedom. Residuals were plotted against predicted values to examine for heteroscedasticity and outliers and histogram of residuals were examined for normality.

Pearson's correlation coefficients were estimated between population means (least square mean estimates) for flushing, flowering phenology and growth (height, diameter, and crown area measured in year 2017). To estimate the population means in growth, model (2) was applied respectively for the diploid and tetraploid populations and the derived least square means were used to test the correlations with phenology. In addition, phenology was correlated to climate variables at the site of origin of populations, and significant correlations visualized by plots. The correlation coefficients and associated tests of significance based on the population least square mean estimates were carried out for diploids and tetraploids separately using the *corr.test* function in the package *psych* (Revelle, 2019) as implemented in R (R Core Team, 2020).

### 3. Results

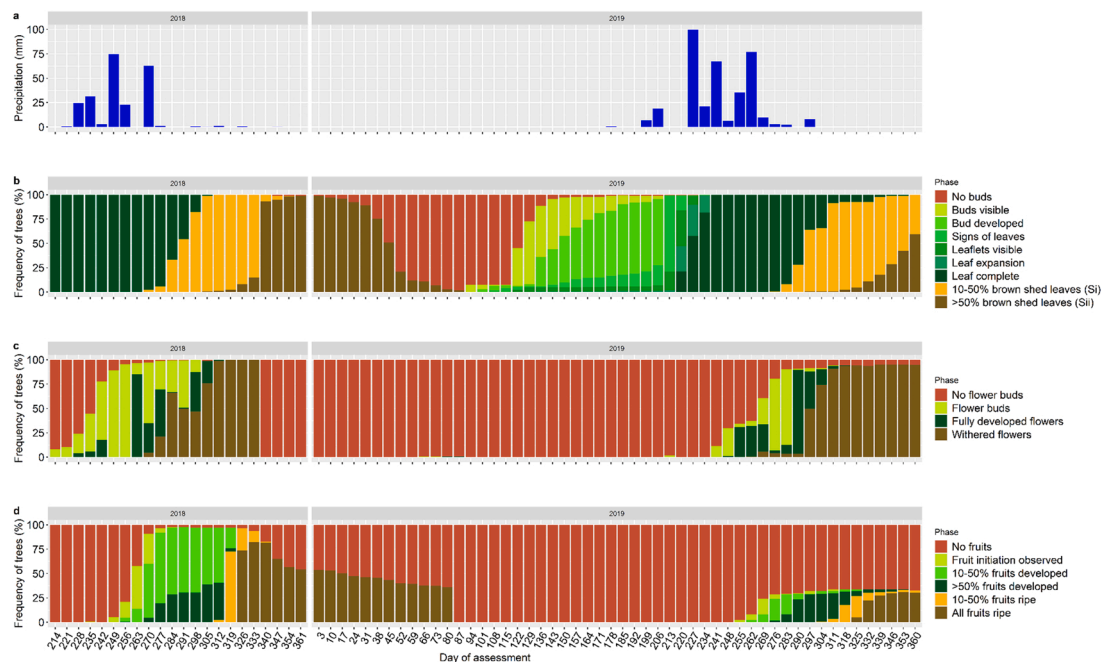
#### 3.1. Timing of leafing, flowering and fruiting

In 2019, leaf buds started to appear on a few trees around day 94 (first week of April) (Fig. 2b). Buds developed progressively before the first day with rain > 2 mm (day 205), while “leaf complete” was registered from day 220 (cf. Fig. 2a, b). All trees had complete leaves at day 241 (Fig. 2b). The first trees showed signs of senescence (i) at day 270 in 2018 (the last week of September), and day 276 in 2019 (first week of October). This was slightly earlier than the end of the rainy season for both years (cf. Fig. 2a, b).

In general, flowers and fruits were produced during the periods of more continuous rainfall (Fig. 2c, d). In 2019, a low frequency of trees (1.5%) produced flowers at day 66 and 213 before the more continuous rainfall, but all these flowers were aborted (Fig. 2c). Flowering took place within 15 weeks (days 214–312) in 2018, and 12 weeks (day 241–318) in 2019 (Fig. 2c). Fruit initiation was observed three and two weeks after the observation of the first flower buds in 2018 (day 236) and 2019 (day 255), respectively. Fruits began to ripen towards the end of the rainy season at day 284 (11th October 2018) and day 304 (31st October 2019) (Fig. 2d). The frequency of trees that completed all fruiting phases was 97% in 2018 while only 32% of the surviving trees succeeded setting fruits in 2019. The frequency of trees showing fruit initiation was also low in 2019 compared with 2018, though the frequency of trees with flower buds reached almost the same level in 2019 as in 2018. These differences suggest a higher frequency of fruit abortion in 2019 (Fig. 2d), which may be due to the fact that trees initiated fruit development almost three weeks later in 2019 (day 255) compared to 2018 (day 236).

#### 3.2. Relationship between leaf flushing and climate at the site of origin

Among diploid populations, the timing of “signs of leaves” and “leaflets visible” was earlier among populations from dry sites, i.e.,



**Fig. 2.** Patterns of rainfall (a), leafing (b), flowering (c) and fruiting (d) phenology of *A. senegal* during the period of survey (August 2018–December 2019). Weekly accumulated rainfall (blue bars) at 10 km (15°24'10"N, 15°25'56"W) from the Dahra field site in 2018 and 2019.



where the first month of the year with  $WAI > 0$  ( $WAI0_i$ ) occurred late (Fig. 3a, b). The speed of LD (ii) and GP (ii) was correspondingly longer for populations from sites where a positive monthly  $WAI0_i$  appeared late (Fig. 3c, d). In tetraploid populations, there were no clear relationship between leafing phases and the climate variables.

### 3.3. Relationship between leaf flushing and growth traits

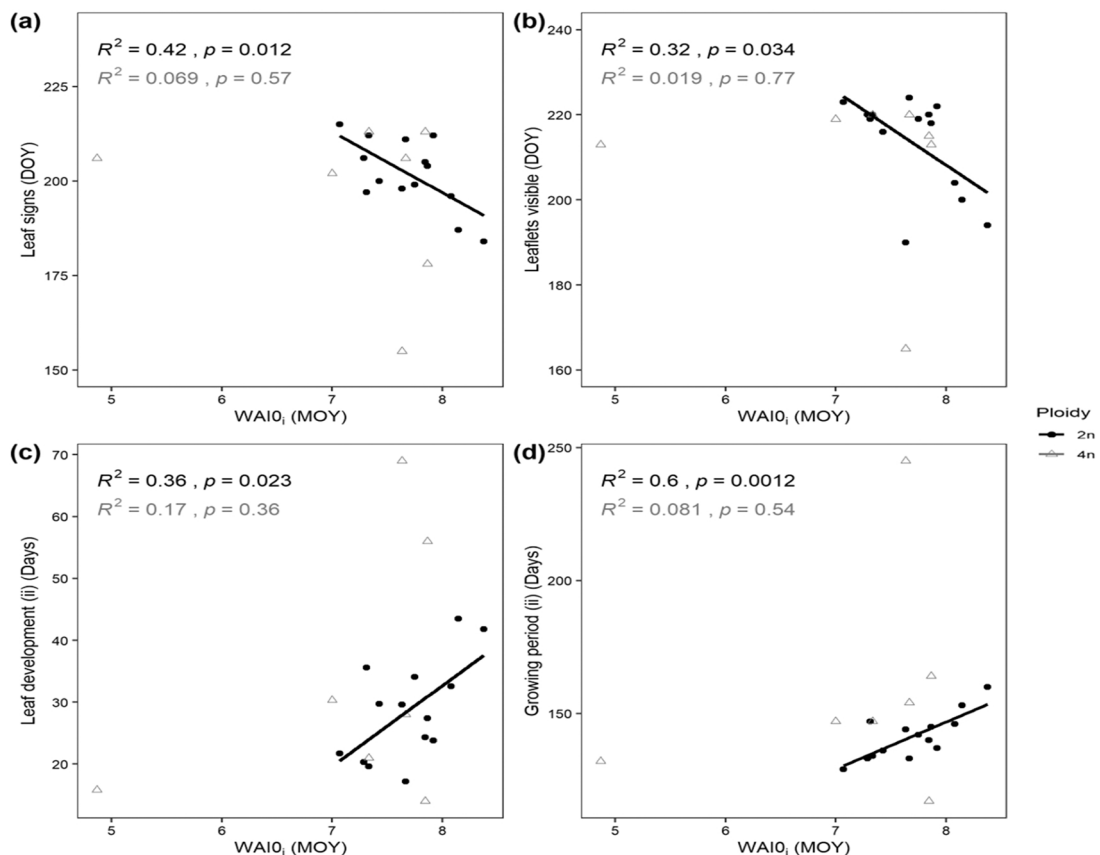
In both diploid and tetraploid populations, first day with “signs of leaves” and “leaflets visible” correlated negatively with the number of days for LD (ii) indicating that late flushing populations in 2019 reached “leaf complete” about the same time as the populations with early leaf flushing. Nevertheless, both estimates of GP (GP(i) and GP(ii)) were negatively correlated with first days of the early flushing phases, particularly first day with “signs of leaves” and “leaflets visible”, which means that the early flushing trees in general had a longer GP (Table S1).

In diploid populations, the first day of “buds developed” (2019) correlated negatively with height and crown area (Fig. 4a, c). Late senescence (i) in 2019 and GP (i) correlated positively with the diameter (Table S1, Fig. 4h). Thus, populations with early development of buds were characterized by taller trees and larger crown areas compared to populations with late bud development, and populations with late senescence had a longer GP and larger diameter.

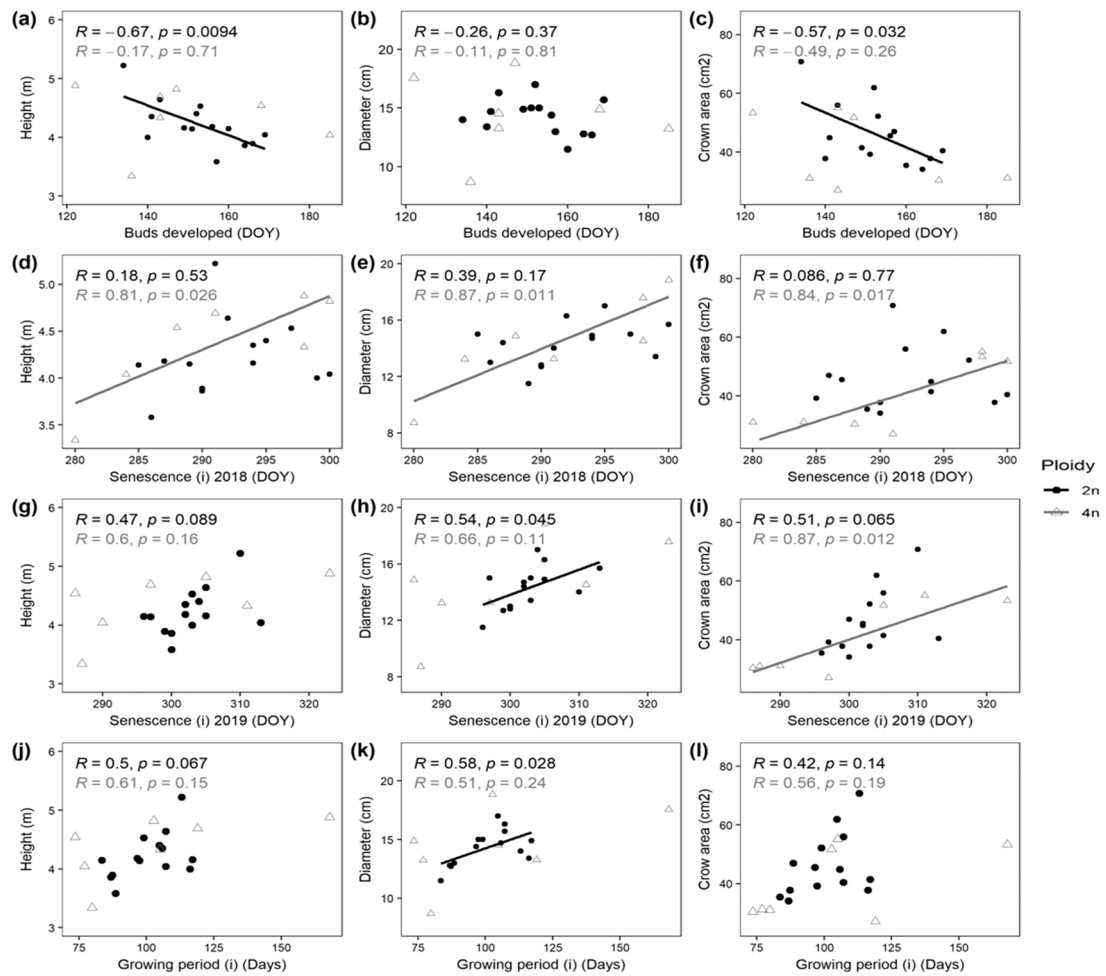
In tetraploid populations, late senescence (senescence (i) and senescence (ii)) correlated positively with growth in 2018 (Table S1, Fig. 4d, e, f). The significant correlations were mainly due to the two populations India60 (India) and Sodera (Ethiopia), and no clear relationships were found when these two populations were removed from the analysis (Fig. S3d, e, f).

### 3.4. Differences in leafing phenology between ploidy levels and among populations

Diploids and tetraploids differed significantly in leafing phenology as regards the day with “signs of leaves”, LD (ii), and the length of the growing period (GP (i)). Tetraploids thus showed earlier “signs of leaves” (day  $187 \pm 7.3$ ) and longer length of LD (ii) (day



**Fig. 3.** Pairwise plots of the leaf signs, leaflets visible, leaf development (ii) and growing period (ii) against the  $WAI0_i$  (first month of year (MOY) with  $WAI > 0$  average for the period 1961–1990) (a, b, c, d), in diploid and tetraploid populations. Symbols represent population least square means. Growing period (ii) is the number of days between the first day with registration of “signs of leaves” and first day with registration of “> 50% brown and shed leaves” (GP (ii)); the leaf development (ii) the number of days between the first registration of “signs of leaves” and first registration of “leaf complete” (LD (ii)).



**Fig. 4.** Pairwise plots of the growth variables (height, diameter and crown area) against estimates of first day with developed buds (a, b, c), first day with senescence (i) in 2018 (d, e, f) and 2019 (g, h, i) and growing period (GP (i)) (j, k, l). Symbols represent population means. Dark symbols denote diploid populations, whereas gray symbols denote tetraploids. DOY means day of the year. The correlations in Fig. 3d, e, f are not significant ( $p = 0.31$ ,  $p = 0.23$ ,  $p = 0.057$ , respectively) when India60 and Soderia were removed.

$43 \pm 7.3$ ) as compared to diploids ones (day  $203 \pm 5.2$  and day  $26 \pm 5.1$ , respectively) (Table 3). Since diploids and tetraploids reached “leaf complete” almost at same time, the diploid trees had a significantly faster LD compared to tetraploids trees (Table 3).

Diploid populations were significantly different from each other in regards to the first day of leaf senescence (i) in 2018, but this result was not repeated in 2019. In addition, diploid populations differed in first day with “buds visible”, “buds developed”, “signs of leaves”, “leaf expansion”, and “leaf complete” (Table 3). The four populations Daiba, Diamenar, Ngane (all Senegal) and Djigueri (Mauritania) had greater frequency of trees ( $\geq 25\%$ ) starting early leaf flushing (first day with “buds visible” and first day with “buds developed”) among the diploid populations (Fig. S1). These populations originate from dry sites where a positive monthly WAI0 occurs late in the year (Table 1).

Tetraploid populations showed differences from each other in senescence in both 2018 and 2019 at least concerning the first day with “10–50% brown or shed leaves” (senescence (i) in Table 3). Significant differences were also found in first day with “buds developed”, “leaflets visible”, and “leaf complete” (Table 3). The local population Ngane had early leaf flushing (first day with “buds visible” and first day with “buds developed”) among the tetraploid populations (Fig. S2).

The population differences in leaf flushing and senescence were also to some extent reflected in significant differences, among diploid populations in LD (i) and GP (i), and among tetraploid populations in both estimates of GP (Table 3).

### 3.5. Differences in flowering phases between ploidy levels and among populations

The mean day with dominance of fully developed flowers and withered flowers differed significantly between diploids and tetraploids in 2019, and was for the tetraploids  $269 \pm 4.7$  and  $291 \pm 3.1$ , respectively. For the diploids, the mean day with dominance of fully developed flowers and withered flowers was  $279 \pm 2.8$  and  $299 \pm 1.9$ , respectively (Table 4). No significant differences between



**Table 3**

Differences in leafing phenology between (a) diploid and tetraploid trees of *A. senegal* based on data from the five populations (Kidira, Ngane, Karofane, Kirane, Aite, Table 1) where diploid and tetraploid trees are present (*model 1* on the left) and (b) among populations analyzed separately in each of diploid and tetraploid populations respectively (*model 2* on the right). Variables where no year is specified were recorded in 2019.

Variables	Mean values				Statistical results								
					Ploidy levels (1)			Population tests (2)					
	Diploid	n	Tetraploid	n				Diploids			Tetraploids		
					Df	F value	P value	Df	F value	P value	Df	F value	P value
Senescence (i) (2018)	291 ± 1.5	55	291 ± 2.5	15	1	0.00	0.9751	13	4.13	< 0001***	6	10.13	< 0001***
Senescence (ii) (2018)	338.8 ± 0.8	55	335.8 ± 1.4	15	1	3.43	0.069	13	2.10	0.0154*	6	1.91	0.1311
Buds visible	127 ± 2.8	55	125 ± 4.0	15	1	0.39	0.537	13	2.80	0.0012**	6	2.37	0.0707
Buds developed	154 ± 3.3	55	151 ± 6.2	15	1	0.16	0.6912	13	2.50	0.0041**	6	6.65	0.0008**
Signs of leaves	203 ± 5.2	55	187 ± 7.3	15	1	5.98	0.0180*	13	2.18	0.0127*	6	2.48	0.0685
Leaflets visible	214 ± 5.6	55	203 ± 7.3	15	1	2.28	0.1408	13	1.71	0.0718	6	3.28	0.0314*
Leaf expansion	224 ± 5.7	55	226 ± 1.8	15	1	1.3	0.2624	13	3.18	0.0006**	6	0.34	0.8886
Leaf complete	229 ± 1.1	55	230 ± 1.8	15	1	0.21	0.6504	13	3.54	0.0001***	6	9.07	0.000***
Senescence (i) (2019)	301 ± 2.1	55	303 ± 4.2	15	1	0.15	0.6986	13	0.87	0.5867	6	3.45	0.0177*
Senescence (ii) (2019)	349 ± 2.9	55	346 ± 4.6	15	1	0.22	0.6426	13	0.77	0.6902	6	1.99	0.1947
Leaf development (LD (i))	101 ± 2.8	55	105 ± 4.4	15	1	0.59	0.4439	13	1.90	0.0335*	6	1.34	0.2878
Leaf development (LD (ii))	26 ± 5.1	55	43 ± 7.3	15	1	6.55	0.0136*	13	1.64	0.0796	6	2.21	0.096
Growing period (GP (i))	98 ± 5.7	55	114 ± 8.1	15	1	3.58	0.064	13	0.08	0.0087*	6	7.52	0.0003***
Growing period (GP (ii))	145 ± 6.03	55	164 ± 8.9	15	1	3.85	0.058	13	0.851	0.6064	6	21.59	0.0003***

LD (i): leaf development (i) number of days between “buds visible” and “leaf complete” LD (ii): leaf development (ii) number of days between “signs of leaves” and “leaf complete” GP (i): Growing period (i) number of days between “signs of leaves” and “10–50% brown shed leaves” GP (ii): Growing period (ii) number of days between “signs of leaves” and “> 50% brown shed leaves”. Asterisks indicate the level of significance; \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001. Least square means ± SE of the distribution and standard error, Df: degrees of freedom, n: number of trees for each level of ploidy. Asterisks indicate the level of significance; \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001; significant P value in bold.

**Table 4**

Differences in flowering phases between (a) diploid and tetraploid trees of *A. senegal* based on data from the five populations (Kidira, Ngane, Karofane, Kirane, Aite, Table 1) where diploid and tetraploid trees are present (*model 1* on the left) and (b) between populations analyzed separately in each of diploid and tetraploid populations respectively (*model 2* on the right).

Variables	Mean values				Statistical results								
	Diploid	n	Tetraploid	n	Ploidy levels (1)			Population tests (2)					
					Df	F value	P value	Diploids			Tetraploids		
								Df	F value	P value	Df	F value	P value
Flower buds (2018)	237 ± 2.2	55	238 ± 3.7	15	1	0.07	0.789	13	0.58	0.8677	6	0.58	0.7391
Fully developed flowers (2018)	257 ± 2.7	55	260 ± 4.0	15	1	0.45	0.505	13	0.49	0.9293	6	0.68	0.6704
Flowers withered (2018)	287 ± 1.5	55	284 ± 3.0	15	1	0.73	0.398	13	2.24	0.0101*	6	1.29	0.3086
Flowering length 2018	51 ± 2.4	55	45 ± 4.6	15	1	1.47	0.231	13	1.74	0.0571	6	0.61	0.7194
Flower buds (2019)	264 ± 2.8	55	254 ± 5.1	15	1	2.87	0.096	13	1.08	0.3855	6	7.49	0.0006**
Fully developed flowers (2019)	279 ± 2.8	55	269 ± 4.7	15	1	4.15	0.0466*	13	1.95	0.0298*	6	1.27	0.3182
Flowers withered (2019)	299 ± 1.9	55	291 ± 3.1	15	1	7.09	0.0104*	13	3.83	< 0001***	6	0.79	0.5896
Flowering length 2019	35 ± 2.3	55	36 ± 4.5	15	1	0.04	0.8488	13	0.91	0.5439	6	43.53	< 0001***

Least square means ± SE of the distribution and standard error, Df: degrees of freedom, n: number of trees for each level of ploidy. Asterisks indicate the level of significance; \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001.

ploidy levels were found for flowering phases in 2018.

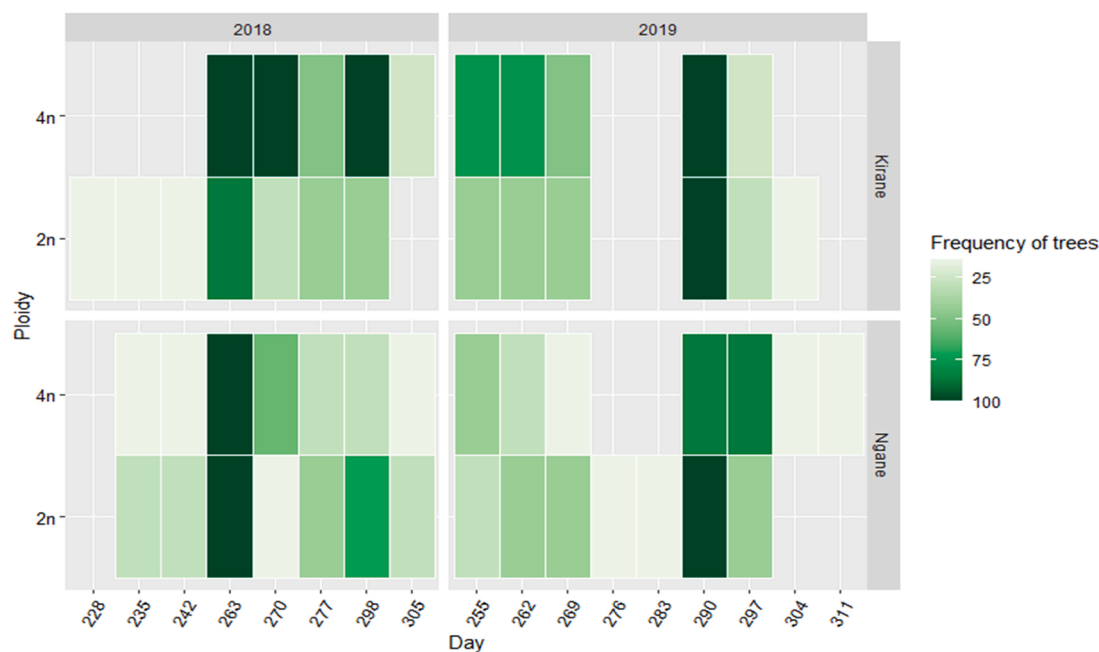
Among diploid populations, significant differences were found in first day with “withered flowers” in 2018 and 2019, and first day with dominance of “fully developed flowers” in 2019.

Among tetraploids populations, significant differences were found in the initiation of flower buds and the length of flowering period (FP) in 2019 (Table 4).

The similar time point for a high frequency of trees that reached “fully developed flowers” within the populations Kirane and Ngane suggested a period of overlap in flowering time between diploid and tetraploid trees (Fig. 5).

### 3.6. Differences in fruiting phases between ploidy levels and among populations

Significant differences were found between diploids and tetraploids as regards the day of year for the early fruiting stages in 2018 (“fruit initiation” and “10–50% developed fruits”) with diploids showing earlier fruit initiation and development at day  $263 \pm 0.8$  and



**Fig. 5.** Frequency of fully developed and likely fertile flowers among diploid and tetraploid groups of trees within the two populations Kirane and Ngane, respectively.

**Table 5**

Differences in fruiting phases between (a) diploid and tetraploid trees of *A. senegal* based on data from the five populations (Kidira, Ngane, Karofane, Kirane, Aite, Table 1) where diploid and tetraploid trees are present (*model 1* on the left) and (b) among populations analyzed separately in each of diploid and tetraploid populations respectively (*model 2* on the right).

Variables	Mean values				Statistical results								
					Ploidy levels (1)			Population tests (2)					
	Diploid	n	Tetraploid	n				Diploids			Tetraploids		
					Df	F value	P value	Df	F value	P value	Df	F value	P value
Fruit initiation 2018	263 ± 0.8	55	270 ± 1.5	15	1	19.30	< 0001***	13	2.36	0.0069**	6	16.44	< 0001***
10–50% fruits developed 2018	271 ± 1.4	55	276 ± 1.8	15	1	13.36	0.0005***	13	2.93	0.0008***	6	6.69	0.0006***
> 50% fruits developed 2018	286 ± 2.4	55	287 ± 5.5	15	1	0.02	0.8967	13	1.18	0.3147	4	2.51	0.3046
10–50% fruits ripe 2018	320 ± 0.5	55	320 ± 0.6	15	1	1.74	0.1930	13	5.4	< 0001***	6	1.7	0.1753
All fruits ripe 2018	328 ± 0.60	55	328 ± 0.87	15	1	0.10	0.7476	13	6.9	< 0001***	6	1.01	0.4492
Fruit initiation 2019	269 ± 3.6	55	270 ± 4.0	15	1	0.29	0.6060	11	2.63	0.012*	4	2.69	0.1803
10–50% fruits developed 2019	278 ± 5.3	55	280 ± 5.8	15	1	0.32	0.5840	11	3.96	0.0006***	4	1.103	0.4348
> 50% fruits developed 2019	289 ± 3.1	55	290 ± 3.7	15	1	0.33	0.5846	11	2.79	0.0081**	4	0.033	0.9968
10–50% fruits ripe 2019	318 ± 2.2	55	322 ± 3.4	15	1	2.28	0.1621	11	2.23	0.0307*	4	2.33E+28	< 0001***
All fruits ripe 2019	332 ± 1.3	55	338 ± 3.0	15	1	3.13	0.1072	11	1.13	0.3682	4	2.33E+27	< 0001***
Mean % trees making fruits 2018	97 ± 1.8	55	100 ± 2.3	15	1	1.5	0.2314	13	1.26	0.2838	6	1.00E+00	0.4326
Mean % trees making fruits 2019	34 ± 13.5	55	29 ± 16.0	15	1	0.11	0.7419	13	1.35	0.2341	6	20.31112	0.0023

Least square means ± SE of the distribution and standard error, Df: degrees of freedom, n: number of trees for each level of ploidy. Asterisks indicate the level of significance; \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001.

$271 \pm 1.4$ , respectively, while tetraploids showed fruit initiation and development at day  $270 \pm 1.5$  and  $276 \pm 1.8$ , respectively (Table 5). Variation among diploid populations was significant in the timing of all fruiting phases, except for “> 50% fruits developed” and “all fruits ripe” in 2018 and 2019 respectively (Table 5). In tetraploid populations, populations were only significantly different in the timing of their early fruiting phases (“fruit initiation” and “10–50% developed fruits”) and fruit ripening (“10–50% fruits ripe” and “all fruits ripe”) in 2018 and 2019, respectively. However, a low number of tetraploid trees had developed ripe fruits in 2019, which explained the higher significance among populations.

No significant differences were found between diploid and tetraploid trees, and among diploid populations in their success of developing ripened fruits in 2018 and 2019 (Table 5).

#### 4. Discussion

##### 4.1. Triggering factors in relation to phenological patterns

In the present study, *Acacia senegal* started shedding its leaves at the end of the rainy season. The trees remained almost leafless during the dry season, but buds and leaf development began before the first rainfall. Our finding of leafing initiation before rainfall is in line with another study on phenology of *A. senegal* in West Africa (Seghieri et al., 2012b) and with the general findings of pre-rain green up in the dry tropics from satellite images (Ryan et al., 2017). The findings are however in contrast to a previous study on phenology of *A. senegal* in Kenya (Omondi et al., 2016), where the initiation of leaves were found to occur at the onset of the rain. In contrast to our study the phenology of Kenyan *A. senegal* was bimodal and followed the rainfall patterns. In the dry tropics, the phenomenon of leafing before the rainy season may be triggered by factors such as photoperiodicity, temperature and air humidity (De Bie et al., 1998; Myers et al., 1998; Do et al., 2005; Seghieri et al., 2012b; Di Lucchio et al., 2018), but the process is still poorly understood. When investigating the phenology of *A. tortilis* subsp. *raddiana* in the Sahelian zone of Senegal, Do et al. (2005) suggested that the relative humidity of the air in connection with low pressures in the Inter-Tropical Convergence Zone (ITCZ) is a determinant factor of early leaf flushing in this region. In a greenhouse experiment, Di Lucchio et al. (2018) found that flushing in *A. digitata* was influenced by the day-length with the lowest degree of meristematic activity observed in the short day-length treatment. The environmental factors that influence our observed leafing in *A. senegal* are still not clear. Thus, further investigations under controlled conditions testing effects of environmental factors (temperature, day-length, drought) on leaf phenology of *A. senegal* will be needed.

The completion of leaf development as well as the development of flowers and fruits during the rainy season attests to the importance of a match between phenology and local seasonality, in relation to changing conditions in soil water availability (Borchert, 1994; Okullo et al., 2004; Omondi et al., 2016). Tree species from dry tropical areas mostly use the favorable, but often very short rainy seasons for leaf development to accumulate sufficient photosynthates and initiate reproduction before the soil moisture starts to fall in the subsequent drier season (Singh and Kushwaha, 2006). The results also suggest that rainfall may trigger flowering (and fruiting) in *A. senegal* (Tandon et al., 2001; Omondi et al., 2016; but see also Tybirk, 1993), and allows fruit growth and maturation (Lieberman, 1982).

While climatic variables are potential factors that trigger leaf flushing in tropical drylands, the ability to access deep soil moisture (Borchert, 1994) or groundwater (Do et al., 2005, 2008), and the storage of water in tree stems (Borchert, 1994; Myers et al., 1998) may also be important for phenology. In deep-rooting woody plants, the strategy of leafing before the start of the rainy season indicates other available water resources providing a fully operating photosynthetic apparatus under favorable conditions (De Bie et al., 1998). In addition, seasonal changes in tree water status with reduction of water loss during leaf shedding in combination with available soil water enabled rehydration of stem tissues and subsequent flowering or flushing during the dry season in tropical dry forest trees (Borchert, 1994). Leaf flushing during the dry season has been found in *Adansonia* species in Madagascar, which was related to the stem water reserves (Chapotin et al., 2005).

##### 4.2. Genetic variation among populations

In the present paper we found significant genetic variation in leafing phenology among populations while grown at the same site in Senegal. This was the case for both diploid and tetraploid trees. In general, populations of *A. senegal* with early leaf flushing had a longer growing period. It can be speculated if such early leafing trees can resist water loss and/or if they show higher drought tolerance to sustain the period from leaf flushing to start of the rainy season. In our study we found that the early flushing trees in general performed better in growth. The early development of leaf buds might be an important adaptation to areas with highly variable start of the rainy season making it possible for the trees to initiate photosynthesis fast.

The genetic differences in leafing phenology among populations suggest presence of local adaptation to seasonality in *A. senegal*. However, in our study we found that it was diploid trees from sites with a late arriving rainy season that developed leaves *earliest* in the year. This is against a simple hypothesis of trees from areas with late arriving rain having late leaf flushing. No significant relationships were found between leafing phases and other climatic variables at the origins. Still, the annual African monsoon looses moisture from the ocean toward the north, and sites with late arrival of the rainy season are therefore also in general sites with low annual rainfall. This is reflected by WAI0<sub>i</sub> being negatively correlated with the annual mean precipitation and positively correlated with the latitude of the origins: sites with high WAI0<sub>i</sub> (late arriving rainy season) are also in general drier. So even though the relationship between phenology and annual mean precipitation is not significant in our analysis, there is an inherent relationship between timing of rainy season and amount of precipitation.

The significant, but negative correlation between WAI0<sub>i</sub> and leaf development in the common garden highlights the importance of

identifying the environmental cues that control leafing phenology and the associated physiological mechanisms. Since bud and leaf development commence before the start of the rainy season, it is tempting to suggest a role for the small variations in daylength observed close to the equator (Di Lucchio et al., 2018). However, the pattern we observe would be possible only if bud development is triggered by longer days before the spring equinox. Buds become visible shortly after the spring equinox, making this a possibility, but it would require knowledge of leaf phenology at the sites of origin, or studies of leaf phenology under controlled light regimes to truly verify this hypothesis.

A better insight into the triggering factors is crucial in order to predict how movement of seed sources will influence their phenology and thereby their ability to grow in non-native environments. The latter is a pre-requisite for development of smart seed transfer guidelines (assisted migration) as a mean to mitigate changing growing conditions related to global warming. Since recent studies in temperate forests has revealed that phenology can also be influenced by maternal effects (Bräutigam et al., 2013), it is also important to take this option into consideration in further studies of mechanisms controlling the phenology.

The observation of differences among populations in phenology should be seen in context of Diatta et al. (2021a) that find a clear indication of local adaptation to dry conditions, where *A. senegal* provenances from dry sites performed relatively better in terms of growth at a dry site Dahra (the same common garden used in the present study) compared to provenances from wet sites that performed relatively better when grown at a wetter site. Differences in leafing phenology likely explains some of the differences in growth, and additional investigations on factors triggering leafing in *A. senegal* and their associated physiological mechanisms are important.

We did not find any relationships between timing of senescence and climate at sites of origins. This contrasts previous studies of African tropical species such as *A. digitata* (Di Lucchio et al., 2018; Bamba et al., 2019) and *P. biglobosa* (Ouedraogo, 2015). The studies of *A. digitata* demonstrated that the timing of senescence is under genetic control and was related to the climatic parameters at the site of origin, and the senescence of *P. biglobosa* populations followed a latitudinal gradient. In general, genetic differences in phenology can reflect adaptation to prevailing climates. In the context of future climate change that may challenge current adaptation of trees to their local growth conditions (Ouedraogo, 2014), species will be able to change phenology through phenotypic plasticity or natural selection. The relationship between timing of senescence and climatic parameters at the site of origin supports that the patterns are generated by local adaptation (Bamba et al., 2019). In order to enhance knowledge on the adaptation of *A. senegal* to different climatic conditions, more investigations over successive years and in different geographic locations are needed.

#### 4.3. Genetic variation between ploidy levels

Although it is generally accepted that *A. senegal* is a heteroploid species with different levels of ploidy and that different cytotypes can either co-exist in the same populations or be found in pure populations (Assoumane et al., 2013; Odee et al., 2015; Diallo et al., 2015), it is still not clear how well the cytotypes are delimited and what mechanisms reinforce the potential boundaries. In the present study we found differences between diploids and tetraploids in some leaf phenological characters (the first signs of leaves and the speed of leaf development). Although tetraploids started to flush earlier, diploids had a significantly faster leaf development. As regards flowering and fruiting, flower development and senescence occurred earlier in tetraploids than in diploids, while differences in fruit development between the two cytotypes were non-significant. The phenological differences between cytotypes suggest that ploidy level may be of importance for the fitness of *A. senegal*. Since the leaf phenological phases “sign of leaves” and “complete leaves” appeared respectively before and after the rainy season, and diploids had faster leaf development despite their late leaf initiation, we can hypothesize that diploid and tetraploid individuals employ different water-use strategies to adapt to contrasting environments. An explanation could be a better performance of *A. senegal* polyploids under drought stress (Diallo et al., 2016), perhaps because tetraploids display higher water use efficiency (WUE<sub>i</sub>) compared to diploid individuals (Diatta et al., 2021b). It has been demonstrated that under conditions of changing water availability, deciduous species such as *A. senegal* do not maintain a consistent water use strategy (Gebrekirstos et al., 2011). In general, plants that display higher or lower WUE under drought conditions, may exhibit contrasting water use strategies in wet conditions (Gebrekirstos et al., 2011; Gray et al., 2013). Further investigations in both dry and growing seasons will be needed to clarify the differences between diploid and polyploids in their water use strategies.

Diploid and tetraploids differed in their flowering in 2019, where tetraploid individuals had fully developed flowers earlier and shorter flowering time than diploid individuals. However, the same patterns were not observed in 2018 where the two ploidy levels seemed to flower simultaneously. However, even in the case of overlapping flowering time, other pre-zygotic factors are likely to limit gene flow between ploidy levels (Diallo et al., 2021).

## 5. Conclusion

This study is to our knowledge the first to investigate the variation in phenology among different origins of *A. senegal*. It showed that phenology in *A. senegal* is to some extent under genetic control, but the environmental factors that trigger leafing phenology and create variation among populations when grown in a common garden are not yet known and need further investigations. The results revealed apparent local adaptation with early budburst, long growing season and better performance as characteristics of populations from dry areas. To face the ongoing climatic changes, further research on physiological mechanisms in relation to the leaf life-span in *A. senegal* will be needed for future use in conservation programs in Africa.

## Funding

This study was funded by the Islamic Development Bank (IsDB), Saudi Arabia, Ph.d. Merit Scholarship program grant number

600032772, University of Copenhagen, Denmark.

## 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 are publicly available through the University of Copenhagen - Electronic Research Data Archive (ERDA): <https://erda.ku.dk/archives/56d00a9c0e66b33619c3db45afd239af/published-archive.html>.

## Acknowledgements

We acknowledge the funding support provided by the Islamic Development Bank (IsDB), Saudi Arabia, under the Ph.D. Merit Scholarship program grant number 600032772, and by the University of Copenhagen, Denmark. We are thankful to Ibra Padane from Institut Sénégalais de Recherches Agricoles/Centre National de Recherches Forestières (ISRA/CNRF) for the data collection in Senegal, and to Håkan Torbern Tagesson and Rasmus Fensholt from the Department of Geosciences and Natural Resource Management at University of Copenhagen for providing weather data from Dahra.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01957](https://doi.org/10.1016/j.gecco.2021.e01957).

## References

- Assoumane, A., Zoubeirou, A.M., Rodier-Goud, M., Favreau, B., Bezançon, G., Verhaegen, D., 2013. Highlighting the occurrence of tetraploidy in *Acacia senegal* (L.) Willd. and genetic variation patterns in its natural range revealed by DNA microsatellite markers. *Tree Genet. Genomes* 9 (1), 93–106. <https://doi.org/10.1007/s11295-012-0537-0>.
- Bamba, H., Korbo, A., Sanou, H., Ræbild, A., Kjær, E.D., Hansen, J.K., 2019. Genetic differentiation in leaf phenology among natural populations of *Adansonia digitata* L. follows climatic clines. *Glob. Ecol. Conserv.* 17, e00544 <https://doi.org/10.1016/j.gecco.2019.e00544>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Borchert, R., 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75 (5), 1437–1449.
- Bräutigam, K., Vining, K.J., Lafon-Placette, C., 2013. Epigenetic regulation of adaptive responses of forest tree species to the environment. *Ecol. Evol.* 3, 399–415.
- Chapotin, S.M., Razanameharizaka, J.H., Holbrook, N.M., 2005. Baobab trees (*Adansonia*) in Madagascar use stored water to flush new leaves but not to support stomatal opening before the rainy season. *New Phytol.* 169 (3), 549–559. <https://doi.org/10.1111/j.1469-8137.2005.01618.x>.
- Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A., Schwartz, M.D., 2007. Shifting plant phenology in response to global change. *Trends Ecol. Evol.* 22 (7), 357–365. <https://doi.org/10.1016/j.tree.2007.04.003>.
- De Bie, S., Ketner, P., Paasse, M., Geerling, C., 1998. Woody plant phenology in the West Africa savanna. *J. Biogeogr.* 25 (5), 883–900. <https://doi.org/10.1046/j.1365-2699.1998.00229.x>.
- Di Lucchio, L.M., Fensholt, R., Markussen, B., Ræbild, A., 2018. Leaf phenology of thirteen African origins of baobab (*Adansonia digitata* (L.)) as influenced by daylength and water availability. *Ecol. Evol.* 8 (22), 11261–11272. <https://doi.org/10.1002/ece3.4600>.
- Diallo, A.M., Nielsen, L.R., Hansen, J.K., Ræbild, A., Kjær, E.D., 2015. Study of quantitative genetics of gum arabic production complicated by variability in ploidy level of *Acacia senegal* (L.) Willd. *Tree Genet. Genomes* 11 (4). <https://doi.org/10.1007/s11295-015-0902-x>.
- Diallo, A.M., Nielsen, L.R., Kjær, E.D., Petersen, K.K., Ræbild, A., 2016. Polyploidy can confer superiority to West African *Acacia senegal* (L.) Willd. trees. *Front. Plant Sci.* 7 (June), 1–10. <https://doi.org/10.3389/fpls.2016.00821>.
- Diallo, A.M., Kjær, E.D., Ræbild, A., Nielsen, L.R., 2021. Coexistence of diploid and polyploid *Acacia senegal* (L. Willd.) and its implications for interploidy pollination. *New For.*
- Diatta, O., Sarr, M.S., Hansen, J.K., Diallo, A.M., Nielsen, L.R., Ræbild, A., Kjær, E.D., 2021a. Survival and growth of *Acacia senegal* (L.) Willd. (*Senegalia senegal*) provenances depend on the rainfall at the site of origin. *Ann. For. Sci.* <https://doi.org/10.1007/s13595-021-01098-5>.
- Diatta, O., Kjær, E.D., Diallo, A.M., Nielsen, L.R., Novak, V., Sanogo, D., Laursen, K.H., Hansen, J.K., Ræbild, A., 2021b. Leaf morphology and stable isotope ratios of carbon and nitrogen in *Acacia senegal* (L.) Willd. trees vary with climate at the geographic origin and ploidy level. *Trees*, 0123456789. <https://doi.org/10.1007/s00468-021-02206-8>.
- Do, F.C., Goudiaby, V.A., Gimenez, O., Diagne, A.L., Diouf, M., Rocheteau, A., Akpo, L.E., 2005. Environmental influence on canopy phenology in the dry tropics. *For. Ecol. Manag.* 215 (1–3), 319–328. <https://doi.org/10.1016/j.foreco.2005.05.022>.
- Do, F.C., Rocheteau, A., Diagne, A.L., Goudiaby, V., Granier, A., Lhomme, J.P., 2008. Stable annual pattern of water use by *Acacia tortilis* in Sahelian Africa. *Tree Physiol.* 28 (1), 95–104. <https://doi.org/10.1093/treephys/28.1.95>.
- Eamus, D., Prior, L., 2001. Ecophysiology of trees of seasonally dry tropics: comparisons among phenologies. *Adv. Ecol. Res.* 145, 87–99. [https://doi.org/10.1016/s0065-2504\(01\)32012-3](https://doi.org/10.1016/s0065-2504(01)32012-3).
- Fagg, C., Allison, G., 2004. *Acacia senegal* and the Gum Arabic Trade. Monograph and Annotated Bibliography. Tropical Forestry Papers No. 42. Oxford Forestry Institute, Oxford. [https://doi.org/10.1663/0013-0001\(2005\)059\[0405:dfabre\]2.0.co;2](https://doi.org/10.1663/0013-0001(2005)059[0405:dfabre]2.0.co;2).
- Gebrekirstos, A., van Noordwijk, M., Neufeldt, H., Mitlöhner, R., 2011. Relationships of stable carbon isotopes, plant water potential and growth: an approach to assess water use efficiency and growth strategies of dry land agroforestry species. *Trees* 25 (1), 95–102. <https://doi.org/10.1007/s00468-010-0467-0>.
- Göttsche, F.M., Olesen, F.S., Trigo, I.F., Bork-Unkelbach, A., Martin, M.A., 2016. Long term validation of land surface temperature retrieved from MSG/SEVIRI with continuous in-situ measurements in Africa. *Remote Sens.* 8 (5). <https://doi.org/10.3390/rs8050410>.
- Gray, A., Odee, D., Cavers, S., Wilson, J., Telford, A., Grant, F., Diouf, M., Ochieng, J., Grant, H., Stott, A., 2013. Does geographic origin dictate ecological strategies in *Acacia senegal* (L.) Willd.? Evidence from carbon and nitrogen stable isotopes. *Plant Soil* 369 (1–2), 479–496. <https://doi.org/10.1007/s11104-013-1593-4>.



- Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H., 2014. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *Int. J. Climatol.* 34, 623–642. <https://doi.org/10.1002/joc.3711>.
- Khanduri, V.P., 2014. Annual variation in floral phenology and pollen production in *Lagerstroemia speciosa*: an entomophilous tropical tree. *Songklanakarin. J. Sci. Technol.* 36 (4), 389–396.
- Kyalangalilwa, B., Boatwright, J.S., Daru, B.H., Maurin, O., van der Bank, M., 2013. Phylogenetic position and revised classification of *Acacia* s.l. (Fabaceae: Mimosoideae) in Africa, including new combinations in *Vachellia* and *Senegalia*. *Bot. J. Linn. Soc.* 172 (4), 500–523. <https://doi.org/10.1111/boj.12047>.
- Larwanou, M., Raebild, A., Issa, R., Kjær, E.D., 2010. Performance of *Acacia senegal* (L.) Willd provenances in dryland Savannah of Niger. *Silvae Genet.* 59 (5), 210–218. <https://doi.org/10.1515/sg-2010-0025>.
- Lieberman, D., 1982. Seasonality and phenology in a dry tropical forest in Ghana. *J. Ecol.* 70 (3), 791–806.
- Lim, O.P., Kim, H.J., Nam, H.G., 2007. Leaf senescence. *Annu. Rev. Plant Biol.* 58, 115–136. <https://doi.org/10.1146/annurev.arplant.57.032905.105316>.
- Milla, R., Castro-Díez, P., Maestro-Martínez, M., Montserrat-Martí, G., 2005. Costs of reproduction as related to the timing of phenological phases in the dioecious shrub *Pistacia lentiscus* L. *Plant Biol.* 8 (1), 103–111. <https://doi.org/10.1055/s-2005-872890>.
- Myers, B.A., Williams, R.J., Fordyce, I., Duff, G.A., Eamus, D., 1998. Does irrigation affect leaf phenology in deciduous and evergreen trees of the savannas of northern Australia? *Austral Ecol.* 23 (4), 329–339. <https://doi.org/10.1111/j.1442-9993.1998.tb00738.x>.
- Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U., Poot, P., Purugganan, M.D., Richards, C.L., Valladares, F., van Kleunen, M., 2010. Plant phenotypic plasticity in a changing climate. *Trends Plant Sci.* 15 (12), 684–692. <https://doi.org/10.1016/j.tplants.2010.09.008>.
- Odee, D.W., Wilson, J., Omondi, S., Perry, A., Cavers, S., 2015. Rangeland ploidy variation and evolution in *Acacia senegal*: a north-south divide? *AoB PLANTS* 7 (1). <https://doi.org/10.1093/aobpla/plv011>.
- Okullo, J.B.L., Hall, J.B., Obua, J., 2004. Leafing, flowering and fruiting of *Vitellaria paradoxa* subsp. *nilotica* in savanna parklands in Uganda. *Agrofor. Syst.* 60, 77–91.
- Omondi, S.F., Odee, D.W., Ongamo, G.O., Kanya, J.I., Khasa, D.P., 2016. Synchrony in leafing, flowering, and fruiting phenology of *Senegalia Senegal* within Lake Baringo Woodland, Kenya: implication for conservation and tree improvement. *Int. J. For. Res.* 2016. <https://doi.org/10.1155/2016/6904834>.
- Ouedraogo, M., 2015. Improving and conserving sahelian fruits trees: a case study of *Parkia biglobosa* (Jacq.) Benth. Dissertation, Department of Geosciences and Natural Resource Management, Faculty of Science, University of Copenhagen.
- Panchen, Z.A., Primack, R.B., Gallinat, A.S., Nordt, B., Stevens, A.D., Du, Y., Fahey, R., 2015. Substantial variation in leaf senescence times among 1360 temperate woody plant species: implications for phenology and ecosystem processes. *Ann. Bot.* 116 (6), 865–873. <https://doi.org/10.1093/aob/mcv015>.
- Parnes, C., 2006. Ecological and evolutionary responses to recent climate change. *Ann. Rev. Ecol. Syst.* 37, 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>.
- Polgar, C., Gallinat, A., Primack, R.B., 2014. Drivers of leaf-out phenology and their implications for species invasions: insights from Thoreau's Concord. *New Phytol.* 202 (1), 106–115. <https://doi.org/10.1111/nph.12647>.
- R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (URL). (<https://www.R-project.org/>).
- Raddad, E.A.Y., 2007. Ecophysiological and genetic variation in seedling traits and in first-year field performance of eight *Acacia senegal* provenances in the Blue Nile, Sudan. *New For.* 34 (3), 207–222. <https://doi.org/10.1007/s11056-007-9049-4>.
- Raddad, E.A.Y., Luukkanen, O., 2006. Adaptive genetic variation in water-use efficiency and gum yield in *Acacia senegal* provenances grown on clay soil in the Blue Nile region, Sudan. *For. Ecol. Manag.* 226 (1–3), 219–229. <https://doi.org/10.1016/j.foreco.2006.01.036>.
- Raddad, E.Y., Luukkanen, O., Salih, A.A., Kaarakka, V., Elfadl, M.A., 2006. Productivity and nutrient cycling in young *Acacia senegal* farming systems on vertisol in the Blue Nile region, Sudan. *Agrofor. Syst.* 68 (3), 193–207. <https://doi.org/10.1007/s10457-006-9009-6>.
- Ræbild, A., Graudal, L., Ouedraogo, M., 2003a. Evaluation of a provenance trial of *Acacia senegal* at Gonsé, Burkina Faso. Trial no. 12 in the arid zone series. Results and Documentation No. 5. Danida Forest Seed Centre, Humlebaek, Denmark, p. 14.
- Ræbild, A., Graudal, L., Cesar, P., Lima, F., 2003b. Evaluation of a provenance trial of *Acacia senegal* at Dori, Burkina Faso: trial no. 8 in the arid zones series. DFSC Results and Documentation No. 3. Danida Forest Seed Centre, Humlebaek, Denmark.
- Ræbild, A., Diallo, B.O., Graudal, L., Dao, M., Sanou, J., 2003c. Evaluation of a provenance trial of *Acacia senegal* at Djibo, Burkina Faso. Trial no. 5 in the arid zone series. Results and Documentation No. 7. Danida Forest Seed Centre, Humlebaek, Denmark.
- Ræbild, A., Larsen, A.S., Jensen, J.S., Ouedraogo, M., de Groot, S., van Damme, P., Bayala, J., Diallo, B.O., Sanou, H., Kalinganire, A., Kjaer, E.D., 2010. Advances in domestication of indigenous fruit trees in the West African Sahel. *New For.* 41 (3), 297–315. <https://doi.org/10.1007/s11056-010-9237-5>.
- Rathcke, B., Lacey, E.P., 1985. Phenological patterns of terrestrial plants. *Ann. Rev. Ecol. Syst.* 16, 179–214. <https://doi.org/10.1146/annurev.es.16.110185.001143>.
- Revelle, W., 2019. psych: Procedures for Personality and Psychological Research. Northwestern University, Evanston, Illinois, USA. Version = 1.9.12. (<https://CRAN.R-project.org/package=psych>).
- Ryan, C.M., Williams, M., Grace, J., Woollen, E., Lehmann, C.E.R., 2017. Pre-rain green-up is ubiquitous across southern tropical Africa: implications for temporal niche separation and model representation. *New Phytol.* 213 (2), 625–633. <https://doi.org/10.1111/nph.14262>.
- Seghier, J., Carreau, J., Boulain, N., de Rosnay, P., Arjounin, M., Timouk, F., 2012b. Is water availability really the main environmental factor controlling the phenology of woody vegetation in the central Sahel? *Plant Ecol.* 213 (5), 861–870. <https://doi.org/10.1007/s11258-012-0048-y>.
- Singh, K.P., Kushwaha, C.P., 2006. Diversity of flowering and fruiting phenology of trees in a tropical deciduous forest in India. *Ann. Bot.* 97 (2), 265–276. <https://doi.org/10.1093/aob/mcj028>.
- Tagesson, T., Fensholt, R., Guirio, I., Rasmussen, M.O., Huber, S., Mbow, C., Garcia, M., Horion, S., Sandholt, I., Holm-Rasmussen, B., Götsche, F.M., Ridler, M.E., Olén, N., Lundgaard Olsen, J., Ehammer, A., Madsen, M., Olesen, F.S., Ardö, J., 2015. Ecosystem properties of semiarid savanna grassland in West Africa and its relationship with environmental variability. *Glob. Chang. Biol.* 21 (1), 250–264. <https://doi.org/10.1111/gcb.12734>.
- Tandon, R., Shivanna, K.R., Mohan Ram, H.Y., 2001. Pollination biology and breeding system of *Acacia senegal*. *Bot. Linn. Soc.* 135 (3), 251–262. <https://doi.org/10.1006/boj.2000.0401>.
- Tian, F., Wigneron, J.P., Ciais, P., Chave, J., Ogée, J., Peñuelas, J., Ræbild, A., Domec, J.C., Tong, X., Brandt, M., Mialon, A., Rodriguez-Fernandez, N., Tagesson, T., Al-Yaari, A., Kerr, Y., Chen, C., Myneni, R.B., Zhang, W., Ardö, J., Fensholt, R., 2018. Coupling of ecosystem-scale plant water storage and leaf phenology observed by satellite. *Nat. Ecol. Evol.* 2 (9), 1428–1435. <https://doi.org/10.1038/s41559-018-0630-3>.
- Tyrbirk, K., 1993. Pollination, breeding system and seed abortion in some African acacias. *Bot. J. Linn. Soc.* 112, 107–137.
- Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.
- Wu, C., Gough, C.M., Chen, J.M., Gonsamo, A., 2013. Evidence of autumn phenology control on annual net ecosystem productivity in two temperate deciduous forests. *Ecol. Eng.* 60, 88–95. <https://doi.org/10.1016/j.ecoleng.2013.07.019>.