



**Coexistence and performance of diploid and polyploid *Acacia senegal* (L.) Willd
implications for adaptation and domestication in the Sahel**

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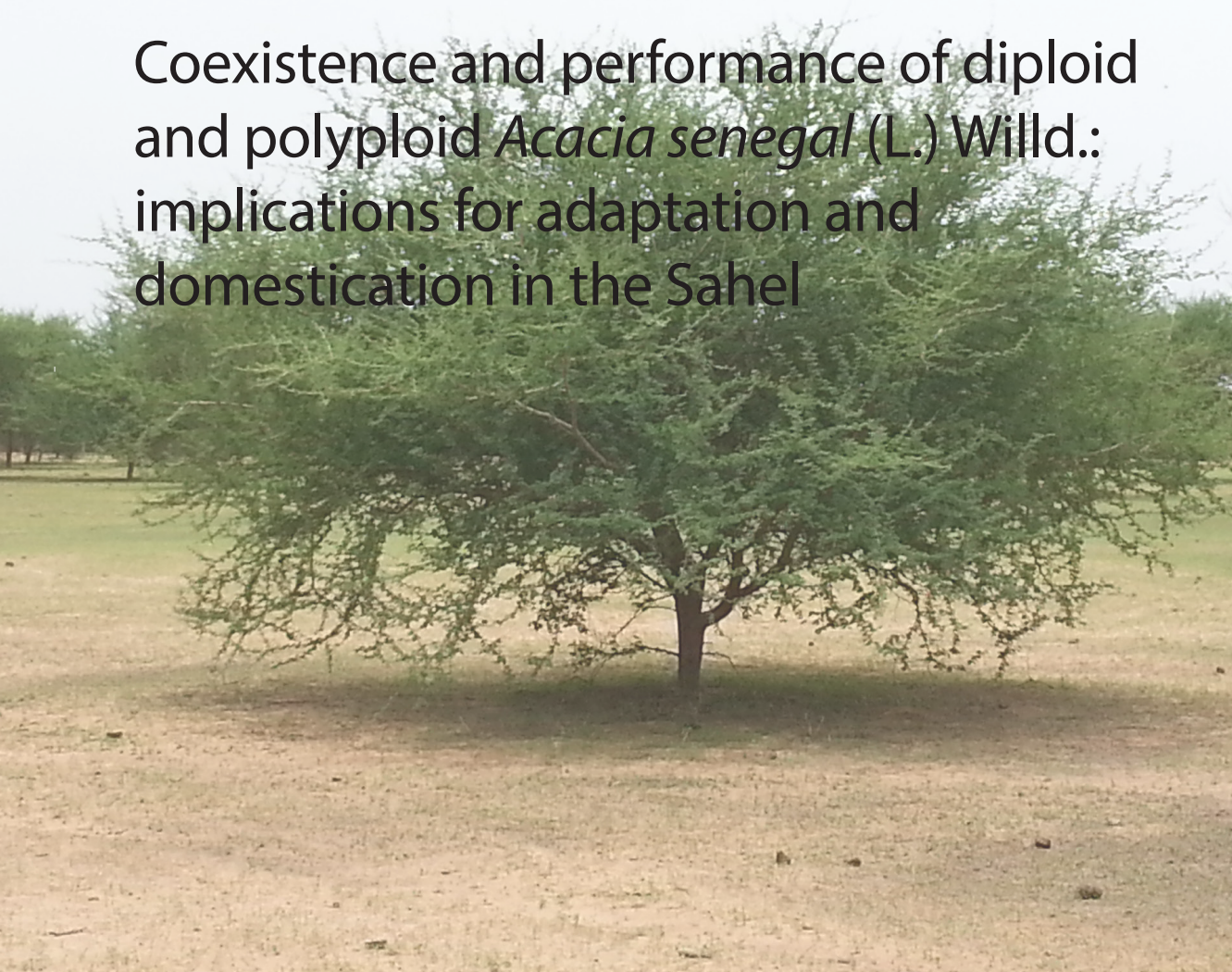
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PREFACE AND ACKNOWLEDGEMENTS

This thesis has been submitted to fulfil the requirement for a degree of Doctor of Philosophy at the University of Copenhagen.

The work reported here was carried out at the Department of Geosciences and Natural Resource Management, University of Copenhagen. The PhD project received funding from the Islamic Development Bank (IDB) and has focused on analyzing and identifying effects of polyploidization in *Acacia senegal* in its natural distribution in Senegal. The research was mainly based on a progeny trial established in 1994 by the Centre National de Recherches Forestieres, of Institut Senegalais de Recherches Agricoles (ISRA/CNRF).

The thesis consists of results from three submitted manuscripts and comprises of two parts. The first part is a general introduction to the concept of polyploidy, presentation of the studied species, and potential impact of polyploidy in adaptation to the dry Sahel region of West Africa, summarization of results of each study, and a general discussion of the findings followed by conclusion and perspectives of this thesis. The second part consists of three submitted manuscripts.

I am grateful to my team of supervisors Prof. Erik Dahl Kjær, Associate Prof. Lene Rostgaard Nielsen and Associate Prof. Anders Ræbild. You are the best supervisors in the world, I'm sure. You have been a great support through the “difficult subject of polyploidy”. Even though the subject was totally new for all of us, you showed great interest in this study. You have put a lot of attention to the quality of the work.

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The assistance of the Centre National de Recherches Forestieres is acknowledged. Abibou Gaye Abdourahmane Tamba, Ibrahima Thomas and Dr Mayecor Diouf are acknowledged.

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Many thanks go to the members of the Department of Geosciences and Natural Resource Management who have cordially welcomed me through the whole study period for their gracious hospitality. Thanks to my colleagues at the Section of Forest Genetics and Diversity and Tropical Trees from whom I have gained knowledge of many things, for example, how to maintain good spirit in a research group. I really enjoyed cakes and tours.

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Nothing would have been possible without the support of my family. I would like to thank my mother and my father for their constant prayers, for being there all my life as a constant support especially during my thesis writing period.

Last but not least, very special thanks are due to my husband Birane Diop who has been my constant moral support throughout my study. His support has provided the incentive for the successful completion of this study.

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DANSK SAMMENDRAG

Polyploidi (det forhold at organismer har mere end to sæt kromosomer som det kendes fra diploide organismer) er velkendt inden for planter og menes at have en vigtig evolutionær rolle i planters tilpasningsevne. Det er imidlertid uvist om polypløide tropiske træer har en evolutionær fordel i forhold til diploide træer i områder med meget lav nedbør. I denne PhD afhandling bringes nu viden til dette område gennem undersøgelser af *Acacia senegal* i Senegal.

Acacia senegal er interessant, fordi den vokser naturligt under forskellige vilkår, herunder i områder med meget lav nedbør på grænsen af, hvor der overhovedet kan vokse træer. Det er samtidig en meget vigtig art for befolkningerne i det tørre afrikanske Sahel-område hvor man bl.a. tapper *gummi arabicum* fra træerne: et produkt som bruges i fødevarerindustrien og er en vigtig eksportvare for flere lande i regionen. *Acacia senegal* er også en interessant art, fordi man fornyligt har opdaget at bestande af arten kan indeholde både diploide og polypløide træer. Det vil sige at nogle træer har de normale to sæt kromosomer (diploide), mens andre har flere sæt (polypløide).

Som led i PhD studiet er andelen af polypløider i 10 forskellige bestande i Senegal undersøgt. Bevoksningerne er valgt langs med to transekter. Det ene transekt dækker lidt mere nedbørsrige områder til ganske tørre områder, mens det andet inkluderer områder med moderat saltkoncentration i jorden og områder med meget høj salinitet. Andelen af polypløider varierer meget fra sted til sted. De to områder med høj salinitet har en højere andel af polypløider sammenlignet med områder med lavere salinitet. Der var ikke noget tydeligt mønster i ploidi-grad i forhold til nedbør, selvom andelen af polypløider også varierede meget langs dette transekt.

Undersøgelse af træerne med DNA-markører peger på, at polypløide træer fra forskellige bestande generelt er mere forskellige end det er tilfældet for de diploide artsfæller. Dette tyder på, at polypløidi er opstået flere gange og måske har mindre spredning af gener mellem bestande. Studiet gav anledning til at undersøge samspillet mellem ploidi-grad og salttålsomhed, og dette blev undersøgt ved at sammenligne hvordan polypløide og diploide frøplanter voksede når de blev udsat for stigende saltkoncentration i vandingsvandet under væksthushold. Dette afslørede imidlertid ingen tydelige forskelle mellem ploidi-graderne.

En vigtig del af PhD afhandlingen bygger på resultater fra et afkomsforsøg, som er plantet i et tørt og varmt område i Senegal. Planterne i forsøget stammer fra frø, som blev samlet på 60 træer (15 i hver af 4 populationer). Forsøget er målt løbende siden det blev plantet, og i 2011 og 2012 blev der

desuden høstet *gummi arabicum* på en del af træerne. Både mængde og kvalitet blev registeret og analyseret. Slægtskab mellem træer i de enkelte afkomsgrupper blev undersøgt ved hjælp af DNA-markører. Analyserne viste, at de polyploide træer generelt vokser hurtigere end de diploide træer på denne tørre lokalitet, men der var ikke systematiske forskelle mellem diploider og polyploider i produktion af *gummi arabicum*. I et væksthuseksperiment med frøplanter kunne det observeres at polyploider og diploider voksede lige hurtigt, når de fik rigelig vanding, men når de blev vandstressede voksede de polyploide frøplanter hurtigere end de diploide. Dette underbygger et samspil mellem ploidi-grad og evne til at klare sig godt under tørre vækstvilkår, selvom dette ikke fremgik af transektstudiet beskrevet ovenfor.

Analyserne i feltforøget afslørede at variation mellem træerne i *gummi arabicum* til en vis grad er genetisk styret, og af det derfor vil være muligt at forædle sig frem til større udbytter gennem selektion, afprøvning og opformering af særligt interessante træer. Denne viden vil indgå i det fremadrettede arbejde med at udvikle bedre frøkluder til fremtidig brug i Senegal. Den opnåede viden vil også indgå i overvejelser om brug og sikring af de genetiske ressourcer af arten under indtryk af de store udfordringer, der kan blive skabt af fremtidige klimaændringer.

Afhandlingen berører en række spørgsmål som det vil være relevant at undersøge nærmere. For eksempel påvises det at der forekommer flere niveauer af polyploider, og at der muligvis er udveksling af gener imellem nogle af niveauerne. Det vil derfor være meget interessant at undersøge, i hvilket omfang og hyppighed de højere niveauer af polyploiditet findes i naturen, og i hvilket omfang de krydser med hinanden. I afhandlingen præsenteres nogle foreløbige observationer baseret på mikroskopering af bestøvede og ubestøvede blomster, som giver anledning til hypoteser vedrørende bestøvningsbarrierer. Afhandlingen afslører også interessante forskelle mellem diploider og tetraploider i, hvor mange forskellige individer der tilsyneladende har bidraget med pollen til bestøvning af de enkelte modertræer. DNA-resultaterne stiller spørgsmålstegn ved, om de polyploide træer er normalt udkrydsende, eller om de evt. undergår en mere kryptisk reproduktion med delvis selvbestøvning og/eller andel af apomixi. Det vil derfor være interessant at kortlægge og sammenligne reproduktionssystemet i de forskellige ploidi-niveauer.

Det er umiddelbart svært at afgøre træernes ploidi-grad alene ud fra deres udseende. Baseret på mikroskopering præsenterer afhandlingen imidlertid data, som viser at antal og størrelse af stomata på bladene er meget forskellige. Det vil derfor være oplagt at kortlægge effekten af ploidi-grad på

træernes fotosyntese og økofysiologi for bedre at kunne forstå mekanismerne bag artens tilpasningsevne til ekstreme vækstvilkår.

SUMMARY IN ENGLISH

Polyploidy is defined as possession of more than two sets of chromosomes of an organism. It is known to play a major role in evolution of organisms, but few studies are available on Sahelian trees. In the case of *Acacia senegal* (distributed across the Sahel), it is important to clarify the potential role of polyploidy in adaptation to dry growth conditions. This thesis therefore aims at increasing the understanding of polyploidization in adaptation of *A. senegal* by the means of population genetics and quantitative genetic tools.

An assessment of the distribution of polyploids across ten natural sites with different rainfall and salinity showed no simple geographical pattern in the frequency of polyploids. However, salinity was found to be positively correlated with frequency of polyploids. Analysis of population differentiation between cytotypes compared to genetic relationship among populations within cytotypes revealed that the studied polyploid populations were more differentiated than diploid ones. The analysis of genetic relationships further suggest multiple origins of polyploid *A. senegal* and provide novel information for understanding the evolutionary history of the recently revealed polyploidy in *A. senegal*.

Estimation of the frequency of polyploids were also made among four natural populations based on trees planted in a progeny trial located in dry and hot region of Senegal; Dahra: annual rainfall < 300 mm and temperature 35-45 °C. Here also, polyploid trees were observed in all tested populations. In this study the growth rate of each tree could be estimated very precisely, because the sampled trees were part of a research trial, and the comparison between cytotypes in the progeny trial showed significantly higher growth rate of polyploids compared to diploid at this test site. A drought stress trial under controlled conditions (growth chamber) showed that diploid and tetraploids had similar growth rate when grown under well-watered conditions, but tetraploids grew faster than diploids when subjected to drought stress. The findings suggest that presence of polyploids play an important role for the species ability to adapt to harsh growing conditions.

The level of genetic variation for growth and gum yield for diploids and polyploids was estimated from quantitative genetic analysis based on assessments in the progeny trial during two years (2012 and 2013). Sibling relationship among and between trees from the different open pollinated progenies was tested by application of genetic markers to support the quantitative genetic analysis. The results suggested different mating systems in diploid and polyploids, and this complicated the

quantitative genetic analysis and reduced the precision of the estimated quantitative genetic parameter. Still, the results from the quantitative genetic traits analysis showed strong genetic variation in growth and gum production between provenances and families for each level of ploidy. Ploidy level appeared to have a consistent effect on growth rate of the trees, but not on the economically important gum yield in the investigated years. Still, estimates of genetic parameters showed that gum yield is a heritable trait (based on analysis of diploids). The results therefore suggest that breeding for high gum yield could be effective. These results represent a good start-up for a future program of conservation, reforestation and restoration of *A. senegal* in the Sahel region.

ABSTRACT

Acacia senegal, is the most important gum arabic producer and represents an active component in traditional dryland agroforestry systems in Africa. The species has been recently found to consist of both diploid and polyploid individuals, which opens for interesting questions since polyploidy is considered a major evolutionary process in plants. This thesis consists of a comprehensive introduction followed by three manuscripts with the aim to contribute new knowledge about potential role of polyploidization in *A. senegal* in relation to adaptation, gum arabic production and evolutionary success.

The study presented in *manuscript I* showed that polyploid individuals are also found in Senegal, but frequencies vary among populations. Comparison of growth performance in both a progeny trial and in a growth chamber under drought stress test indicated that polyploids perform better than diploid under dry conditions. The results show that polyploidisation is likely to play a role in the species ability to grow under very dry conditions and the presence of multiple ploidy levels therefore increases the adaptive potential of *A. senegal*.

Manuscript II investigates sibling-relationship between diploid and polyploid families and presents for the first time, estimates of genetic parameters for growth and gum yield traits in diploids. Different sibling-relationship between diploids and polyploids were observed. Diploids were mainly outcrossed and families consisted of half-sib progenies. In contrast, polyploid individuals within families were more related than half-sib. Narrow sense heritability was estimated to 0.38 for gum yield suggesting that a breeding program for increased gum yield can be effective in providing gain after selection of trees with superior phenotypes based on careful testing.

Manuscript III presents the distribution of polyploids across different environmental ranges and compare genetic structure between diploids and polyploids. The results reveal no simple geographic pattern in the level of polyploids in natural populations, but frequency of polyploids appeared to be positively correlated with increased salinity. Polyploids were found to be more genetically differentiated compared to diploids and based on study of genetic relationship between cytotypes, it is argued that polyploid *A. senegal* are likely to have multiple origins. This indicate presence of a dynamic system with repeated polyploidization events

Key words: *Acacia senegal*, adaptation, distribution, drought, genetic differentiation, genetic relationship, gum arabic, heritability, origins, polyploidy, Sahel regions

OBJECTIVES OF THE STUDY

With the recent discovery of polyploid individuals in *A. senegal*, it is important to understand their role in relation to the species ability to adapt to future and drier conditions in the Sahel region, but also the interaction between diploid and polyploid individuals in nature. Knowledge about the genetic of the gum arabic tree is also attracting increased interest, but many questions remain unanswered. In context of domestication and future tree breeding program for increased gum arabic production and quality, the aim of the present thesis is to contribute to the development of effective strategies for conservation and breeding programs of climatically adapted and high yielding trees by shedding light on the impact of polyploidization in *A. senegal* on growth and yield under stressful conditions.

In order to meet the overall objective, the thesis includes population genetic analyses based on DNA markers with the objective to clarify the genetic differentiation between diploid and polyploid *A. senegal*. Also, the marker based genetic analyses are applied to allow estimation of genetic relationship among single families collected after open pollination, because this information is crucial for effective quantitative genetic analysis of the progeny trials that form the backbone of breeding activities. Drought and saline trials were established as supplement to the field trial and sampling from natural populations in order to test under controlled conditions if polyploids are better adapted for growth under harsh conditions compared to diploids.

The research was organized in three studies with specific objectives. The objective of the first study was to verify presence of polyploid individuals in Senegalese populations and to study if polyploidy confers superiority to trees grown under stressful conditions since these had not previously been investigated.

The objective of the second study was to quantify variation within and among diploid and polyploid families based on a comprehensive set of phenotypic observations in order to estimate presence of additive genetic variation and narrow-sense heritability for gum yield and growth traits. The findings of the study are discussed in relation to development of future breeding programs.

The objective of the third study was to investigate if cytotype frequencies within natural populations coincide with ecological patterns within Senegal. Further, to infer on genetic relationships between polyploid and diploid individuals within and among 10 natural populations across Senegal. More specially, the study was designed to sample populations along two transects covering different

environmental conditions in terms of soil salinity and annual rainfall, respectively, to observe if the fraction of polyploid trees in natural populations increases with increasingly stressful growing conditions (increased salinity and reduced precipitation). A comparison of genetic distances within and among sampled trees was applied to infer on whether polyploids in Senegal are likely to be of single or multiple origins.

Correspondingly, the main hypotheses in these studies are:

- Polyploid trees in the Sahel are better suited for extreme growth conditions than their diploid counterparts
- Breeding for high gum yield can be effective if based on careful field testing
- Polyploids of *A. senegal* are of multiple origins reflecting several polyploidization events in natural populations

POLYPLOIDY IN FLOWERING PLANTS

Polyploidy or whole genome doubling is defined as possession of three or more sets of chromosomes (Ramsey and Schemske, 1998), and exists in nearly all major divisions of vascular plants (Stebbins 1971; Lewis 1980; Soltis et al. 2009; Jiao et al. 2011). Polyploidy is considered a major pathway for instant speciation, increasing biodiversity and provision of new genetic material for evolution (Levin 2002; Ramsey and Ramsey 2014). Polyploids are classified based on their formation: autopolyploids form by union of intraspecific unreduced gametes, while allopolyploids form from interspecific reduced gametes followed by genome doubling. Allopolyploidy was for a long time considered the more significant mode of polyploid formation, however recent evidence suggests that the frequency of autopolyploids in nature is highly underestimated (Ramsey and Schemske 1998; Soltis et al. 2007) and it has been estimated that the rate of autopolyploidy is on the same order as the genic mutation rate (10^{-5}) and that a high frequency of hybridization (3 %) is required for the rate of allopolyploidy to equal autopolyploidy (Ramsey and Schemske 1998).

Traditionally, polyploidization has been considered a rare process, and polyploid species was therefore seen to be of single origin (Soltis and Soltis 1993). Recent studies based on molecular markers demonstrate that the majority of polyploid plants are of recurrent origins, while single origin of polyploids is rare (Soltis et al. 2003, Patterson et al. 2006; Adams 2007; Leitch and Leitch 2008; Tang et al. 2008). It has been hypothesized that presence of triploids could facilitate recurrent polyploid formation through a so-called triploid bridge as a triploid plant may produce gametes with one ($n = x$), two ($n = 2x$) and three ($n = 3x$) chromosome sets enabling recurrent polyploid formation, or gene flow from diploids to polyploids subsequent to the polyploid formation (Husband and Sabara, 2003, Husband, 2004).

Polyploid plants can have numerous genotypic and phenotypic characteristics that distinguish them from their diploid parents. Through new gene combinations and doses, polyploids may develop new ecological preferences and become advantageous compared to their diploid counterparts in special environments (Ramsey, 2011). At phenotypic level, polyploidy often lead to increased cell size, enlarged floral structures, larger pollen and stomata, and more robust stems (Ramsey & Schemske 1998; Madlung 2013).

An often observed association with polyploidy is self-fertilization and/or apomixis (Hörandl 2010). Polyploids are reported to self-fertilize more often than their diploid progenitors (Barringer, 2007), although autopolyploids tend to outcross more often than allopolyploids (Husband et al. 2008). Stone (2002) reported that the transition from diploidy to polyploidy can be accompanied by mating

shift towards self-fertilization by disrupting certain genetic self-incompatibility systems or even towards apomictic reproduction (Mable, 2004; Robertson et al. 2011). For example, the allotetraploid *Arabidopsis kamchatica* has been found to be self-compatible while both its diploid parents are self-incompatible (Mable et al. 2004) and allotetraploid *Tragopogon* (Asteraceae) were found to have higher selfing rates compared to diploids (Cook and Soltis 2000). Newly formed polyploids will be at mating disadvantage (“theory of minority cytotype”) (Husband 2000), because most potential mates are from the diploid population. However, self-fertilization or apomixis can allow their establishment in an environment dominated by diploid plants and persist while mating with the parental diploid species often results in sterile progeny (Stebbins 1971; Grant 1981).

STUDIED SPECIES: *ACACIA SENEGAL*

Description of the species

Acacia senegal (L.) Willd. is a leguminous tree species belonging to the genus of *Acacia* and the family of *Fabaceae*. A new classification has been proposed by Orchard and Maslin (2005) in which the genus and species occurring in Africa and Asia have been transferred to *Senegalia*. Here we maintain Willdenow’s classification and thus the name *Acacia senegal*. The species has a wide natural distribution area in the Sudano-Sahelian zone of Africa (Fagg and Allison 2004) (Fig. 1). The species is highly variable, with four distinct varieties recognized based on morphological characters, namely vars. *senegal*, *kerensis*, *rostrata* and *leiorhachis* (Fagg and Allison 2004). The present study is concerned with variety *senegal*, which is the main source of gum arabic and one of the most economically and ecologically important native tree species covering the northern and eastern regions in Senegal. The species is famous for its gum arabic, a dried exudate rich in soluble fibers, which emerges from slits made in the bark and is being tapped from the stems and branches by the local populations (Fig. 2). *Acacia senegal* is a multipurpose species that besides gum arabic provides valuable livestock fodder and fuel wood (Raddad and Luukanen 2006). It can restore soil fertility because of its ability to fix N₂, which is beneficial for crop production in the gum arabic agroforestry systems in drylands of sub-Saharan Africa (Raddad and Luukanen 2006). The gum is

an international commodity used in food, pharmaceutical and cosmetic industries and for a wide range of other purposes (Fagg and Allison 2004).

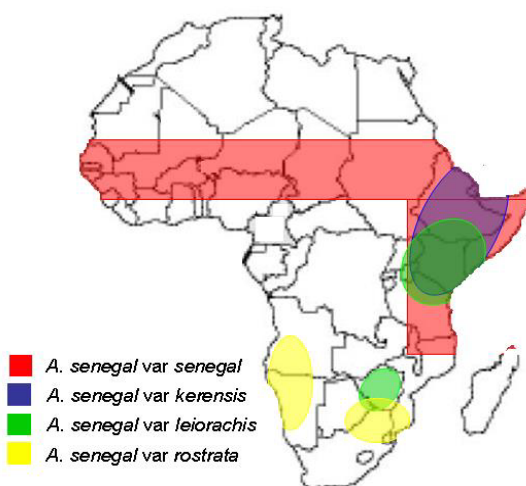


Figure 1. Distribution map showing natural distribution of *A. senegal* in Africa (Fagg and Allison 2004).



Figure 2. Tapping technique and gum production in *A. senegal* in the progeny trial in Dahra, Senegal (November 2012)

Genetics of the species

In *A. senegal*, little was known about the genetics of the species before 2012. Early studies based on cytological techniques have reported only diploids ($2n = 26$ chromosomes) (Ross et al. 1979) and studies of genetic diversity based on iso-enzyme markers reported low levels of heterozygosity (Chevalier et al. 1994). Even though *A. senegal* represents one of the most economically and ecologically important and domesticated species in the Sahel regions of Africa, no estimates of genetic parameters (additive genetic variance and heritability for gum yield) was available to this date. Earlier pre-breeding programs only included establishment of provenance trials.

In 2009, the development of microsatellite markers by Assoumane et al. (2009), allowed new insights on the genetics of the species. Still, the species was first reported to consist of diploid and tetraploid cytotypes by Assoumane et al. (2013). Very recently, presence of triploid, tetraploid, pentaploid, hexaploid individuals has been reported in Senegal, (Diallo et al. 2015 see manuscript 1) and in a large scale across the natural distribution of the species in Africa (Odee et al. 2015). In Senegal a mixture of cytotypes were reported to co-occur in natural populations with the predominant cytotype depending on the site (See manuscript I and III in the present thesis).

Phenotypic changes associated with polyploidy in *A. senegal*

In nature, mature diploid and polyploid *A. senegal* individuals are indistinguishable based on their appearance. Nevertheless, we have found it possible to separate the cytotypes based on morphological differences related to stomata, floral organs (polyade and stigma sizes) and seed size. Also, the leaflet length was found to be positively correlated with increased ploidy at seedling stage (21 % longer in tetraploids compared to diploids, see manuscript 1). The stomata length varied among different levels of ploidy ($2n$, $3n$, $4n$, $5n$ and $6n$) with significant increase in the stomata length from diploid to hexaploid individuals (Fig. 3).

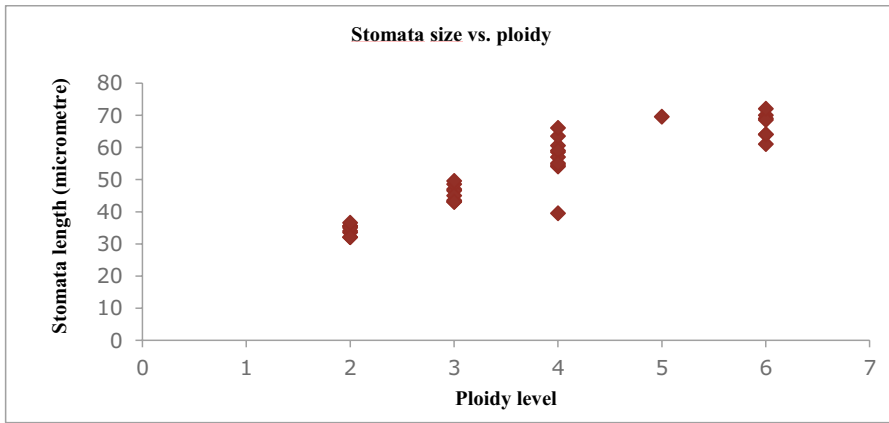
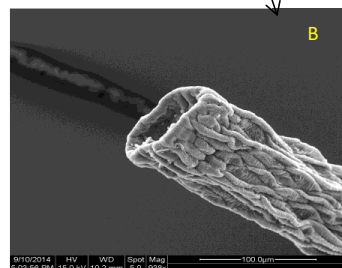
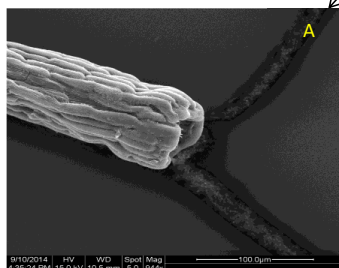
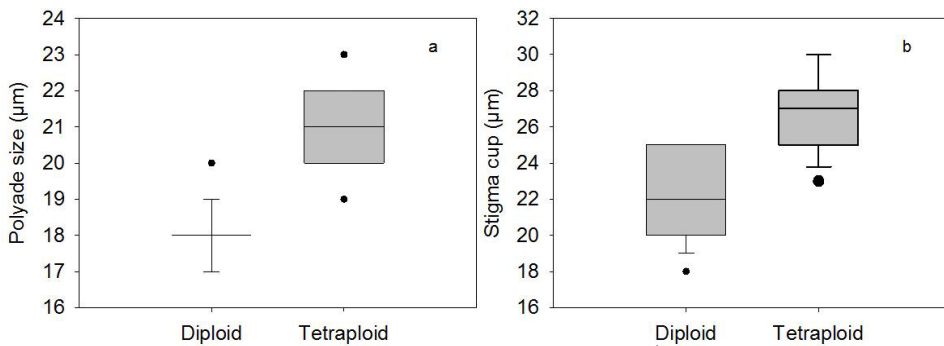


Figure 3. Difference in stomatal size between different levels of ploidy (2n, 3n, 4n, 5n and 6n) in *A. senegal*.

At floral level, polyploid *A. senegal* can be characterized by bigger polyades (unit of 16 pollen grains), larger stigma cup (stigma is as in other Acacias cup-shaped) and development of larger seed size (18 % longer and 12 % larger) (Fig.4).



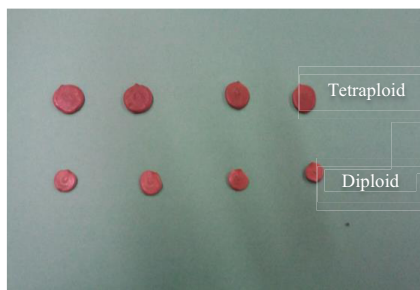


Figure 4. Difference in polyade (a), stigma cup (b) and seed sizes (c) between diploid and tetraploid *A. senegal* individuals

IMPLICATIONS OF POLYPLOIDY IN *A. SENEGAL* IN THE DRY SAHEL REGIONS OF WEST AFRICA

Polyloidization may be a common phenomenon in the tropical dryland species. Two of the four widely distributed African *Acacia* species in the Sahel region, namely *A. tortilis* and *A. nilotica*, were recently discovered to be predominantly polyploids (Bennett and Leitch 2012). Baobab (*Adansonia digitata*), which is widely distributed in Africa including the Sahel region of Africa is known to be tetraploid (Larsen et al 2009), but Pettigrew et al. (2012) recently revealed that diploid populations exist in East Africa.

Polyploidy has been associated with increased performance under drought environments compared to diploids in *Chamerion angustifolium*, (Maherali et al. 2009); *Brachypodium distachyon*, Manzaneda et al. (2012); *Acacia senegal*, Diallo et al. (2015), manuscript 1. The increased tolerance towards water stress may be due heterosis and a high level of genetic diversity (Lowry & Lester, 2006). If polyploids in general are more successful than their diploid progenitors under drought conditions, the occurrence of polyploidy in the Sahel region of Africa characterized by low rainfall and poor soil fertility can be of major importance for adaptation, domestication, forest restoration and also development of conservation and breeding strategies in the context of climate change.

SUMMARY OF MATERIAL, METHODS AND OBTAINED RESULTS

Manuscript I: Polyploidy confers superiority to trees grown under stressful conditions: a case study of *Acacia senegal* (L) Willd. in the Sahel region of West Africa
(Submitted to Botanical Journal of the Linnean Society)

Shift in ploidy level is thought to produce individuals that can cope with fluctuating environments and are more successful in harsh conditions than progenitor species (Leitch and Leitch 2008). The aim of the study was to check occurrence of polyploid individuals in Senegal and investigate whether polyploid *A. senegal* tolerate stressful conditions better than the diploids. Two approaches were used. The first was based on a progeny trial established in 1994 in Northern Senegal, Dahra. The site is characterized by low annual rainfall (< 300 mm) and high temperature (35-45 °C), i.e. a site well suited for studying growth under quite stressful conditions. Height, diameter, crown diameter and survival were assessed in 2012 (18 years from planting) for all 617 living trees in the trial. DNA was extracted from dry cambium and genotyped using eight microsatellite markers (Assoumane et al. 2009). The ploidy level was determined based on the banding pattern of the genotyping and also by using flow cytometry. The second approach was based on a drought stress experiment established in a growth chamber using seedlings tested with flow cytometry to determine the exact level of ploidy.

The results showed considerable variation in the frequency of polyploids among provenances in Senegal, estimated to range from 2 % to 84 % depending on site. In the progeny trial, polyploids were found to grow substantially faster than diploids (i.e. 26 % more in biomass) (Table 1).

Table 1. F-tests for significance in growth traits between ploidy levels and provenances in the progeny trial of *Acacia senegal*.

Traits	Ploidy level ³			Ploidy level ⁴			Provenance ⁴			Ploidy LS means		
	Df ³	F ³	P>F ³	Df, ⁴	F ⁴	P>F ⁴	Df ⁴	F ⁴	P>F ⁴	Mean trial	Diploid	Polyloid
Height 1995 (cm)	1; 39	26.3	<.0001	1; 36	0.79	0.38	3; 36	11.0	<.0001	42 (19)	38 (1.3)	42 (4.0)
Height 2012 (cm)	1; 39	9.68	0.004	1; 36	0.12	0.73	3; 36	3.2	0.03	470 (1)	453 (0.1)	462 (0.2)
Basal area 2012 (cm ²)	1; 39	4.25	0.05	1; 36	0.05	0.83	3; 36	3.12	0.04	160 (90)	161 (6.8)	167 (21)
Log Biomass (kg)	1; 39	9.28	0.004	1; 36	0.02	0.89	3; 36	2.99	0.04	33 (28)	34 (2.4)	43 (7.4)
Crown diameter 2012 (m)	1; 39	0.28	0.6	1; 36	3.81	0.06	3; 36	2.91	0.05	5.4 (1.3)	5.6 (0.1)	5.0 (0.2)

Least square means (LS means) of non transformed data and standard errors (SE) are provided for the two ploidy levels. The superscripts 3 and 4 refer to statistical models (3) and (4); Df: Degrees of freedom and F: F-value.

Under controlled conditions in the growth chamber, the same pattern was observed, where tetraploid seedlings grew in greater magnitude (26 % more) in height when drought stress was applied (Fig. 5).

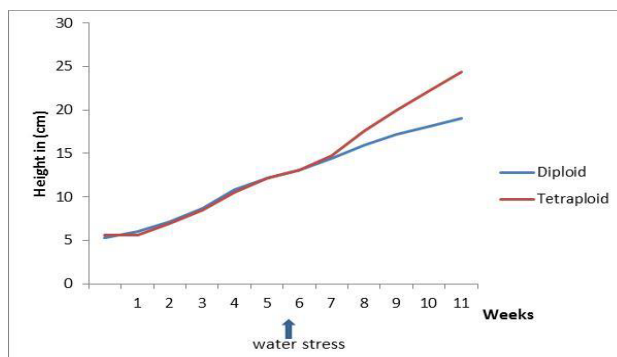
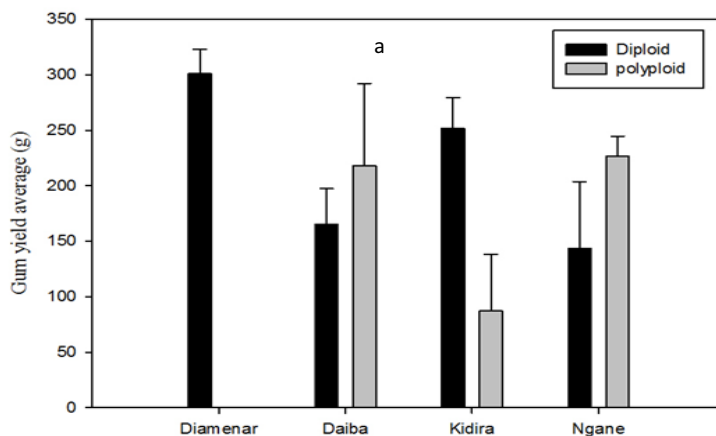


Figure 5. Variation in growth between diploid and tetraploid seedlings of *Acacia senegal* under drought stress conditions

Manuscript II: Study of quantitative genetics of gum arabic production complicated by variability in ploidy level of *Acacia senegal* (L.) Willd. (Accepted by Tree Genetics and Genomes)

The results in manuscript 1 indicate higher performance of polyploids under stressful conditions compared to diploid ones. The objective of the present manuscript was to investigate whether higher ploidy level also confer high ability to produce gum arabic and estimate the genetic parameters for growth and gum traits. This was accomplished through assessment of gum yield during two consecutive years (2012-2013) in the progeny trial. This progeny trial consisted of 60 open-pollinated families originating from four natural populations of *A. senegal* in Senegal. Microsatellite markers confirmed the assumption that diploid families consist of half-sib progenies whereas in polyploid families it was not possible to estimate the outcrossing rate (lack of clear Mendelian segregation). However, an AMOVA analysis lead us to conclude that individuals within polyploid families are much closer related than those within diploid families, which do not support that these families mainly consist of half sibs. Therefore, additive genetic variance was estimated only based on diploid families in order to obtain trustworthy estimates of narrow sense heritability and level of additive genetic variation (V_A). Based on the analysis, the presence of genetic variation in relation to future improvement of gum arabic was quantified by estimating the coefficient of additive variance (CV_A) and narrow sense heritability (h^2_{ns}).

The results showed large genetic variation among provenance and families but there were no clear signs of a consistent effect of ploidy level on gum production (Fig. 6a and 6b).



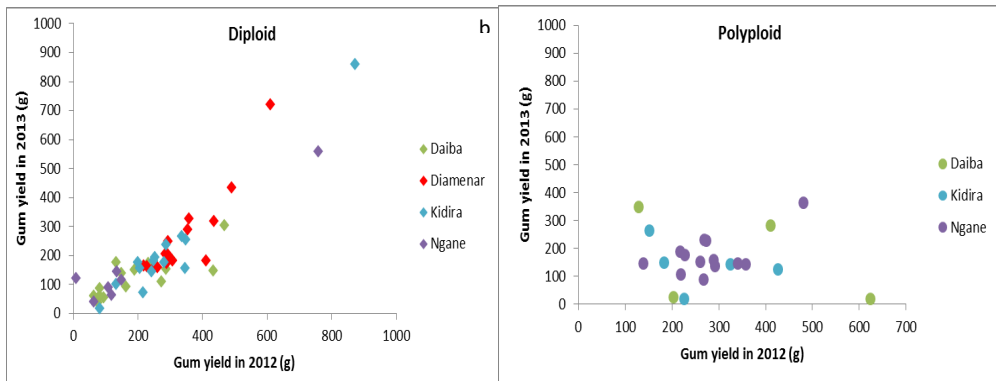


Figure 6. Least square mean estimates of gum yield per tree for different ploidy levels within provenances (a) and family (b) of *Acacia senegal*. Standard errors shown with bars

A highly significant additive genetic variation was observed among families for gum yield across years and in yield average and the estimated narrow sense heritability was relatively high (0.38) as reflected by CV_A values of 32 % (Table 2).

Table 2. Genetic parameter estimates of growth and gum traits for the half sib families in diploid individuals of *A. senegal*. Average performance (least square means) for both diploid and polyplloid trees are provided for reference

Traits	V_A	h^2_{ns}	SE (h^2_{ns})	Lsmeans Diploid	Lsmeans Polyplloid	CV_A (%)
Height (m)	0.05	0.21	0.15	4.53 (0.06)	4.89 (0.14)	5.0
Diameter (cm)	0.61	0.22	0.14	11.71 (0.22)	14.37 (0.51)	6.8
Crown (m)	8.32E-07	0	0	5.43 (0.08)	5.77 (0.18)	0.02
Gum nitrogen content (%)	2.86E-10	0	0	0.39 (0.01)	0.34 (0.02)	0.004
Gum carbon content (%)	5.80E-08	0	0	39 (0.73)	38 (1.11)	0.06
Yield in 2012 (g tree ⁻¹)	948	0.06	0.17	264 (22)	321 (49)	12
Yield in 2013 (g tree ⁻¹)	8216	0.73	0.27	189 (17)	216 (38)	48
Yield average (g tree ⁻¹)	4377	0.38	0.22	227 (18)	269 (40)	32

V_A is the additive genetic variance, h^2_{ns} is the narrow sense heritability SE (h^2_{ns}) is the standard errors of the heritability estimate, Least square means (Lsmeans) of non-transformed data and standard errors (SE) are given for the two ploidy levels and CV_A is the coefficient of additive genetic variance.

Manuscript III: Distribution, coexistence and genetic relationship of diploid and polyploid *Acacia senegal* trees in natural populations in Senegal (Submitted to Evolutionary Ecology)

The results in manuscript I showed that polyploid individuals can co-occur with diploids in nature and in highly variable frequencies, where the highest fraction (84 %) was observed in offspring from a saline area. On this background it was the objective of manuscript III to investigate whether the distribution of polyploids follows any geographical or environmental patterns. Also, based on a wider sampling of natural populations across Senegal, the objective was to study whether polyploid *A. senegal* are likely to be of single or multiple origins. The study was therefore based on sampling and investigating ten natural stands along transects representing different aridity and salinity levels in Senegal. Local-scale cytotype screening of a total of 293 individuals collected from the ten populations was performed using microsatellite markers.

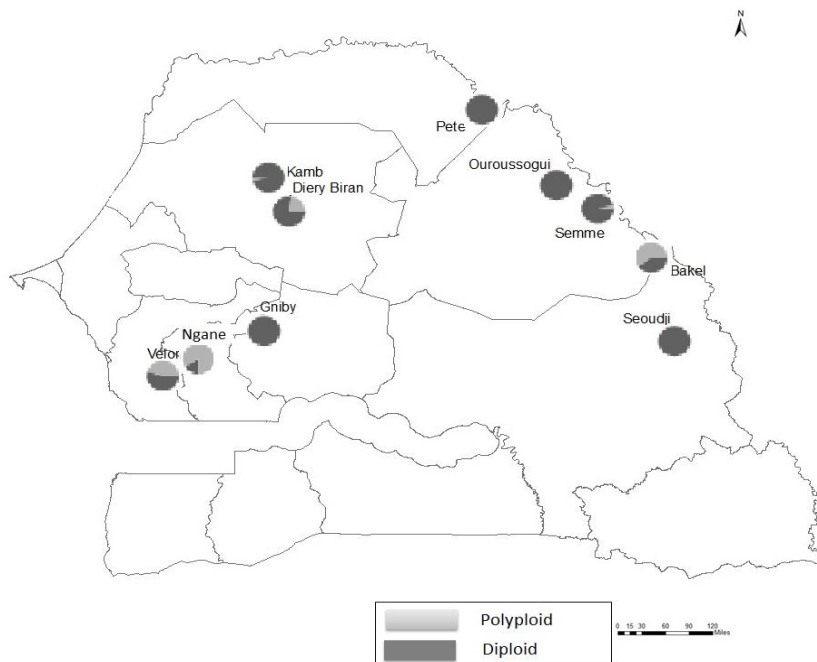


Figure 7. Distribution of diploid and polyploid individuals of *Acacia senegal* in Senegal based on 293 samples from 10 sites analyzed by microsatellite markers.

The results did not reveal a clear geographical pattern in the distribution of polyploids in Senegal (Fig. 7). However, the frequency of polyploids significantly increases with increasing salinity

($P = 0.03$). The analysis of population genetic relationships did not separate the trees clearly according to cytotype (Fig. 8), which suggests multiple origins of the polyploids.

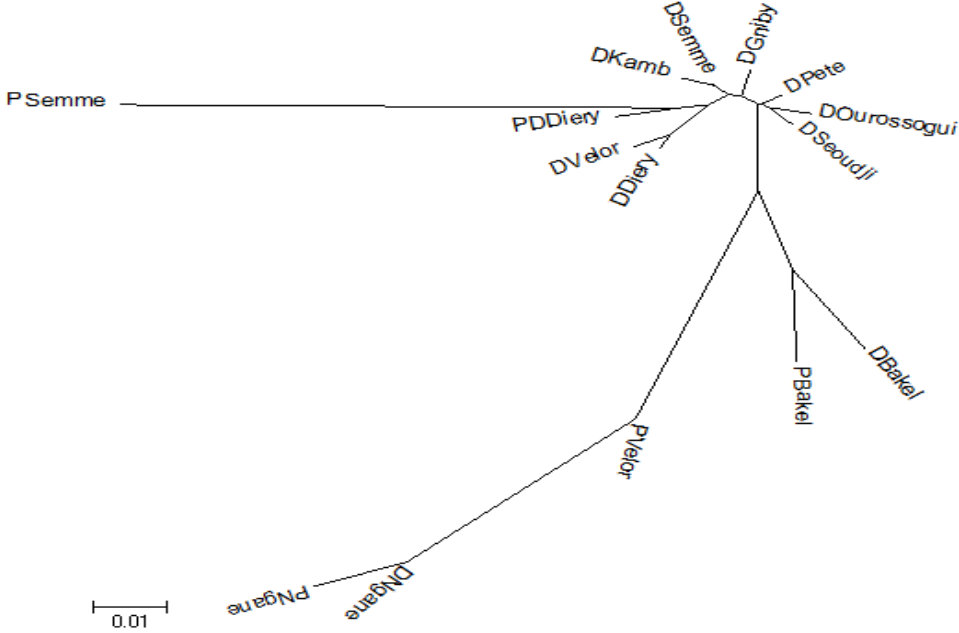


Figure 8. Unrooted neighbor-joining tree of populations (site x cytotypes combinations) based on Nei's genetic distance, calculated using microsatellite markers. The scale indicates the genetic distance.

INTEGRATED DISCUSSION

Adaptive potential of polyploid Acacia senegal in context of climate changes

Polyploids were often reported to be more frequent in harsh conditions (Love and Love 1949; Madlung 2013) and more successful than related diploids in invading relatively disturbed areas (te Beest et al. 2012). The literature provided numerous studies regarding adaptive potential of polyploids under drier conditions in mainly grass species (*Chamerion angustifolium*, Maherali et al. 2009; *Brachypodium distachyon*, Manzaneda et al. 2012; *Atriplex canescens*, Hao et al. 2013). Such studies are scarce in trees, especially for tropical tree species. In a context of climate change, it is important to know whether polyploids can cope better with very dry growth conditions as the Intergovernmental Panel for Climate Change (IPCC) provided strong evidence of accelerated global warming (IPCC 2013). Increase in temperature may lead to decrease in water availability for forest plants and crops in many African countries. Therefore, it is crucial to have information on adaptability of polyploid *A. senegal* to climatic changes for better management strategies and reforestation programs with adapted material for the species.

The progeny trial established in stressful zones proved that polyploid *A. senegal* tree were better performing than diploid ones in terms of growth (biomass production, height) (Manuscript 1). In a short-term growth chamber experiment, tetraploids showed a substantial increase in height when subjected to drought stress (Fig. 5). The analysis of morphological parameters showed that the polyploids tend to be larger than the diploids and are characterized by larger seed size and pinnae length and wider stomata. Whether these aspects provide high adaptive potential to polyploid *A. senegal* is not yet resolved. In addition, in the case that *A. senegal* is allopolyploid, the question whether the observed differences in the phenotype and/or performance are due to hybridization effect and /or genome doubling effect need also to be settle down. Hybridization like polyploidization is reported to facilitate speciation and increase genetic diversity in plants (Hegarty and Hiscock, 2005). Therefore, phenotypic changes observed in polyploid *A. senegal* may be or not a combination effect of natural hybridization with polyploidization (Hegarty and Hiscock, 2005).

Numerous studies have highlighted positive relationship between level of ploidy and drought tolerance (Li et al. 1996; Li et al. 2009; Maherali et al. 2009; Manzaneda et al. 2012; Hao et al. 2013) but the physiological background remains unknown and the role in adaptation controversial. Some authors found improved photosynthetic performance of polyploids under drought stress compared to diploids related to large stomata observed in polyploids conferring change in stomatal conductance by means of increased water use efficiency (Li et al. 1996; Li et al. 2009) while Maherali et al. (2009) reported no change in stomatal conductance and gas exchange between diploid and tetraploid *Chamerion angustifolium* when grown under drought stress conditions. In polyploid *A. senegal*, differences in adjustment of the osmotic potential may play a role, because tetraploid seedlings were found to have higher fresh weight than diploid seedlings, indicating either higher ability to absorb scarce water available in the soil, or improved ability to store larger quantity of water in its cells controlling water loss.

Effectiveness of breeding programs for high gum yield production

Although *Acacia senegal* was one of the earliest domesticated species in tropical drylands because of its benefits (i.e., gum arabic, fuel, fodder, soil fertilizers), till now only few studies have provided reliable information on genetic variation in gum yield (Ouédraogo 2001; Raddad and Luukkanen 2006; Larwanou et al. 2010; Soloviev et al. 2010). Manuscript 1 acknowledges presence of different levels of ploidy in *A. senegal* and higher tolerance to stressful conditions of polyploids. Previous studies have highlighted that gum production is correlated to the reduction of water storage in the soil (Vassal et Dione 1993; Anderson 1995; Wekesa et al. 2009). In a context of sustainable improvement of gum arabic production, it is of highly relevance to study whether polyploids and diploids differ in their ability to produce gum arabic. Manuscript 2 showed no differences in gum yield between cytotypes. However, gum yield appear to be under moderate genetic control as heritability estimates for diploids were found to be moderate to high. In our study, substantial genetic variation in gum arabic production was observed at both provenance and family levels for both levels of ploidy. This result is in line with previous findings of Gray et al. (2013) who reported large provenance to provenance variation in provenance trial suggesting that selection for high gum yield could be based at provenances level. Together with the findings in the present study, this suggests that establishment of breeding seed orchards for diploids (BSO) would be an interesting option (cf. Dhakal et al 2005).

In polyploids, attention should be paid to their mating system. Polyploid *A. senegal* was found to differ from diploid *A. senegal* in their sibling-relationships, which is in line with findings from other species where shift from diploidy to polyploidy has been reported to be associated with shift in mating system from outcrossing towards selfing or apomixes (Stone 2002; Hörandl 2010). If polyploid *A. senegal* are revealed as partly of predominantly apomictic, this will have importance for deployment of selected trees, because in case of apomictic reproduction, clonal propagation of superior genotypes can be made through seed.

Evolution of polyploidy in A. senegal

Polyploids have previously been reported to often have different ecological requirements compared to their diploids ancestors, probably due to new gene combinations allowing them to invade harsh areas where they are better fitted than the diploid ancestors (Ramsey 2011). Manuscript I and III document co-occurrence of both cytotypes in Senegal with diploids being predominant in most, but not all, populations. The finding of local co-occurrence of different cytotypes is not unusual. Lumaret et al. (1987) reported different cytotypes in *Dactylis glomerata*. Local co-occurrence of cytotypes can enable gene exchange between cytotypes in case of moderate or weak reproductive barriers (Herrera et al. 2004; Martonfiova 2006). The findings of manuscript I suggest that diploid individuals always produced diploid offspring while tetraploid plants gave rise to mainly tetraploid offspring, but also few individuals with higher levels of ploidy were also observed. This pattern could be explained by the observed difference in pollen and stigma cup between cytotypes (Fig. 4). Potentially tetraploid polyades will not be able to fit into diploid stigma cups because of the size whereas the opposite may be possible.

The pattern of genetic differentiation (presented by the NJ tree, Fig. 8) does not suggest that trees with similar cytotypes from different populations are more related than trees with different cytotypes for the same population. This suggests multiple origins of polyploidy in *A. senegal*, which is in agreement with the results of Assoumane et al. (2013) and Odee et al. (2015). Multiple origins of polyploidy was for long time considered as a rare phenomenon (Soltis and Soltis 1993; Ramsey and Schemske 1998), but is now considered more common since numerous studies have highlighted this phenomenon (i.e., Soltis and Soltis 1999; Segreaves et al. 1999; Soltis et al. 2004; Parisod and Besnard 2007; Arrigo et al. 2010).

CONCLUSION AND PERSPECTIVES

In summary, the studies undertaken in this PhD pointed out the importance of polyploidy in *A. senegal*. By promoting evolutionary novelties, prevalence of polyploidy in tropical tree species (i.e. *Adansonia digitata*, *Acacia senegal*, *Acacia tortilis* and *Acacia raddiana*) could be important for development of novel strategies to face harsh growing conditions occurring in Sahel. Even though valuable information has been accumulated since 2012, many questions still remain unresolved.

The present studies revealed that polyploids grew faster than diploids. Whether this difference in performance is attributable to different eco-physiological responses (i.e., photosynthetic responses, stomata conductance, osmotic adjustment) under stressful conditions are still not yet studied. However, such research is on-going. A trial representing individuals with different levels of ploidy (diploid, triploid, tetraploid, pentaploid and hexaploid) has been established in a greenhouse and physiological traits such as stomata conductance, stomata opening and closure, photosynthetic traits have been assessed from 2014 and will be finalized during spring 2015. The results of this study will hopefully provide new insights on physiological differences between ploidy levels and allow identification of traits conferring the high adaptive potential of polyploids.

Also the mating system in polyploid *A. senegal* is to be clarified. Results from manuscript II confirm that the mating system is different in polyploids compared to diploids. Diploids were mainly outcrossing and single tree collections mainly consisted of half-sib progeny. This was in contrast to polyploids, where self-fertilization or apomixis seems to be likely more common than outcrossing. More research into this field is important, because a good understanding of the mating system is basic for operational breeding activities, data analysis and deployment activities.

To investigate the mating system in polyploids, controlled crosses were initiated in August 2014 in the progeny trial in Senegal. The experiment included eight parents (four diploids and four tetraploids) and the main purpose was to check any presence of reproductive barriers between cytotypes. The difference in pollen and stigma cup size combined with the observed ploidy level in offspring from diploid mother trees, suggest presence of reproductive barriers, but mainly in one direction. The results from the crossing experiments were inconclusive and should be repeated under protection and with the inclusion of a triploid mother. This would allow us to test the potential role of triploid trees in forming a reproductive bridge between diploid and tetraploid trees.

Another debate that needs to be settled is about the origin of polyploid *A. senegal*. Results from chloroplast markers of three tetraploid populations of *A. senegal* across its natural distribution in Africa supported allopolyploid origin (Assoumane et al. 2013) while Odee et al. (2015) suggested a possible autopolyploid origin. Our study reported recurrent formation of polyploidy at local scale. Therefore, further investigations on whether different parental genotypes are involved in producing different polyploid genotypes having different evolutionary potentials are needed.

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LIST OF MANUSCRIPTS

Manuscript I: Polyploidy confers superiority to trees grown under stressful conditions: a case study of *Acacia senegal* (L.) Willd. in the Sahel region of West Africa. Submitted to Botanical Journal of the Linnean Society.

Manuscript II: Study of quantitative genetics of gum arabic production complicated by variability in ploidy level of *Acacia senegal* (L.) Willd. Tree Genetics and Genomes (2015).

Manuscript III: Distribution, coexistence and genetic relationship of diploid and polyploid *Acacia senegal* trees in natural populations in Senegal. Submitted to Evolutionary Ecology.

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