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Original Research Article

Genetic differentiation in leaf phenology among natural populations of *Adansonia digitata* L. follows climatic clines

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ABSTRACT

Leafing phenology is an important component of climatic adaptation in semi-arid regions. The questions are to what extent phenology is under genetic control and represent adaptation to local climates? In the present study, we compare leaf phenology among *Adansonia digitata* L. trees of 27 different origins from West and East Africa and test if the differences follow climatic clines. Timing of bud burst was largely synchronized with the start of rainy season, but some few individual trees showed bud burst before the first rain. Timing of leaf senescence was under genetic control with substantial differences among origins. The timing of senescence was for some origins at the end of rainy season and for some in the beginning of the dry season. Differences among origins in timing of leaf senescence were related to the variation in drought just before- and in the first months of the rainy season at the sites of origin. Populations from drier sites had the earliest leaf shed at the common test site indicating that trees have been adapted to the prevailing climatic conditions at the sites of origin. We discuss the results in the light of possible triggering factors.
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1. Introduction

Tropical trees in many arid and semi-arid environments with a marked seasonality in rainfall have phenology synchronized to the periods of humidity and aridity. It most likely reflects that timing of phenological events is crucial for survival and in arid environments, and that selection therefore works against genotypes that are out-of-tune with the season. For example, setting or maintaining leaves in the dry season can lead to excessive loss of water, leading to leaf dieback and loss, depletion of nutrients and carbohydrates due to the loss of leaves and other drought associated damages such as xylem cavitation.

For tropical deciduous tree species, investigations *in situ* have suggested that temperature, photoperiod, soil water availability, tree water status, air humidity or vapor pressure deficit influence the initiation of the leaf phenology (e.g. Njoku, 1964; Chidumayo, 2001; Borchert et al., 2005; Do et al., 2005; Seghieri et al., 2012). In tropical Africa, satellite imagery demonstrates a pre-rain greening of trees, which suggests that phenology may be triggered by changes in photoperiod or an

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increase in solar irradiation (Ryan et al., 2017). A greenhouse experiment, where *Adansonia digitata* L. (African baobab) populations were subjected to combinations of water stress- and day-length treatments, showed that leaf flushing was depending on both day-length and water regime and that population responded differently on the water regime (Di Lucchio et al., 2018). Studies of genetic variation in phenology of tropical trees of temporal dry zones are however rare (Ræbild et al., 2011). Therefore, it is not clear whether reported differences in phenology are purely phenotypic reactions to varying environmental conditions, or whether there are genetic differences between origins, reflecting adaptation to the prevailing climate. This is a serious lack of knowledge, as climate change may challenge a current adaptation of trees to their local growth conditions (Ouedrago, 2014). Sub-Saharan Africa will likely face increased annual temperatures between 2 and 6 °C during the next century. The development in annual precipitation is more uncertain (Niang et al., 2014), but there is a risk for shorter rainy seasons with extreme precipitation in West Africa (Sylla et al., 2016).

If there are large genetic differences in phenology reflecting adaptation to prevailing climates, it will lead to the question whether species will be able to cope with rapid changed in climate by changing phenology through phenotypic plasticity or natural selection. It will also stress the need for gene conservation to retain genetic diversity. If the phenotypic plasticity and adaptation potential of the species is considered poor, an alternative will be to actively increase genetic diversity through assisted migration (e.g. Aitken and Bemmels, 2016; Lobo et al., 2018). Studies of genetic variation in phenology are therefore highly needed to guide management of plant genetic resources.

The aim of this study is contribution to a better understanding of tropical tree phenology, using the *A. digitata* as a study species. We examine the variability in leaf phenology of *A. digitata* originating from different geographic and climatic zones, and test if the differences among origins follow geographical or climatic clines. The hypothesis is that differences between sites of origin are reflected in differences in leaf phenology among the origins as result of local adaptation. To study this, we take advantage of a common garden trial with a unique pool of genotypes representing a large part of the distribution area.

A. digitata (African baobab) belongs to the family of *Malvaceae* (Baum, 1995) and is widely distributed in the driest parts of the Savannas of West Africa, East Africa and South East Africa. Present populations of West Africa, East and South Africa are isolated from each other due to a gap in Central Africa (Wickens, 1982; Sidibé and Williams, 2002). The distribution of *A. digitata* is mainly associated with precipitation and temperature rather than soil (Sanchez et al., 2010). The species is often found in smaller groups or as single trees mainly due to human influence in West Africa or wildlife in East and South East Africa (Dhillion and Gustad, 2004; Assogbadjo et al., 2005; Duvall, 2007; Venter and Witkowski, 2010; Larsen, 2010).

A. digitata is highly adapted to semi-arid areas with frequent wild fires with its thick bark and thick fruit shells (Kempe et al., 2018). In natural populations, *A. digitata* sheds its leaves during the start of the dry season and flushes new leaves towards the end of the dry season (Sidibé and Williams, 2002; Assogbadjo et al., 2005), but some genotypes has been reported to retain leaves during the dry season (Gebauer and Luedeling, 2013).

A. digitata is tetraploid. Seed and pollen of the species is mainly dispersed by fruit bats (Baum, 1995). Genetic marker studies indicate regional population structures and a modest gene flow (Kyndt et al., 2009; Larsen, 2010).

A. digitata is a priority species for domestication in several African countries (Gebauer et al., 2016) and is of high importance for the food security in Africa providing minerals, vitamins and proteins also in years with famine (Yazzie et al., 1994; Nordeide et al., 1996; Sidibé et al., 1998; Glew et al., 1997; Diop et al., 2005; Parkouda et al., 2009; Gebauer et al., 2016) as well as medicine and fibers for ropes (Owen, 1970; Diop et al., 2005).

2. Materials and methods

2.1. Plant material and experiment

Leaf phenology was studied among 27 origins in a field trial at Samanko in Mali (12.53 N, 8.07 W). The origins were from 11 East and West African countries representing widely different annual rainfalls ranging from 260 to 1200 mm (Table 1). The origins represented baobab populations from both North and South of the Equator (Fig. 1), and each population was represented by plants from seeds collected from approximately 20 open pollinated mother trees and mixed in equal proportions (10 seeds per sampled mother tree). Seedlings were germinated and raised in the nursery at the Regional Centre of Agronomic Research of Sotuba (Institute of Rural Economy, Bamako, Mali) from July 2007. The 1-year-old seedlings were planted in the field in August 2008 in a randomized block design with 4 replications and where each population was represented by one to five non-contiguous randomized 4-tree-plots in each replication. The trees of each population were chosen randomly among the seedlings raised from the seed mix of the 20 open pollinated mother trees. The spacing between trees was 2 × 2 m. The long-term aim of the trial was to study the variation among African Baobab populations in their growth and development. Annual precipitation estimates for the field trial site was 781 mm and 630 mm in 2012 and 2013, respectively, with a long dry season extending from November to April (Fig. 2). Average monthly temperatures in 2012 and 2013 ranged between 21.4 and 32.8 °C based on gridded climate estimates from the University of East Anglia Climatic Research Unit (Jones and Harris, 2014; Harris et al., 2014). The growth of the plants from May 2009 to May 2011, and survival in the nursery are reported in Korbo et al. (2012), while the present study reports the variation in phenology in 2012 and 2013 among the different origins.

Table 1
Origins included in the field trial.

No.	Origin	Country	Latitude (°)	Longitude (°)	Daylength diff. (h)[a]	Annual rainfall	LSM senescence[b]	Std. err.	LSM senescence[c]	Std. err.	N replications 2012 and 2013	N trees 2012	N trees 2013
1	North Kordofan	Sudan	–	–		–	249	13	261	13	2	9	9
2	Bandia	Senegal	14.62	−17.03	1.5	516	268	7	286	7	4	36	32
3	Komodiguili	Mali	14.40	−3.40	1.4	498	271	7	288	8	3	32	30
4	Samé	Mali	14.30	−11.65	1.4	702	274	7	294	7	4	35	31
5	Kourougué	Mali	14.17	−9.12	1.4	633	273	6	289	7	3	42	39
6	South Kordofan	Sudan	13.60	29.97	1.4	275	255	9	277	10	3	18	15
7	Nabougou	Mali	13.27	−5.90	1.3	676	289	11	300	10	3	13	13
8	Zambougou	Mali	13.15	−6.50	1.3	685	291	7	311	8	2	31	25
9	Maradi	Niger	13.13	8.50	1.3	512	284	7	297	8	3	31	29
10	Torodi	Niger	13.12	1.78	1.3	574	273	7	287	8	3	29	28
11	Kolangal	Burkina Faso	12.95	0.93	1.3	682	276	7	294	7	3	34	34
12	Parc W	Niger	12.42	2.32	1.2	749	293	8	304	8	3	23	23
13	Nobéré	Burkina Faso	11.55	−1.20	1.1	857	325	9	341	10	3	17	16
14	Koumadiobo	Mali	11.50	−6.92	1.1	998	289	8	301	9	3	26	26
15	Péni	Burkina Faso	10.82	−4.60	1.1	1052	294	6	303	7	4	39	37
16	Boukoumbé	Benin	10.27	1.32	1.0	1118	314	19	328	18	1	4	4
17	Lomé	Togo	6.15	0.97	0.6	1091	311	7	329	8	4	28	26
18	Kibwezi	Kenya	−2.55	38.00	0.2	636	254	7	270	7	4	34	34
19	Kilimanjaro	Tanzania	−3.45	37.53	0.3	1155	264	8	284	8	3	27	27
20	Dodoma	Tanzania	−5.93	35.13	0.6	557	239	8	262	8	4	26	26
21	Rivage	Tanzania	−6.62	37.37	0.6	941	269	12	296	12	2	11	10
22	Urban Morogoro	Tanzania	−6.67	37.60	0.7	822	257	11	268	11	3	12	11
23	Rural Morogoro	Tanzania	−6.78	37.73	0.7	822	268	12	285	12	3	10	7
24	Iringa	Tanzania	−7.55	36.43	0.7	1057	252	8	270	8	3	24	18
25	Rumphi	Malawi	−11.00	34.00	1.1	1145	238	7	253	8	3	32	30
26	Mangochi	Malawi	−17.00	35.00	1.7	998	261	6	277	7	4	43	41
27	Manica	Mozambique	−17.03	33.32	1.7	873	248	7	263	7	4	36	32

[a] Difference in hour between longest and shortest day of the year. Estimates of daylength based on the equation of Forsythe et al. (1995) with sunrise/sunset value p = 0.8333.
[b] Least square mean (LSM) for phase 3 to 4, or 3 to 0 in 2012.
[c] LSM for first day with phase 0 in 2012.

2.2. Phenology monitoring

Leaf phenology was assessed 2012–2013, approximately every two weeks, from 29th May 2012 to 25th June 2013 (day 150, 164, 178, 206, 220, 234, 248, 276, 290, 304, 318, 332, 346 and 360 in 2012 and day 9, 23, 37, 51, 65, 79, 93, 107, 121, 135, 149 and 163 in 2013). At each assessment, the phenological stage of all trees was recorded using 4 phases: phase 0 without leaves, and no signs of bud swelling; phase 1 with some leaf buds swelling, and bud breaking; phase 2 when young leaves are opened, but not totally expanded; phase 3 when leaves are fully opened, and adult; phase 4 when the leaves start to show signs of senescence in terms of a change in colors from normal green to yellow brown. Different parts of the trees could be in different stages of phenology, but only the dominant phase of the tree was used for further analysis. The change between two subsequent dominant phases was estimated as the median day between the two assessments where the change was recorded. Two measures of the timing of senescence were estimated: (i) change to phase 4 and (ii) change to phase 0. Time of bud burst was estimated as change from phase 0 or phase 1 to a more progressed phase. The mean number of living trees per provenance used for senescence assessment in autumn 2012 was 26 and the minimum number per provenance was four trees. The mean number of living trees per provenance used for the assessment of bud burst in spring 2013 was 23 and again the minimum number of trees was four trees. Not all populations were represented in all replications at the time of the phenology assessments (Table 1).

2.3. Climate estimates

For each of the sites of origin, estimates of monthly precipitation, evapotranspiration and mean temperature were obtained from gridded data available from the University of East Anglia Climatic Research Unit (CRU), (Jones and Harris, 2014; Harris et al., 2014). A monthly drought index (DI) was estimated as the difference between monthly precipitation and potential evapotranspiration. Cumulated DI - and precipitation were calculated for all possible combinations of consecutive months from January to December and for all possible combinations of consecutive months from June to May. Temperature means were calculated for the same periods.

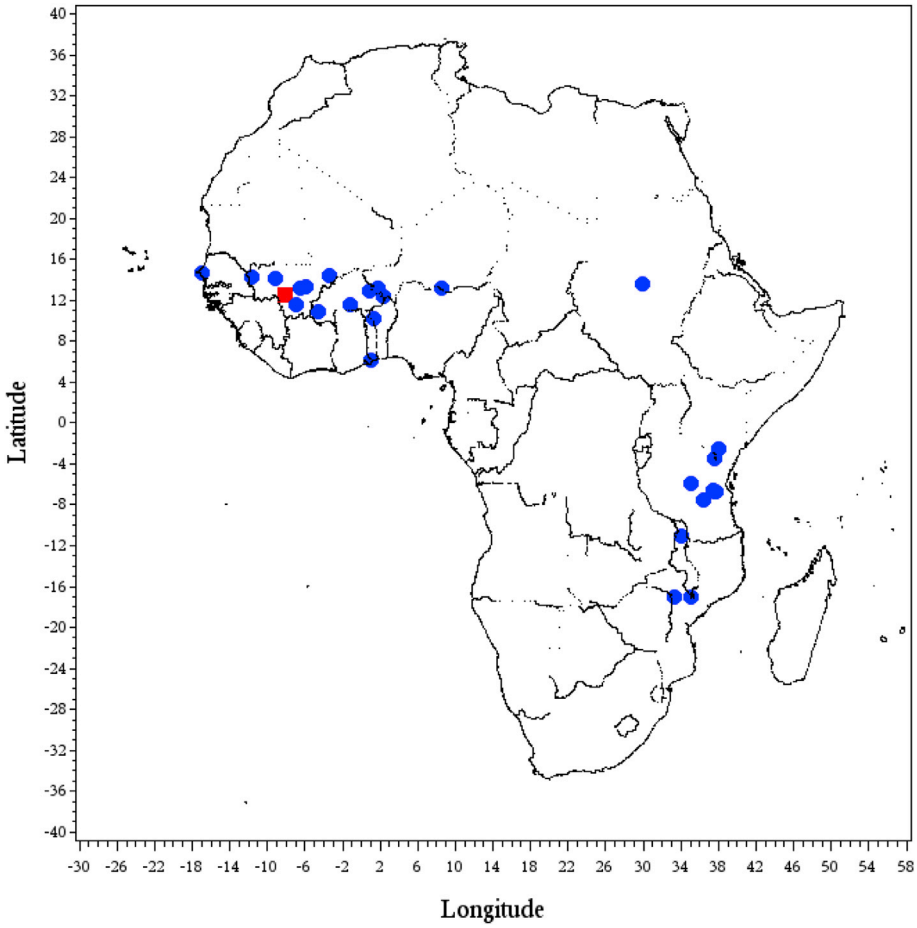

Fig. 1. Origin of populations (dots) and location of the test site (filled square).

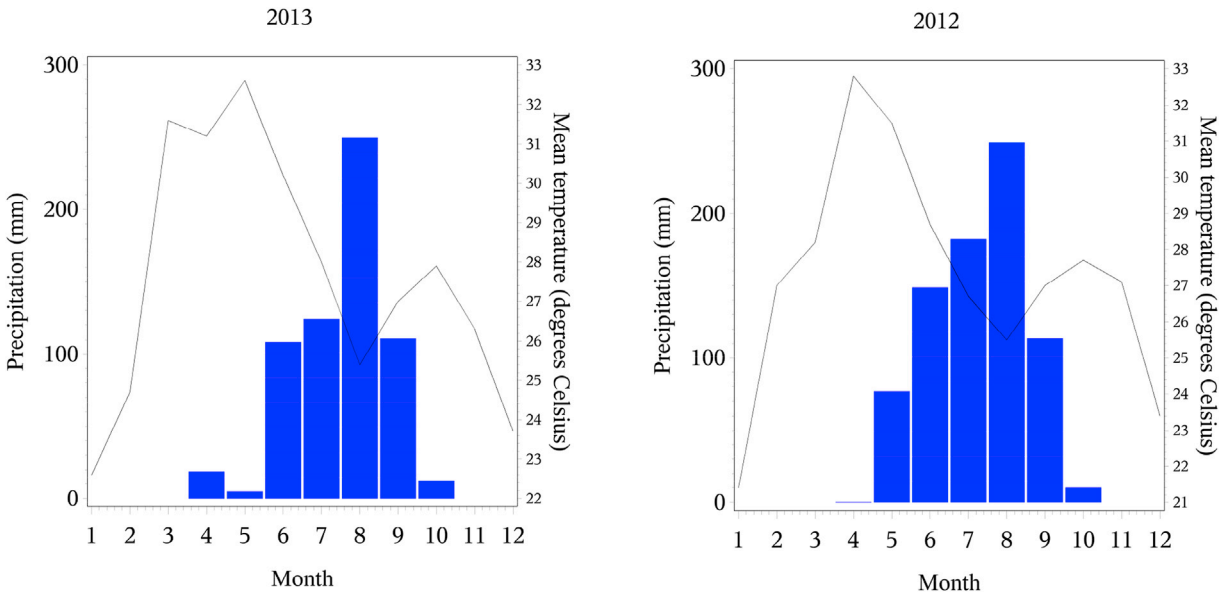

Fig. 2. Mean monthly temperature (line plot) and precipitation (columns) in 2012 and 2013 at the test site at Samanko in Mali (12.53 N, 8.07 W). Estimates from University of East Anglia Climatic Research Unit, Climate Research Unit (Harris et al., 2014; Jones and Harris, 2014).

2.4. Statistical analysis

The following linear model was applied to test for differences among origins concerning the estimated days for changes in dominant phenology phases:

$$Y_{ijk} = \mu + b_i + P_j + \rho_{ij} + e_{ijk} \quad (1)$$

Where Y_{ijk} is the estimated day of the individual tree where it is changing from one phenology phase to another, μ is the general mean, b_i is the random effect of replication i in the trial P_j is the fixed effect of origin number j, ρ_{ij} is the random effect of plot expressing the origin by block interaction and e_{ijk} is the residual, which is assumed to follow the normal distribution $N(0, \sigma_e^2)$. The significance of origins was tested using the Satterthwaite, (1946) option in the procedure GLM (general linear models) in SAS (SAS Inc. 2015), i.e. the origin effects were mainly tested by the origin by block interaction. Least square means (LSM) for origins were obtained from the procedure MIXED (SAS Inc. 2015) using model [1] above.

Regressions of phenology on monthly precipitation, DI, and cumulated precipitation and DI over different periods at the sites of origins were tested. Similarly, mean monthly temperatures and mean temperatures for different periods at the sites of origins were tested. The reference period was 1961–2006. Origins from north and south of Equator were analyzed separately, because the annual patterns in rainfall are different for the two groups with a rainy season starting January–June north of Equator and September–November south of Equator (including tendencies to bimodal rainy seasons) (Fig. 3). To account for different precision of origin least square means, the least square means (LSM) were weighted by the reciprocal of their variance in the procedure REG in SAS (SAS Inc. 2015). The regressions showing lowest Criterion of Akaike (AIC) were chosen (Burnham and Anderson, 2002).

3. Results

3.1. Variation between origins

All origins were mostly leafless during the dry season and with foliage during the rainy season (Fig. 4). Analyses of variance showed significant ($P < 0.001$) differences among origins in the timing of senescence in 2012 (Table 2) with mean date ranging among the origins from 25th of august 2012 (day 238) to 20th of November 2012 (day 325), (Table 1). When assessed as change to phase 0, the origins ranged from 9th of September 2012 (day 253) to 6th of December 2012 (day 341), i.e. a difference of 88 days (Table 1). Origins with early senescence were shedding the leaves at a time when there was still considerable rainfall, while origins with late senescence shed leaves long time after rainfall had stopped at the trial site (for rainfall at trial site see Fig. 2).

The majority of the origins initiated bud burst around the time where the first small rain showers were recorded, but some individual trees set new leaves by the end of March before the first rain occurred in April (Fig. 4). The mean date of bud burst (estimated date for change from either phase 0 or 1 to a higher phase) did not vary significantly among origins at a 5% level ($P < 0.090$ and $P < 0.065$, respectively; Table 2).

3.2. Climatic clines in timing of senescence

Among origins from the northern hemisphere, the day of senescence was significantly earlier among populations from drier climates, i.e. with highly negative cumulated DI from April–July/May–July (Table 3, Fig. 5a). DI estimates for September, October and November at the start of the dry season at the sites of origins were not, or only vaguely significant as explanatory variables with $P < 0.06$, $P < 0.03$ and $P < 0.07$, respectively. Latitude proved significant as explanatory variable (Table 3). Latitude and DI at the sites of origins north of Equator are highly confounded with a correlation between latitude and DI April–July of 0.87 and between latitude and DI May–July of 0.84.

For origins south of the Equator, DI in October (start of the rainy season at the sites of origins), showed the highest significant association with the timing of senescence (Table 3, Fig. 5b). DI estimates for April, May and June at the start of the dry season at the sites of origins were not significant as explanatory variables with $P < 0.41$, $P < 0.17$ and $P < 0.18$, respectively. Neither latitude, nor longitude was significant as explanatory variable, but longitude was at the borderline (Table 3). The correlation between longitude and DI in October was 0.68 so the DI in October is to some extent confounded with longitude.

Overall, the main result is that origins from drier sites, in this case expressed in terms of DI in spring or autumn, show earlier senescence.

4. Discussion

4.1. Timing of senescence

This study is to our knowledge the first to show that the timing of leaf senescence of *A. digitata* is under genetic control. The results are based on a single year of observations at one site, and more studies are required to test for genotype by year

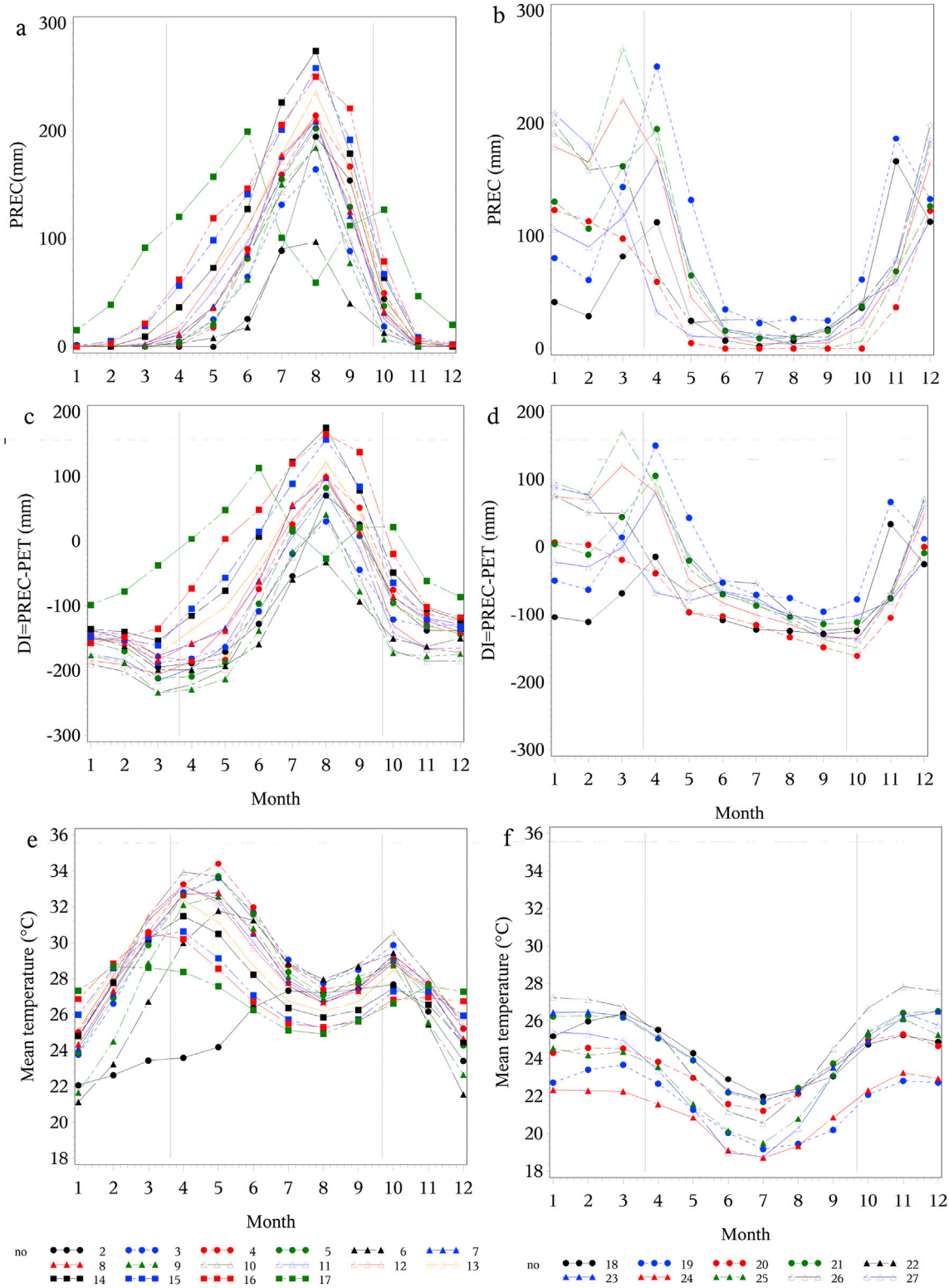

Fig. 3. Monthly precipitation estimates for the origins from the northern (a) and southern (b) hemispheres, monthly DI estimates (precipitation minus potential evapotranspiration) for the origins from the northern (c) and southern (d) hemispheres and monthly mean temperatures for the origins from the northern (e) and southern (f) hemispheres. Climate estimates from University of East Anglia Climatic Research Unit, Climate Research Unit (Harris et al., 2014; Jones and Harris, 2014). Vertical lines equals the equinox in spring and autumn, respectively. Legend numbers refer to the origin numbers in Table 1.

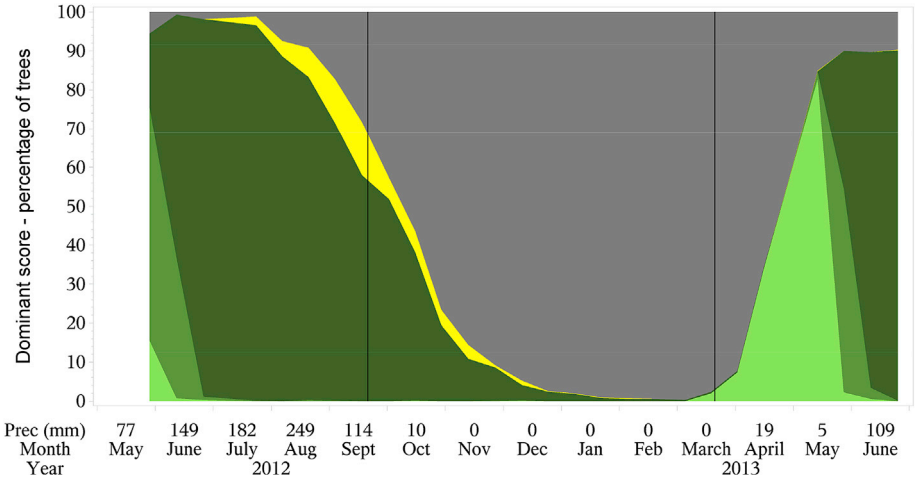

Fig. 4. Development of dominant phenology phases 2012–2013. Light green: phase 1 with some leaf buds swelling and bud breaking. Green: phase 2 when young leaves are opened, but not totally expanded. Dark green: phase 3 when leaves are fully opened and adult. Yellow: phase 4 when the leaves start to show signs of senescence. Gray: phase 0 with no leaves and no signs of bud swelling. Monthly precipitation (Prec) estimates from University of East Anglia Climatic Research Unit (CRU) (Jones and Harris, 2014; Harris et al., 2014). Equinox in spring and autumn are shown with vertical lines. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Results from the test of differences between origins concerning the day with change in phenology phase.

Year	First day with change of dominant phenology phase	Mean day of year	Source	DF	MS	F-value	Pr > F
2011	Phase 1 to phase >1	135	Origin	26	100	1.35	0.1609
			Block	3	567	8.12	<.0001
			Origin x block	54	77	1.45	0.0220
			Error	648	53		
2011	Phase 2 to phase >2	154	Origin	26	99	1.04	0.4281
			Block	3	813	9.05	<.0001
			Origin x block	54	98	1.36	0.0480
			Error	612	72		
2012	Phase 3 to 4, or 3 to 0	272	Origin	26	9613	5.86	<.0001
			Block	3	2217	1.41	0.2446
			Origin x block	54	1697	1.30	0.0797
			Error	618	1306		
2012	First day with phase 0	288	Origin	26	8826	5.45	<.0001
			Block	3	1524	1.01	0.3937
			Origin x block	54	1709	1.56	0.0076
			Error	618	1093		
2013	Phase 0 to phase >0	112	Origin	26	509	1.51	0.0899
			Block	3	1632	5.17	0.0023
			Origin x block	54	354	1.45	0.0225
			Error	557	243		
2013	Phase 1 to phase >1	141	Origin	26	17	1.58	0.0647
			Block	3	21	1.92	0.1291
			Origin x block	53	10	0.88	0.7036
			Error	525	12		
2013	Phase 2 to phase >2	155	Origin	26	15	0.81	0.7133
			Block	3	2	0.10	0.9608
			Origin x block	48	19	1.28	0.1125
			Error	306	15		

and genotype by environment interactions and the observed phenology-climate clines. Nevertheless, the clear relationship between timing of senescence and climatic parameters at the site of origin supports that the patterns are generated by local adaptation. More studies are also needed to clarify to what degree the adaptive patterns are due to epigenetics as observed recently for several tree species (see Sow et al., 2018 for a recent review).

Genetic differences in timing of bud burst and senescence was reported in *Parkia biglobosa* among West African origins tested in Burkina Faso, showing a north-south cline in senescence (Ouedrago, 2014). Although studies on more species are needed, the two studies collectively indicate substantial variation in the timing of leafing senescence among origins of semi-arid species, and that such variation is linked to adaptation to the prevailing climates at the origins.

Table 3
Results from the regression analyses of relations between changes in phenology phases and climate of origins.

Origins	Year	First day with change of dominant phenology phase	Variable	Estimate	Std. err.	t-value	Pr > |t|	adj. R^2
North of Equator	2012	Phase 3 to 4, or 3 to 0	Intercept	296.76	3.74	79.36	<.0001	0.60
			DI57	0.07	0.02	4.84	0.0003	
	2012	Phase 3 to 4, or 3 to 0	Intercept	355.31	16.85	21.09	<.0001	0.54
			Latitude	−5.67	1.31	−4.32	0.0007	
	2012–2013	First day with phase 0	Intercept	316.76	4.79	66.12	<.0001	0.54
			DI47	0.05	0.01	4.35	0.0007	
	2012–2013	First day with phase 0	Intercept	366.39	16.41	22.33	<.0001	0.52
			Latitude	−5.31	1.28	−4.14	0.0010	
South of equator	2012	Phase 3 to 4, or 3 to 0	Intercept	299.63	9.21	32.54	<.0001	0.74
			DI1010	0.37	0.07	5.15	0.0009	
	2012	Phase 3 to 4, or 3 to 0	Intercept	124.72	58.46	2.13	0.0655	0.30
			Longitude	3.58	1.63	2.2	0.0594	
	2012–2013	First day with phase 0	Intercept	317.10	13.33	23.78	<.0001	0.56
			DI1010	0.37	0.10	3.55	0.0075	
	2012–2013	First day with phase 0	Intercept	128.01	65.57	1.95	0.0867	0.29
			Longitude	3.98	1.83	2.18	0.0613	

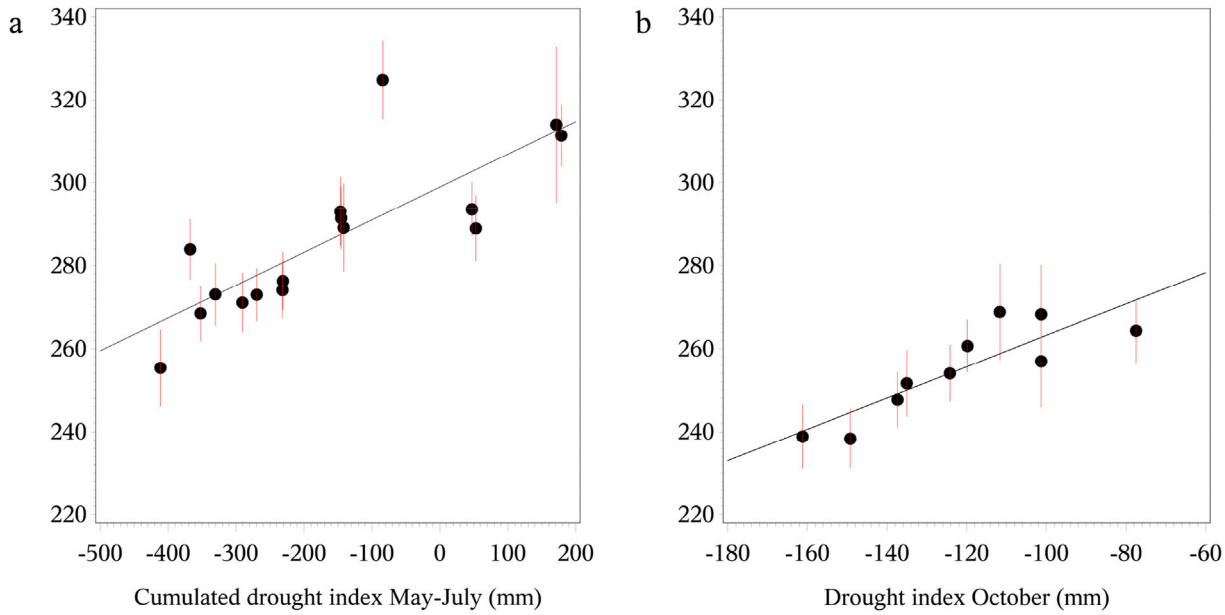

Fig. 5. Least square mean (LSM) estimates for first day of senescence (phenology phase change to 4 or 0) for origins from the northern hemisphere as function (a) cumulated DI for May–July at the sites of the origins ($P < 0.0003$, adj. $R^2 = 0.60$). LSM for first day of senescence in 2012 for southern hemisphere origins as function of (b) DI for October at the sites of origins ($P < 0.0013$, adj. $R^2 = 0.71$). Standard errors of least square mean estimates are shown with bars.

It remains uncertain if the timing of leaf senescence is induced by day-length, temperature, reduced soil water availability, or other factors. However, reduced water availability can possibly be ruled out for the origins starting to show leaf senescence already at the end of August (day 238 in 2012, Table 2), where the rainfall was still reasonably high at the test site (Fig. 2). Interestingly, Korbo et al. (2013) found variation in leaf production among *A. digitata* origins along the course of the year in a trial where plants were continuously irrigated. This indicates that timing of leaf production is not simply controlled by soil water availability in *A. digitata*. A decrease in leaf production despite irrigation was also observed among seedlings of species from drier climates in Nigeria (Njoku, 1964). Populations from drier sites of the Central American tropical dry forest species *Quercus oleoides*, also shed their leaves earlier during a drought treatment (Ramírez-Valiente and Cavender-Bares, 2018). Conversely, among irrigated trees of the arid savanna tree species *Colophospermum mopane*, there was a weak seasonality in leaf area index compared with water stressed trees (Stevens et al., 2016).

Studies on Madagascan *Adansonia* species indicate that the trees use water stored in the parenchyma rich wood to support leaf flushing (Chapotin et al., 2006). The early development requires that the trees are not losing excessive amounts of water from the stems after the end of the rainy season due to the transpiration. The large genetic differences in timing of senescence may therefore reflect that trees from drier regions retrieve nutrients and shed their leaves in time to secure that the water

reserves in the stems are sufficiently large to support leaf flushing the next season. This is a hypothesis that deserves to be tested in further studies.

4.2. Bud burst

No firm conclusion can be made concerning the genetic variation in bud burst from this study. It might be that the occurrence of first rain is an important trigger of budburst in *A. digitata* and that early rain at the test site synchronized the timing of the bud burst among the different origins.

Yet, in our study, a few trees set leaves in March before the first occurrence of rain, and the coincidence between the spring equinox and start of leaf flushing before the start of the rain makes it tempting to suggest a role for daylength as a determining factor for the start of bud burst. In the study of Di Lucchio et al. (2018), longer photoperiods resulted in higher levels of meristematic activity, also suggesting a role for daylength in relation to bud break. Even at small distances from the Equator, there are differences in daylength along the course of the year and the difference between the shortest and the longest day exceed 1 h at many of the sites of the origins (Table 1).

Early leaf flushing is an important strategy to benefit from early rainfall and to make leaves ready to start photosynthesizing when the rainy season starts (Chapotin et al., 2006). Bud burst starts earlier than the rainy seasons over several vegetation types and years in the tropics, suggesting that bud burst is not controlled by rainfall (Swanepoel, 1993; Ryan et al., 2017). The role of daylength for tropical tree phenology constitutes an interesting topic for follow up research (Borchert et al., 2005) and additional studies with control of day length will allow a specific test of the hypothesis.

4.3. Adaptation in semi-arid areas and adaptation potential

Tree species in dry seasonal climates can be divided into groups according to their phenology: deciduous species with short or long leafing periods, semi-evergreen species which shed their leaves over a short period, and evergreen species in which old leaves are still on the tree when the new leaf flush occurs (Seghieri et al., 2012). While *A. digitate* represents a deciduous species, there may be reason to extend the study to other species representing other areas of distribution and representing other phenology groups. To our knowledge, few studies on genetic variation in phenology from arid and semi-arid areas are based on experiments where population and environmental effects are not confounded, emphasizing that we have only started to understand how species may have adapted their phenology to the prevailing climates.

An important question is also to what extent observed variations in phenology among populations are due to epigenetics as observed in temperate tree species (Bräutigam et al., 2013; Sow et al., 2018). In times with climatic changes the degree of phenotypic plasticity including epigenetics and speed of adaptation in phenology is crucial.

We do not yet know to what degree the observed differences in phenology of *A. digitate* influence fitness, but the trial will be followed in the future to help in determining whether – in response to climatic changes - it will be advisable to resort to assisted migration to increase the genetic variation in the species, as suggested for temperate trees (Aitken and Bemmels, 2016). In this context, the quite large genetic variation in leaf senescence shown in this study combined with an indicated limited gene flow could make *A. digitata* populations vulnerable to climate change.

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