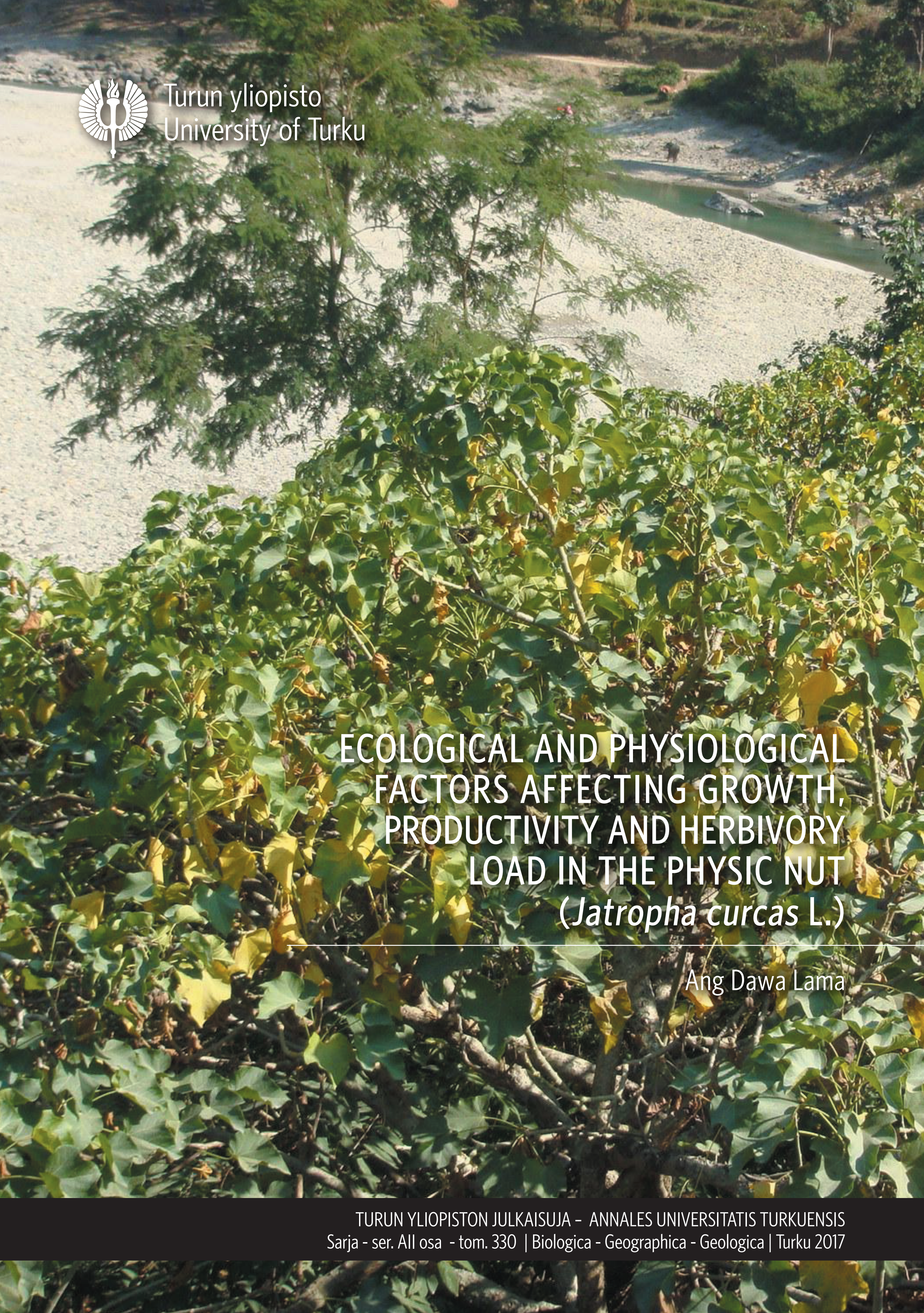

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Ang Dawa Lama

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LIST OF ORIGINAL ARTICLES

The thesis is based on the following articles, referred to in the text by their Roman numerals.

I. Lama AD, Kim J, Martiskainen O, Klemola T, Salminen J-E, Tyystjärvi E, Niemelä P & Vuorisalo T (2016) Impacts of simulated drought stress and artificial damage on concentrations of flavonoids in *Jatropha curcas* (L.), a biofuel shrub. – **Journal of Plant Research** 129: 1141—1150

II. Lama AD, Klemola T, Tyystjärvi E, Niemelä P, Vuorisalo T. Physiological and compensatory growth responses of *Jatropha curcas* (L.) seedlings to simulated herbivory and drought stress.– Submitted Manuscript

III. Lama AD, Vuorisalo T & Niemelä P (2015) Global patterns of arthropod herbivory on an invasive plant, the physic nut (*Jatropha curcas* L.). – **Journal of Applied Entomology** 139: 1—10

IV. Lama AD, Klemola T, Saloniemi I, Niemelä P, Vuorisalo T. Factor affecting genetic and seed yield variability of *Jatropha curcas* (L.) across the globe: a review.– Submitted Manuscript

Article **I** has been reprinted with permission of Springer Verlag and The Botanical Society of Japan and article **III** has been reprinted with permission from Wiley-Blackwell publishing.

Author contribution to the original publications

	I	**II**	**III**	**IV**
Original idea	ADL, PN, TV	ADL, PN, TV	ADL, PN, TV	ADL, TV
Experimental design	ADL, PN, TV	ADL, PN, TV		
Data collection	ADL	ADL	ADL	ADL
Chemical analysis	JK, OM, JKS			
Statistical analysis	ADL, TK	ADL, TK	ADL	ADL, TK
Manuscript preparation	ADL, JPS, TK, ET, PN, TV	ADL, TK, ET, PN, TV	ADL, PN, TV	ADL, IS, TK, PN, TV

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Tero Klemola (TK), Juha-Pekka Salminen (JKS), Esa Tyystjärvi (ET), Pekka Niemelä (PN),
Timo Vuorisalo (TV)

ABSTRACT

Jatropha curcas (L.) is a multipurpose oil bearing shrub assumed to be able to survive in a wide range of ecological conditions across the tropical regions of the world. The thesis is composed of two parts, the first one based on experimental research, and the second one on literature reviews. In the experimental part, I assessed the effects of simulated herbivory and drought stress on defence, physiology and compensatory growth of *J. curcas* seedlings (**I** and **II**). In the latter part I reviewed arthropod herbivores, seed yield and genetic variability of *J. curcas* across the globe (**III** and **IV**). Experimental results showed that the highest concentration of flavonoids was found in the leaves of *J. curcas* seedlings exposed to 50 % herbivory stress and grown in 200 mm y^{-1} rainfall, whereas the lowest growth and biomass was produced by *J. curcas* seedlings exposed to 25 % herbivory stress and grown in 200 mm y^{-1} rainfall (**I** and **II**). *J. curcas* seedlings exhibited an undercompensatory growth response to herbivory stress in all the drought stress levels (**II**). Our literature review showed that arthropod herbivore load associated with *J. curcas* was relatively low (78 species) across the globe. Flower and fruit feeders were more common than foliage feeders (**III**). The highest average genetic diversity was observed, as expected, within the native range of *J. curcas* (**IV**) with record levels observed in populations sampled in the State of Chiapas of Mexico. The annual seed yield varied greatly across the globe from 26 to 11,150 kg ha^{-1}; the global mean annual seed yield was 2,220 kg ha^{-1}. Age had a linear whereas rainfall and plant density had a significant quadratic effect on seed yield. Differences in seed yields of *J. curcas* across the globe might be due to differences in site-specific agro-climatic, soil fertility and genetic factors as well as agronomic practices applied to achieve a high seed yield (**IV**). Further genetic improvements will be required to produce cultivars which can provide consistently high seed and oil yields. My results contribute to promote commercial production of *J. curcas* by providing more information on the ecological requirements of the species.

TIIVISTELMÄ

Jatropha curcas (L.) on monikäyttöinen öljykasvi, joka menestyy hyvin vaihtelevissa ekologisissa olosuhteissa maapallon trooppisilla alueilla. Väitöskirjani koostuu kahdesta osasta, kokeellisesta ja kirjallisuuteen perustuvasta. Kokeellisessa osassa tutkin simuloidun herbivorian ja kuivuus käsittelyjen vaikutusta *Jatropha curcaksen* siementaimien fysiologiaan, puolustukseen ja kompensaatiokasvuun (**I** ja **II**). Työni jälkimmäisessä osassa tarkastelen kirjallisuuteen perustuen lajilla tavattavia niveljalkais herbivoreja sekä siemensadon ja geneettisen monimuotoisuuden vaihtelua levinneisyysalueen eri osissa (**III** ja **IV**). Kokeissa havaittiin korkeimmat flavonoidipitoisuudet niiden kasvien lehdissä, joiden lehtipinta-alasta oli poistettu 50 % ja joiden saama sademäärä oli 200 mm v^{-1}, kun taas kasvu oli hitainta ja biomassa pienin niillä kasveilla, joiden lehtipinta-alasta oli poistettu 25 % ja joiden saama sademäärä oli 200 mm v^{-1} (**I** ja **II**). *Jatropha curcaksen* kasvuvaste herbivoriaan oli alikompensoiva kaikissa kuivuus käsittelyissä (**II**). Kirjallisuuskatsaus osoitti niveljalkais herbivorian olevan melko vähäistä (kokonaislajimäärä 78 lajia) levinneisyysalueen eri osissa. Kukkien ja hedelmien syöjät olivat lehtibiomassan syöjiä yleisempiä (**III**). Odotusten mukaisesti geneettinen monimuotoisuus oli suurin lajin alkuperäis alueilla (**IV**); korkein monimuotoisuus aste havaittiin Meksikossa Chiapasin osavaltion populaatioissa. Vuotuinen siemensato vaihteli levinneisyysalueen eri osissa suuresti välillä 26-11,150 kg ha^{-1} keskisadon ollessa 2,220 kg ha^{-1}. Kasvin ikä vaikutti satoon lineaarisesti mutta sademäärä ja kasvitiheys kvadraattisesti. *Jatrophan* siemensadon vaihtelu eri alueiden välillä voi johtua paikallisista ilmasto- ja maaperä olosuhteista, geneettisistä tekijöistä tai sadon lisäykseen käytetyistä viljely tekniikoista (**IV**). Siemen- ja öljysadon lisääminen vaatii geneettisesti parempien lajikkeiden käyttöönottoa. Työni tulokset hyödyttävät *Jatrophan* viljely hankkeita tuottamalla tarvittavaa tietoa lajin ekologisista kasvupaikka vaatimuksista.

1. INTRODUCTION

1.1. Biology and productivity of *J. curcas*

J. curcas (Euphorbiaceae) is a perennial deciduous and multipurpose oil bearing shrub with great but so far not fully realized economic potential (Achten et al. 2008; Achten et al. 2010; Heller 1996; Maes et al. 2009a). It grows upto 8-10 m height under appropriate environmental conditions, and individual plants may produce seed for 50 years (Fairless 2007; Heller 1996). It is a monoecious shrub with female and male flowers located in the same inflorescences, female flowers located at the apical and male flowers at the subordinate positions (Brittaine and Lutaladio 2010; Heller 1996; Raju and Ezradanam 2002). Flowers are small and white, and there are usually significantly more male than female flowers (Raju and Ezradanam 2002). Initially the fruit is green but its colour changes from yellow to black in the course of ripening (Heller 1996). A fruit contains three seeds and each seed contains 35 - 60 % of non-edible oil that can be used as biofuel directly blended with fossil fuels (Heller 1996; Jongschaap et al. 2007; Kumar and Sharma 2008; Openshaw 2000). Due to climate change and gradual depletion of fossil fuel reserves many researchers and policy makers have shown interest in this shrub as a potential source of biofuel production (Fairless 2007; Jongschaap et al. 2007; Kumar and Sharma 2008; Openshaw 2000).

J. curcas can thrive in a wide range of ecological conditions from arid to humid tropical environments (250 - 3,000 mm y^{-1} and 15 - 40 °C) (Achten et al. 2008; Carels 2009; Khair and Atta 2009). It grows up to 1,500 m altitude above the sea level in Nepal (Lama 2010), and is very common below 500 m altitude in the tropical parts of the world (Heller 1996). *J. curcas*, grows rapidly, requires a lot of light and prefers well drained and aerated soils (Carels 2009; Kumar and Sharma 2008). As its root system has one tap root and four lateral shallow roots, it can effectively extract water and nutrients from all soil layers (Carels 2009; Krishnamurthy et al. 2012; Heller 1996). Although *J. curcas* may survive in arid and semi-arid conditions, rapid growth and high seed yields are only achieved on sites with a fair amount of rainfall and deep enough soils (45 cm) (Carels 2009; Krishnamurthy et al. 2012). It is sensitive to water logging and frost (Gimeno et al. 2012; Heller 1996), and is not browsed by vertebrate herbivores (Heller 1996). Due to its ecological flexibility, it has been considered a useful plant for biofuel production, erosion control and land rehabilitation (Achten et al. 2008; Fairless 2007; Openshaw 2000; Pandey et al. 2011; Wani et al. 2012).

As noted above, *J. curcas* is considered a drought resistant species able to grow and survive in drought prone areas (Heller 1996; Jongschaap et al. 2007; Kumar et al. 2012). It utilizes drought avoidance strategies during periods of drought (Maes et al. 2009a). These include reduction of stomatal conductance and leaf size (Diaz-Lopez et al. 2012; Maes et al. 2009a), an effective osmotic adjustment mechanism (Silva et al. 2010), and accumulation of organic solutes in leaves during the drought periods (dos Santos et al. 2013). Furthermore, *J. curcas* leaves have effective mechanisms against drought-induced photo-oxidative damage (Silva et al. 2012). As it is a stem succulent shrub, small water losses in leaves may be balanced by water import from stem (Maes et al. 2009a).

Although *J. curcas* can tolerate moderate drought, its profitable cultivation in arid or semi-arid regions may be questioned (Fini et al. 2013). At least the seed yield in low rainfall sites is considered economically unprofitable (Maes et al. 2009b). Despite low direct economic benefits in such sites, it may still provide important ecosystem services such as carbon sequestration or soil erosion control in vulnerable areas (Wani et al. 2012). *J. curcas* is still considered as a semi-wild plant (Rajaona et al. 2013; Singh et al. 2013) and its compensatory growth responses to herbivore damage in various ecological conditions are poorly known. Earlier studies have focused on growth responses of *J. curcas* against drought and herbivory stress separately (Achten et al. 2010; Grimm and Maes 1997; Maes et al. 2009a; Sharma and Srivastav 2011). Many studies have, however, shown that multiple stress factors may have non-additive effects on plants and thus interactions cannot be reliably modeled on the basis of studies performed on single stress factors (Bansal 2015).

Although *J. curcas* is considered herbivory resistant, some arthropod herbivores have been reported to be associated with it (Grimm and Maes, 1997; Ranga Rao et al. 2010). Grimm and Maes (1997) reported 15 Hemipteran herbivores and Ranga Rao et al. (2010) 40 insects pests observed to feed on *J. curcas*. All these pieces of evidence implicate that *J. curcas* may be vulnerable to invertebrate herbivores. Plants under herbivory stress may produce secondary metabolites, especially phenolics, as their defense mechanism (Agrawal 2011; Coley et al. 1985). The principal plant defense hypotheses are the growth differentiation balance hypothesis, carbon-nutrient balance hypothesis, optimal defense hypothesis and growth rate or resource availability hypothesis (Bryant et al. 1983; Coley et al. 1985; Herms and Mattson 1992; Rhoades and Cates 1976). Making accurate predictions and testing of these hypotheses is not easy for a number of reasons (Stamp 2003). Little information is available on secondary metabolites of *J. curcas* and their roles.

Although there has been no definite consensus on the geographical origin of *J. curcas*, a recent study indicates that Mexico belongs to its centres of origin (Guo et al. 2016). *J. curcas* has been disseminated across the tropical regions of the world first by Portuguese seafarers and later by others interested in its economic value (Heller 1996). However, comprehensive information on genetic diversity of *J. curcas* in different parts of its current range has been lacking, and earlier studies have provided contradictory results (Gupta et al. 2008; Kumar et al. 2009; Pioto et al. 2015; Rosado et al. 2010). One of my objectives was to consolidate available genetic information scattered in a high number of studies to generate a more complete genetic picture of this plant both within its native and non-native range.

Since its introduction to new areas, it has been utilized for oil-based soap production, medicinal purposes and as a hedgerow plant around agricultural fields (Heller 1996; Prasad et al. 2012). *J. curcas* plantations in arid and semi-arid sites improve the biological, physical and chemical properties of soil by depositing a large amount of organic material (Wani et al. 2012). Although some authors have been optimistic about its productivity also in degraded and low precipitation areas (Fearless 2007; Openshaw

2000), others have been more sceptical mainly based on modest seed yields obtained from mono plantations (GTZ 2003; Pohl 2010).

1.2. Purpose of the thesis

My thesis is composed of two parts, the first one based on experimental research (**I** and **II**) and the second one (**III** and **IV**) on literature reviews. The objective of article **I** was to measure the composition and changes in concentrations of flavonoids in leaves of *J. curcas* seedlings under simulated herbivory and/or drought stress and to assess their possible role either as antioxidants or as antiherbivory chemicals. Article **II** mainly focused on the effects of simulated herbivory and drought stress on physiology, compensatory growth responses and resource allocation in *J. curcas* seedlings to identify the ecological threshold levels necessary for the successful establishment of *J. curcas* seedlings at different agro-climatic conditions in the field. Article **III** focused on first compiling a list of all arthropod herbivores associated with *J. curcas* across the globe, secondly on performing a biogeographical analysis of observed herbivory patterns, thirdly on investigating the importance of native versus alien herbivores in all the continents, and finally on compiling data on the feeding ecology and taxonomic distribution of arthropod herbivores in different areas of the current range of *J. curcas*. The last article **IV** focused to review the genetic and seed yield variability of *J. curcas* across the globe, and more specifically, to review factors responsible for the observed genetic diversity and wide seed yield variability.

2. MATERIALS AND METHODOLOGY

2.1. Experimental setup

For articles **I** and **II**, the experiment was carried out in a greenhouse in the Ruissalo Botanical Garden of the University of Turku, Finland. Seeds of *J. curcas* were collected on November 2010 in Nepal. Seeds were sown in seed beds on 2 May 2011 and transplanted into pots after emergence of two true leaves. A 3^2- factorial experiment was set up with two factors: artificial herbivory and drought stress. Both treatment factors had three intensity levels and all treatment combinations had nine replications. Seedlings were irrigated simulating three different levels of annual rainfall (1,900 mm, 800 mm and 200 mm), and subjected to three different levels of artificial herbivory stress (0 %, 25 % and 50 %) mimicking damage caused by foliage feeder arthropod herbivores. Invertebrate herbivory was simulated by cutting 0 %, 25 % or 50 % of each leaf blade of the seedlings by scissors and different rainfall levels by variable irrigation levels. Treatments were imposed on 74 days old *J. curcas* seedlings, which were raised in optimal growth conditions. Eighty one seedlings were grown in nine different growth conditions (9 seedlings in each growth condition) in terms of artificial herbivory stress and drought stress. All other abiotic factors were the same and kept constant for all the seedlings during the treatment period (**I** and **II**).

2.2. Leaf sample collection and flavonoid analysis

Leaf samples were collected three times from the same *J. curcas* seedlings, once before and twice after imposing treatments. Leaf samples were packed in aluminium foil immediately after detaching them from the seedlings and put into a collection box at 0 °C before transport to freezer. Leaf samples were stored at -20 °C before freeze-drying and chemical analysis. Flavonoid analysis was performed in the Natural Chemistry Research Group, Department of Chemistry, University of Turku, Finland. Ultra-high performance liquid chromatography coupled with diode array detection and mass spectrometry (UPLC-DAD-MS/MS) was used to analyse flavonoids from plant extracts (**I**). Frozen leaves were lyophilized and extracts were prepared. All *J. curcas* extracts were analysed by the rapid and selective finger printing tools developed by Engström et al. (2015). All flavonoids were detected and quantified at 349 nm by using quercetin rutinoside as an external standard (**I**).

2.3. Photosynthesis data

PAM-2100 Chlorophyll Fluorometer was employed to measure photosynthesis in study plants (PSII). Yield of PSII electron transfer (Y) was calculated as $Y= (F'_M-F_S)/F'_M$. The second leaf (20-30 days old leaves) from the stem base to tip was used to measure photosynthesis. Measurements were taken three consecutive days from the same leaf. Erratic fluorescence data points were omitted from the data before further analysis (**II**).

2.4. Growth and biomass measurements

Diameter (mm) at base and height (cm) of *J. curcas* seedlings was measured on the 30th day of every month for thirteen months during the experiments. In final harvesting, leaves, branches and roots were separated from the stem and their fresh weights were recorded immediately after harvest. Dry weights were measured after oven drying at 84 °C for 48 h until constant weights were obtained. Root-shoot ratio of seedlings was calculated dividing total dry roots biomass by dry total aboveground biomass (**II**).

2.5. Data collection in literature reviews

Articles **III** and **IV** were based on literature. Data were extracted from the online available published and unpublished literature with the help of various online research engines using key words (e.g. insect, arthropod herbivores, genetic diversity, seed yield, productivity of *J. curcas*). For article **III**, all the available data on arthropod herbivores associated with *J. curcas* was extracted from the available online documents. Native ranges of arthropod herbivores were checked from online sources and references books. In the biogeographical analysis arthropod herbivores were categorized within each region (Central and South America, Africa and Asia) based on their origin and status in the new area. *J. curcas* was considered a native species in Latin America, and introduced elsewhere (Heller 1996). Arthropod herbivores were further segregated based on their feeding guild (**III**). For article **IV**, genetic data were extracted from 46 published articles. Percentages of polymorphic bands detected by different molecular markers on *J. curcas* across the globe were extracted to measure genetic diversity. Seed yield data were extracted from 92 published and unpublished literary sources collected with help of various online search engines. Seed yield data were analysed separately for each region (Latin America, Africa and Asia). All available background information (both biotic and abiotic) that could explain seed yield variability of *J. curcas* was extracted (**IV**).

2.6. Reliability of online collected data

The validity of results of my review papers depends on the reliability and coverage of data in published or unpublished literature. For article **III**, the most comprehensive studies were performed by Grimm and Maes (1997), Nielsen (2010) and Shanker and Dhyani (2006). For article **IV**, genetic data were extracted from 46 published articles whereas seed yield data were collected from 49 published peer-reviewed articles, 4 dissertations and 39 blue documents covering 38 countries (19 from Africa, one from South Asia, 8 from South East Asia and 10 from Latin America). Cai et al. (2010), Maghuly et al. (2015), Santos et al. (2016), and Zhang et al. (2011) analyzed genetic diversity of *J. curcas* on a quite large number of accessions across the globe. Some authors have also done remarkable studies on seed yield (Achten et al. 2008; Jongschaap et al. 2007; Santoso et al. 2014; Singh et al. 2013; van Eijck et al. 2014; Wahl et al. 2012). In articles **III** and **IV**, I synthesized data collected from these and other literary sources.

2.7. Statistical analyses

All flavonoid and growth data with repeated measures were analyzed by SAS 9.4 statistical software (**I** and **II**). Data of biomass, biomass characteristics and photosynthesis were analyzed by IMB SPSS 22 Statistics using a two-way ANOVA (**II**). Arthropod herbivory, genetic diversity and seed yield variability data were also analyzed by the GLM procedure of the SAS statistical software (v. 9.4) and the IMB SPSS 22 Statistics (**III** and **IV**).

3. RESULTS AND DISCUSSION

3.1. Defensive responses of *J. curcas*

Among the nine treatment combinations, the highest concentrations of flavonoids were found in the leaves of seedlings grown in the least favourable treatment combination (50 % defoliation × 200 mm y^{-1} rainfall; **I**). Concentration of flavonoids in leaves of seedlings was primarily influenced by drought stress caused by simulated rainfall and the effects of simulated herbivory were considered negligible (**I**). Results of article **I** thus emphasize the antioxidant role of flavonoids in leaves of *J. curcas* rather than their possible antiherbivory function. These results are supported by an earlier study (Close and McArthur 2002).

Under drought stress, plants reduce utilization of incoming light energy (Henández and Breusegem 2010) which increases production of reactive oxygen species (ROS) (Close and McArthur 2002). Under this situation, plants produce antioxidant enzymes to scavenge ROS and thereby reduce oxidative damage (Close and McArthur 2002; Henández and Breusegem 2010; Massad et al. 2012) and photodamage (Agati et al. 2011; Agati and Tattini 2010; Close and McArthur 2002; Hakala-Yatkin et al. 2010; Herms and Mattson 1992; Miean and Mohamed 2001). As leaf samples were collected from the lower canopy of seedlings, they represented in the most extreme treatment combination those leaves that had been exposed to higher intensity of light than leaves representing less stressful treatment combinations (**I**). This is because leaf sizes in the most extreme treatment combination were due to severe drought much smaller than those in other treatments (Fini et al. 2013; Maes et al. 2009a). According to our interpretation, sunlight and drought were the main factors that had triggered increases in flavonoid concentrations in the leaves of seedlings (**I**).

In the experiment, we originally assumed that concentrations of flavonoids in the leaves of seedlings might increase as a response to herbivory stress (**I**). The resource availability hypothesis states that slowly growing plants from resource-poor sites are better defended against herbivory stress than fast growing plants from resource rich sites (Agrawal 2011; Coleyet al. 1985). Similarly, the growth differentiation hypothesis claims that plants invest more in secondary metabolism than growth in sites with resource scarcity (Herms and Mattson 1992). The seedlings grown under extreme treatment combination might be incapable to uptake all the nutrients unlike the seedlings grown in more favourable treatment combinations. However, the seedlings exposed to extreme treatment combination produced three times more defensive flavonoid compounds in their leaves than seedlings with the same level of herbivory stress but grown under higher precipitation conditions (≥ 800 mm y^{-1}, **I**). Similar results were observed by Khan et al. (2011). We therefore concluded that the high concentrations of flavonoids in the leaves of *J. curcas* seedlings grown in the extreme treatment combination were mainly due to effects of drought stress rather than to effects of simulated herbivory stress (**I**).

3.2. Photosynthesis of *J. curcas*

Among the nine treatment combinations, the lowest PSII yield was observed in the leaves of *J. curcas* seedlings exposed to the extreme treatment combination (**II**). This might be due to drought stress, which forces closing of stomata and reduces CO_2 concentration inside drought-stressed leaves (Diaz-Lopez et al. 2012; Fini et al. 2013; Maes et al. 2009a). Drought stress also triggers production of ROS, which hamper photo-inhibition of PSII (Cruz de Carvalho 2008) and hinder the repair of photoinhibited PSII centers (Tyystjärvi 2013; Wadhwa et al. 2013). Despite these inhibitory effects of drought, the plant is able to continue photosynthesis during long periods of drought due to its efficient protective mechanisms such as synthesis of compatible solutes and use of the stem as a water reservoir for leaves (see Introduction; dos Santos et al. 2013; Maes et al. 2009a). Possible further increases in water deficit would decrease the turgor pressure in leaves of *J. curcas* progressively and could lead to cessation of photosynthesis (Silva et al. 2010). Effects of simulated herbivory stress on PSII yield of *J. curcas* were negligible in comparison to effects of drought stress (**II**). Simulated herbivory and drought stress in combination reduced total leaf area and thereby opened the canopy so that higher intensity of sunlight could reach the leaves in lower portions of seedlings, where we measured the PSII yield. Increased exposure to sunlight may have lowered the PSII yield in these treatments due to partial closure of the reaction centers due to higher light intensity (Retuerto et al. 2006).

3.3. Growth and biomass allocation of *J. curcas*

Herbivory stress had maximum effects on stem biomass production in the extreme drought stress (200 mm y^{-1}) and higher effects on root biomass production on seedlings grown under lower drought stress conditions ($\geq$ 800 mm y^{-1}; **II**). Seedlings grown in medium drought stress (800 mm y^{-1}) benefitted from herbivory stress (**II**). These results parallel those of an earlier study, which showed that growth of *J. curcas* starts to decline when the optimal rainfall level of 1,500 mm y^{-1} is exceeded; relatively good growth was already observed at the level of 900 mm y^{-1} (Trabucco et al. 2010). According to another study *J. curcas* requires 200 mm y^{-1} rainfall to survive, 600 mm y^{-1} to bear fruits and at least 900 mm y^{-1} for proper growth (Foidl et al. 1996; Krishnamurthy et al. 2012). Our experiment confirmed that seedlings grown under 200 mm y^{-1} rainfall just survived but did not grow well (**II**). Herbivory stress increased the root-shoot ratio of seedlings in extreme drought stress but reduced the root-shoot ratio in lower drought stress conditions (**II**). These phenomena might be explained by retarded root growth and development caused by herbivory (Erbilgin et al. 2014; Masters et al. 1993).

3.4. Compensatory growth response of *J. curcas*

Plants response to herbivore damage by compensating damaged vegetative tissue as quickly as possible (Strauss and Agrawal 1999). When growth of a damaged plant is lower than that of an undamaged plant, the response of plant is considered an undercompensatory growth response (Strauss and Agrawal 1999). Our experimental results showed that the response of seedlings to herbivory stress was undercompensatory because growth of all the herbivory stressed seedlings was lower than growth of unharmed seedlings and compensatory growth response varied among the different drought stress levels (**II**). Responses of plants to herbivory stress depend on surrounding environments (Maschinski and Whitham 1989; Wise and Abrahamson 2005). Apparently no single herbivory model can explain the responses of plants to herbivory as the responses vary greatly not only among sites but also among plant species (Hawkes and Sullivan 2001; Karban et al. 1999).

3.5. Arthropod herbivory load of *J. curcas* across the globe

Our literature review showed that there were 78 arthropod herbivores associated with *J. curcas* across the globe, 54 % of them belonging to Hemiptera and 49 % of species reported from the native range (**III**). Ranga Rao et al. (2010) reported 40 arthropod herbivore species of *J. curcas* across the globe. Based on these results, the arthropod herbivore load associated with it seems low in comparison to other tropical plant species (Bellotti et al.1985; Bellotti and Schoonhoven 1978).

The low arthropod herbivore load of *J. curcas* may be explained by three factors. First, the low herbivore load may be caused by the presence of toxic chemicals such as phorbol ester in its seeds and leaf tissue. Phorbol esters are toxic even in low concentrations (Goel et al. 2007). Studies show that many insect herbivores have been reported to be significantly affected by *J. curcas* extracts (Ratnadass and Wink 2012). Zhang et al. (2009) reported 41 different chemical compounds from *J. curcas*. Second, invasive plants may experience relatively low herbivore pressure in their exotic range due absence of their native specialized herbivores (Cripps et al. 2006), and the fact that generalist herbivores in the new areas usually do not prefer newly introduced hosts (Keane and Crawley 2002). My results seem consistent with this hypothesis. The highest number of arthropod herbivores species were observed within its native range (**III**). Third, introduced plant species having many confamilial species suffer greater amounts of herbivory stress than species without confamilials in their new area (Alain et al. 2006; Tahvanainen and Niemelä 1987). Although this seems to be the case for some invasive plants (Cappuccino and Carpenter 2005; Dawson et al. 2008), it does not seem to hold for *J.curcas* because it is not isolated taxonomically outside its native range (**III**). Although the literature review showed generally low arthropod herbivore loads on *J. curcas* (**III**), herbivore load may increase in future if monoculture plantations gain more prevalence.

3.6. Genetic diversity of *J. curcas* across the globe

Our literature review showed that genetic diversity is high within the native and moderate in the non-native range of *J. curcas* (**IV**). Genetic uniformity was reported among the plants from Africa and Asia (Montes Osorio et al. 2014; Santos et al. 2016; Xu et al. 2012) whereas Zhang et al. (2011) reported genetic differences between the Asian and African populations. African plants may have separated from the main group after introduction to Cape Verde, and Indian plants may descend from two distinct germplasms (Guo et al. 2016; Pamidimarri and Reddy 2014). Genetic analysis done on the largest number (907) of accessions collected from 53 regions covering 15 countries showed that genetic diversity does not increase with increasing geographical distance (Maghuly et al. 2015). The highest genetic diversity (42 unique fragments) was observed among plants from the State of Chiapas in Mexico in the native range of *J. curcas* (Pecina-Quintero et al. 2014; Pecino-Quintero et al. 2011). High genetic diversity is typical for plant populations in their centre of origin, and may be promoted by pollination biology (Guo et al. 2016; Pamidimarri and Reddy 2014; Rincón-Rabanales et al. 2016). A more complete analysis of history of global dissemination of the species might help to explain the observed geographical patterns of genetic diversity (**IV**). Further genetic improvements will be required to produce cultivars which can provide consistently high seed and oil yields. For instance, germplasms from the State of Chiapas in Mexico, the area of highest recorded genetic diversity, might provide useful genetic material for such improvements.

3.7. Seed yield of *J. curcas*

Results of linear models showed that age had a linear and rainfall and plant density had quadratic effects on seed yield (**IV**). Rainfall had different effects on seed yield in the three different continents whereas age had significant linear effects on seed yield in all continents. In addition to these factors, there are other potentially even more important factors such as soil fertility and agronomic practices of which enough data were not available. The impact of these factors on seed yield has, however, been discussed in literature (**IV**).

The seed yield of *J. curcas* varied hugely from 26 kg ha^{-1} y^{-1} in Africa to 11,250 kg ha^{-1} y^{-1} in South Asia (**IV**). Earlier studies have reported similar results (Achten et al. 2008; Brittaine and Lutaladio 2010; Jongschaap et al. 2007; Heller 1996; van Eijck et al. 2014; Wahl et al. 2012). Parawira (2010) reported that 1-2 years old plants can yield 7,800 kg ha^{-1} y^{-1} in optimal growth conditions. As the first mono plantations of *J. curcas* have been established relatively recently (GEXSI 2008), earlier high seed yield reports may be extrapolations from hedgerow plants (**IV**). More realistic achievable seed yields range from 500 to 2,000 kg ha^{-1} y^{-1}(van Eijck et al. 2010). Half of the reported seed yields fall below 1,536 kg ha^{-1} y^{-1}, which also parallels earlier studies (**IV**). A study done by GTZ (2004) in India concluded that a realistic expected seed yield would be 700 kg ha^{-1} y^{-1}, but observed a yield of only 70 kg ha^{-1} y^{-1} in rain fed conditions in Maharastra (Prueksakorn et al. 2010). Seed yields on barren lands in China varied from 1,700 to 2,200 kg ha^{-1} y^{-1} (Pohl 2010). In Cape Verde, seed yields were 700 - 2,250 kg ha^{-1} y^{-1}(GTZ 2003). One-year-old plantations produced a seed yield of 595 kg ha^{-1} y^{-1} in Brazil (Dalchiavon et al. 2013). All these studies show that seed yields of *J. curcas* in different parts of the world may be surprisingly low and vary greatly. Seed yield variability of *J. curcas* may be due to variation in site specific agro-climate, soil fertility, adopted agronomic practices and genetic differences among plants (**IV**).

4. CONCLUSION

My experimental results show that growth and defense of *J. curcas* seedlings are primarily influenced by drought stress and not by herbivory stress (**I** and **II**). *J. curcas* produces flavonoids in its leaves primarily to protect leaf tissues against oxidative and photodamage caused by drought and light stress (**I**). It has an undercompensatory growth response to herbivory stress, with growth decreasing with increasing drought stress level (**II**). Experimental results show that it needs at least 800 mm y^{-1} rainfall for an economically viable productivity level (**II**). Levels of arthropod herbivory are generally low; the highest herbivory pressure was recorded within its native range (**III**). Latin American plants have the highest genetic diversity, and the low genetic diversity observed elsewhere may be caused by founder effects (**IV**). Reported seed yields vary hugely across the globe due to differences in site specific agro-climatic conditions, soil fertility, agronomic practices and genetic background of the plants (**IV**). Further genetic improvements will be required to produce cultivars which can provide consistently high seed and oil yields.

Topics for further research

1. Effects of genetic and climatic factors on seed yield
2. Epigenetic elasticity of *J. curcas* and its effects on seed yield
3. Identifying plants with elite seed yield traits from local populations for production of cultivars for local plantations
4. Allelopathic effects of *J. curcas* on agricultural crops
5. In situ ecophysiology of *J. curcas*
6. Impact of nutrients and water on sex ratio of *J. curcas* flowers
7. Impact of topography on seed yield and oil content of *J. curcas*
8. Effects of inbreeding depression and heterosis on seed yield of *J. curcas*

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