Environmental Drivers of Vegetative and Flowering Phenology in Drylands

by

Fransiska Ndiiteela Kangombe

A Dissertation Presented in Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

Approved April 2023 by the
Graduate Supervisory Committee:

Heather Throop, Chair
Osvaldo Sala
Enrique Vivoni
Kathleen Pigg
Kevin Hultine
Ezekeil Kwembeya

ARIZONA STATE UNIVERSITY

August 2023

ABSTRACT

Flowering phenology offers a sensitive and reliable biological indicator of climate change because plants use climatic and other environmental cues to initiate flower production. Drylands are the largest terrestrial biome, but with unpredictable precipitation patterns and infertile soils, they are particularly vulnerable to climate change. There is a need to increase our comprehension of how dryland plants might respond and adapt to environmental changes. I conducted a meta-analysis on the flowering phenology of dryland plants and showed that some species responded to climate change through accelerated flowering, while others delayed their flowering dates. Dryland plants advanced their mean flowering dates by 2.12 days decade^{-1}, 2.83 days °C^{-1} and 2.91 days mm^{-1}, respectively, responding to time series, temperature, and precipitation. Flowering phenology responses varied across taxonomic and functional groups, with the grass family Poaceae (-3.91 days decade^{1}) and bulb forming Amaryllidaceae (-0.82 days decade^{1}) showing the highest and lowest time series responses respectively, while Brassicaceae was not responsive. Analysis from herbarium specimens collected across Namibian drylands, spanning 26 species and six families, revealed that plants in hyper-arid to arid regions have lower phenological sensitivity to temperature (-9 days °C^{-1}) and greater phenological responsiveness to precipitation (-0.56 days mm^{-1}) than those in arid to semi-arid regions (-17 days °C^{-1}, -0.35 days mm^{-1}). The flowering phenology of serotinous plants showed greater sensitivity to both temperature and precipitation than that of non-serotinous plants. I used rainout shelters to reduce rainfall in a field experiment and showed that drought treatment advanced the vegetative and reproductive phenology of *Cleome gynandra*, a highly nutritional and medicinal semi-wild vegetable species. The peak leaf length date, peak number of leaves date, and peak flowering date of *Cleome gynandra* advanced by six, 10 and seven days, respectively. Lastly, I simulated drought and flood in a greenhouse experiment and found that flooding conditions resulted in higher germination percentage of *C. gynandra* than drought. My study found that the vegetative, and flowering phenology of dryland plants is responsive to climate change, with differential responses across taxonomic and functional groups, and aridity zones, which could alter the structure and function of these systems.

DEDICATION

I dedicate this dissertation to my dad Joachim Ndjwaki Kangombe who instilled the spirit of hard work and the love of scholarship in me. I also dedicate this dissertation to my second dad, Manuel Vidal Jeje. To my brother Henock Shivute who passed away in 2021 due to COVID-19, and my aunts Verena Tuyoleni Ndumbu and Pia Igidheni Ndumbu who both passed away during my tenure as a PhD student. May your souls rest in eternal peace.

ACKNOWLEDGMENTS

Firstly, I would like to thank my creator and protector, my heavenly father for guiding and keeping me safe throughout this meandering but legendary journey. I would like to thank my mother Germana Nuugwanga Abraham for her prayers and unwavering support during this time that I spent so far away from home. I wish to extend my thanks to my committee, Heather Throop (Chair), Osvaldo Sala, Enrique Vivoni, Kathleen Pigg, Kevin Hultine, and Ezekeil Kwembeya for their input throughout the evolution of my research, for asking thoughtful questions, sharing resources and providing valuable guidance and reassurance throughout my doctoral journey. I would like to express my gratitude to my advisor Dr. Heather Throop, for the mentorship opportunity to work on my research, which often entailed inter-continental collaboration between Namibia and ASU. Her commitment, guidance and support throughout my doctoral journey has not only inspired me to become the best scientist version of myself but has also fostered an interest in collaborative and integrated research. This research would not have been possible without the funding support from multiple sources including Arizona State University (ASU) through the School of Life Sciences internal Research and Training fund, the Lisa Dent Memorial Ecology Fellowship, and the Michael A. Cichan Award Scholarship. I am grateful for the funding support from the World Wildlife Fund, Education for Nature Fellowship program. This work was also financially and in kind supported by the University of Namibia through the staff development program and the Faculty of Agriculture, Engineering & Natural Sciences. I would like to thank the University of Namibia, Neudamm Campus community and management, especially Dr. Simon Angombe, Mr. Edmond Beukes, and Mr. Johnny Amutenya for the opportunity to work

at an amazing field site in the central highland savanna in Namibia. I am indebted to my field team Simeon Nanyeni, Jonas Booysen, Annelie Boois and Elizabeth Joel for working enthusiastically on the renovations and maintenance of the rainout shelters at the Neudamm field site. My appreciation goes to Imms Lisias and his team at Neudamm Campus for diligently installing my weather station, keeping it safe, facilitating the end of season plastic clean up, and upholding environmental compliance at the field site. I thank all the University of Namibia students who have assisted me through crowdsourcing of herbarium phenology data over the years. Special thanks to Liina Kathena, Helena Elago, Kuume Iiyambo, and Kelly Tashiya for their support and assistance with material and equipment preparations, watering plants, collecting, capturing and organizing data from the greenhouse experiment. Thank you to Albertha Sipapo and the team at Agricultural Laboratory, Ministry of Agriculture, Water and Land Reform in Namibia, for soil analysis services. I would also like to thank the Dryland Ecosystems Research Team Lab members and alumni, including (but not limited to) Edauri Navarro-Perez, Luiza Aparecido, Elise Nghalipo, Isabel Torres, and Mary Chisolm, for their input in my research and day-to-day support over the years. I thank my cohort friends, Brittney Monus, Courtenay Ray, Deanna Zembrzuski and Kate Weiss; these amazing women have been a huge support and source of inspiration from the time I started off this journey together until now. I am indebted to Leevi Nanyeni for availing his vehicle for me to use during my fieldwork. I wish to especially thank Tulimegameno Amutenya and Cameron-Hope Nafidi for their positive words, for believing in me and traveling this journey with me. To my friends and family, I am forever grateful for your support, patience and encouraging words.

TABLE OF CONTENTS

Page

LIST OF TABLES ... xi

LIST OF FIGURES ... xii

CHAPTER

INTRODUCTION ... 1

1 FLOWERING PHENOLOGY IN DRYLAND ECOSYSTEMS: A META-ANALYSIS OF MULTIPLE RESPONSES TO CLIMATE CHANGE ... 8

Abstract ... 8

Introduction ... 9

Materials and Methods ... 14

Data Extraction ... 15

Statistical Analysis ... 18

Results ... 21

Flowering Phenology Responses to Time Series ... 24

Flowering Phenology Responses to Temperature ... 26

Flowering Phenology Responses to Precipitation ... 27

Small Study Bias, Moderator Variables and Publication Bias ... 30

Discussion ... 31

Flowering Phenology Responses to Time Series ... 32

Flowering Phenology Responses to Temperature ... 37

Flowering Phenology Responses to Precipitation ... 44

Small Study Bias, Moderator Variables and Publication Bias 52

Conclusions 54

2 FLOWERING PHENOLOGY FROM HERBARIUM SPECIMENS COLLECTED ACROSS NAMIBIAN DRYLANDS 57

Abstract 57

Introduction 58

Materials and Methods 65

Herbarium Flowering Phenology Data 65

Study Location 68

Study Taxa 69

Climatic Variables 71

Statistical Analysis 72

Analysis of Flowering Phenology Time Series Trends 72

Analysis Of Phenological Sensitivity of Flowering to Temperature 72

Analysis Of Phenological Sensitivity of Flowering To Precipitation 73

Best Fit Model Analysis 73

Results 74

Flowering Phenology Trends Over Time 75

Phenological Responsiveness of Flowering to Temperature 78

Phenological Responsiveness of Flowering To Precipitation 81

Best Fit Model of Flowering Date Response 84

Discussion 85

CHAPTER Page

Flowering Phenology Trends Over Time ... 85

Phenological Responsiveness of Flowering to Temperature ... 88

Phenological Responsiveness of Flowering to Precipitation ... 91

Best Fit Model of Flowering Date Response ... 95

Conclusions ... 98

3 VEGETATIVE GROWTH, REPRODUCTIVE OUTPUT AND PHENOLOGICAL RESPONSES OF *CLEOME GYNANDRA* L. TO DROUGHT IN A SEMI-ARID DRYLAND SAVANNA ... 100

Abstract ... 100

Introduction ... 101

Materials and Methods ... 108

Study Site ... 108

Shelter Design and Rainfall Exclusion Treatments ... 110

Seeding of the Shelters ... 114

Plant Sampling and Measurements ... 114

Soil and Climate Measurements ... 115

Statistical Analyses ... 117

Results ... 118

Soil and Climate Characteristics ... 118

Vegetative Growth Indicators and Phenology ... 121

Flowering and Fruiting Phenology ... 124

Reproductive Output ... 125

Discussion 126
Vegetative Growth Indicators and Phenology 126
Flowering and Fruiting Phenology 129
Reproductive Output 132
Conclusions 132
4 DROUGHT AND FLOODING EFFECTS ON GERMINATION, GROWTH AND FLOWERING PHENOLOGY OF *CLEOME GYNANDRA* L. 134
Abstract 134
Introduction 135
Materials and Methods 141
Statistical Analysis 145
Results 147
Germination Percentage and Vegetative Growth 147
Flowering Phenology 149
Discussion 151
Germination Percentage and Vegetative Growth 151
Flowering Phenology 152
Conclusions 153
CONCLUSION 155
REFERENCES 160

APPENDIX Page

A: SUPPLEMENTARY INFORMATION FOR CHAPTER 1 179

B: SUPPLEMENTARY INFORMATION FOR CHAPTER 2................................... 185

C: SUPPLEMENTARY INFORMATION FOR CHAPTER 3................................... 193

LIST OF TABLES

Table Page

1. The Key Search Words Used in SCOPUS.. 15

2. Estimates of Flowering Phenology Responsiveness of the Herbaceous Plants to Time Series (Collection Year), Temperature and Precipitation for the Different Phenophases. 74

3. Results from the Linear Mixed Effects Model of the Fixed Effects of Drought Treatment on Peak Leaf Length Date of *C. gynandra*.. 121

4. Results from the Linear Mixed Effects Model of the Fixed Effects of Drought Treatment on Peak Number of Leaves Date of *C. gynandra*.. 123

5. Results from the Linear Mixed Effects Model of the Fixed Effects of Drought Treatment on Peak Flowering Date of *C. gynandra*.. 125

6. Descriptive Statistics Summary of Germination Percentage Among Treatments...... 147

7. The Mean Stem Height and Mean Maximum Number of Leaves of *C. gynandra* Under the Different Rainfall Treatments. 149

LIST OF FIGURES

Figure Page

1. The Distribution of Studies (red dots) Included in this Meta-Analysis Across Drylands of the World. 18

2. Boxplots of Phenological Responsiveness of Flowering Date to Time Series (days decade^{-1}), Temperature (days °C^{-1}) and Precipitation (days mm^{-1}) Showing the Distribution of the Data Points. 22

3. Boxplots of Advanced and Delayed Flowering Phenology Responses to Time Series (days decade^{-1}), Temperature (days °C^{-1}) and Precipitation (days mm^{-1}) Showing the Distribution of the Data Points. 23

4. Flowering Phenology Responses to Time Series for (A) All Data, (B) Families and (C) Functional Groups. 24

5. Overall Flowering Phenology Responsiveness to Temperature for (A) All Data & Study Type, (B) Temperature Measures, (C) Plant Families, and (D) Functional Groups. 26

6. Overall Flowering Phenology Responsiveness to Precipitation for (A) All Data and Study Types, (B) Precipitation Measures, (C) Plant Families, and (D) Functional Groups. 28

7. Funnel plots (A-C) Illustrate the Distribution of Flowering Phenology Responses to Time Series, Temperature and Precipitation. 30

8. Representative Specimens of *Cleome gynandra* at Three Different Phenophases. 66

9. Map of Namibia Showing the Mean Annual Precipitation and the Distribution of Plant Specimens Used in this Study, Categorized by Family. 67

Figure Page

10. Flowering Phenology Responsiveness to Time Series of the Herbaceous Species at Early Flowering (1925-2018), Peak Flowering (1913-2018) and Late Flowering (1924-2018). 76

11. Flowering Phenology Responsiveness to Time Series Between Serotiny, Aridity Zones, And Across Phenophases. Each Horizontal Line Corresponds to The Change in Flowering Date.......... 77

12. Flowering Phenology Responsiveness to Temperature for Early Flowering, Peak Flowering and Late Flowering Herbaceous Plants. 79

13. Flowering Phenology Responsiveness to Temperature Between Serotiny, Aridity Zones, and Across Phenophases. 80

14. Flowering Phenology Responsiveness to Precipitation for Early Flowering, Peak Flowering and Late Flowering Herbaceous Plants. 82

15. Flowering Phenology Responsiveness to Precipitation Between Serotiny, Aridity Zones, and Across Phenophases. 83

16. Rainfall Distribution in Namibia. 110

17. An Overview of the Rainout Shelters Used in this Study to Simulate Drought. 112

18. *Cleome gynandra* at the Neudamm Field Site During the Experiment. 113

19. The atmospheric and soil climatic instruments installed at the Neudamm field site. 116

20. Mean Daily Soil Climatic Properties at the Neudamm Field Site During March 2022, Showing (A) Soil Temperature and (B) Soil Moisture. 120

21. Response of Peak Leaf Length Date of *Cleome gynandra* to Drought Treatment. .. 121

Figure Page

22. Response of Peak Number of Leaves Date of *Cleome gynandra* to Drought Treatment. 123

23. Response of Peak Flowering Date of *Cleome gynandra* to Drought Treatment. 125

24. Map of Namibia Showing Seed Collection Site at Onyaanya Village (Blue Star) and Greenhouse Location at the University of Namibia, Windhoek Campus (Red Star). 141

25. The Probability Density Function of the Total Annual Rainfall in Windhoek, Namibia for the Period 1960-2015. 142

26. The View of the Greenhouse at the School of Science Building, University of Namibia (A) Exterior View, (B) Interior View and (C) A *Cleome gynandra* Seedling Growing in a Plant Pot Inside the Greenhouse. 145

27. Boxplot of Germination Percentage of *Cleome gynandra* Seeds Among the Drought, Control and Flood Rainfall Treatments in the Greenhouse. 148

28. Boxplots Comparing the Mean Stem Height of *C. gynandra* at Flowering Onset Between Flood and Control Rainfall Treatments. 150

INTRODUCTION

Phenology, the study of recurring lifecycle events in organisms, has been practiced since ancient times (Willis et al., 2008a). Historical records dating back to the eighth century show that phenological observations were documented by early ecologists (Aono & Kazui, 2008; Nord & Lynch, 2009), with some keeping meticulous details of important events such as flowering. There are few known long-term datasets of phenological events, for example, the documentation of flowering dates of culturally important plants such as cherry trees in China and Japan dating back as far as 812 CE (Willis et al., 2008b; Sparks & Carey, 1995). The annals of phenological events of plants in the Marsham family estates, initiated by Robert Marsham in 1736, in Norfolk, England, yielded a five generation record (Sparks & Carey, 1995). Another renowned long-term record phenological data is the Thoreau phenology dataset from Concord, Massachusetts, United States. This work was initiated by the naturalist and conservationist Henry David Thoreau, who carefully observed and documented the first flowering dates of over 500 plant taxa in various habitats from 1852 to 1858. Thoreau's work was subsequently continued by other scientists, in particular Hosmer (1878, 1888–1902), and Miller-Rushing and Primack (2003–2007), whose collective effort culminated into a 155 year dataset of plant phenological records (Willis et al., 2008a). These pioneer phenological records laid an important foundation for the study of species responses to global change (Root et al., 2003). Indeed, phenological observations are increasingly becoming a valuable data source for assessing global change impacts on ecosystems (Cleland et al., 2007; Ibáñez et al., 2010; Menzel et al., 2006).

Flowering phenology (the seasonal timing of flowers) is demonstrated to be a reliable indicator of climate change, particularly because many plants rely on environmental cues for inducing flowering (Chmura et al., 2019; Cleland et al., 2012; Root et al., 2003). In fact, there is increasing evidence that many plants globally are shifting their flowering phenology in response to anthropogenic global change, leading to ecological consequences such as changes in species performance and community interactions (Ge et al., 2015; Menzel et al., 2006; Parmesan & Yohe, 2003). Flowering phenology is crucial for the reproductive success and long-term sustenance of plant populations (Elzinga et al., 2007; Hegazy et al., 2017), because the timing of flowers affects pollination success, fruit maturity, and seed dispersal. When plants flower too early or too late, they face the risk of reproductive failure due to unfavorable environmental conditions or lack of pollinators. Non-optimal timing of flowering also has implications for other species in the ecological network, including pollinators, competitors, seed dispersers, and predators, potentially altering ecosystem structure and function (Elzinga et al., 2007; Matthews & Mazer, 2016; Memmott et al., 2007).

Analysis of existing data has yielded estimates of shifts in the timing of phenological events, particularly in relation to climate change. One such example is the study by Menzel et al., (2006), who reported in a meta-analysis for the European region that leafing, flowering and fruiting phenological records have advanced by 2.5 days decade^{-1}. Another meta-analysis based on datasets from temperate regions in the Northern

Hemisphere showed an advance of 3 days decade^{-1} and 5 days decade^{-1} for spring phenological events (including flowering) of trees and other plants, respectively (Root et al., 2003). These shifted phenologies have been attributed to increases in temperature (Cleland et al., 2007; Körner & Basler, 2010; Menzel et al., 2006). However, other environmental factors such as precipitation, photoperiod, elevation, latitude and resource availability have also been shown to influence flowering phenology, with different trends observed across ecosystems (Bertin, 2008; Chmura et al., 2019). At the same time, the current literature on flowering phenology shows a clear disproportional focus on mesic systems, which limits the extent to which these studies might be extrapolated to other ecosystems, particularly drylands. The lack of empirical evidence on the flowering phenology trends and responses to climate change in dryland ecosystems is highlighted in recent global meta-analyses (Liu et al., 2021; Stuble et al., 2021). For example, the majority of experimental warming studies included in the meta-analysis by Stuble (2021) focused on temperate forests, grasslands, alpine and sub-alpine grasslands, arctic tundra, and subarctic wetlands, with only 17% of the studies conducted in drylands. Similarly, a review by Willis et al., (2017) found that only 13% of herbarium flowering phenology studies were carried out in drylands, while 71% of the studies were conducted in tropical and sub-tropical ecosystems. Yet, drylands cover more than 41% of the terrestrial surface (Prăvălie, 2016) and influence major global ecological processes such as carbon and nutrient flow (Huang et al., 2017). It is therefore important to expand the span of vegetative and flowering phenology studies into drylands toward narrowing these gaps, thereby contributing to our understanding of how these systems might respond to climate change.

Drylands, which encompass arid and semi-arid ecosystems, are characterized by an aridity index (AI, the ratio of mean annual precipitation to mean annual potential evapotranspiration) below 0.65 (Greve et al., 2019; Maestre et al., 2012). Drylands cover approximately 41% of the Earth's land surface and are projected to expand by 10% by the end of the 21st century (Feng & Fu, 2013; Huang et al., 2016; Prăvălie, 2016). Due to increasing potential evapotranspiration and rising surface air temperatures, a significant portion of global drylands is expected to experience a drier climate in the future (Huang et al., 2017). In addition, soils in drylands are relatively infertile, while the vegetation cover is patchy and nutrient cycling is generally slow. Collectively, these characteristics make dryland ecosystems more susceptible to environmental changes compared to mesic systems, where temperatures are cooler, precipitation occurs throughout the year, and decomposition happens at a faster rate (Huang et al., 2017; Maestre et al., 2012).

According to climate models, surface air temperatures in drylands are projected to increase by 2°C and 4°C under the RCP4.5 and RCP8.5 scenarios, respectively, by the end of the 21st century (Huang et al., 2017). These models also predict an increase in the frequency of extremely warm years in drylands during the same period (Maestre et al., 2012). However, the changes in precipitation patterns are expected to vary across different dryland regions. In most mid-latitude and subtropical dry regions, mean annual precipitation predicted to decrease by up to 30% under the RCP8.5 scenario (Maestre et al., 2012; Pachauri et al., 2015). Nevertheless, some drylands may experience an increase in precipitation by up to 25% over the course of the 21st century (Maestre et al., 2012). With approximately 38% of the global human population residing in drylands (Huang et al., 2017; Maestre et al., 2012), declines in mean precipitation could negatively affect surface and groundwater resources in these systems, posing a threat to the livelihoods of the inhabitants. This direct dependence on natural resources further increases the vulnerability of dryland ecosystems and the communities living within them to the impacts of climate change. As the world's largest terrestrial biome, it is pertinent to determine environmental drivers of flowering phenology including the relative role of temperature, precipitation, and geographic location to better quantify and predict climate change effects on the reproductive timing of flowering in drylands.

In my dissertation, I have sourced data from published studies, herbarium specimens, and field and greenhouse rainfall manipulation experiments to investigate environmental drivers of vegetative and flowering phenology in drylands. In chapter one of this dissertation, I have systematically compiled and reviewed empirical evidence from published, peer-reviewed literature on dryland plants to assess flowering phenology sensitivity to climate change, by determining the magnitude and direction of response in flowering date to time series, temperature, and precipitation. In chapter two of this dissertation, I reconstructed historical flowering dates from herbarium specimens of selected herbaceous flora collected from across Namibian drylands, to determine the relationship between flowering date and specimen collection year (as a proxy for time, measured in years) as well as how changes in rainfall and temperature may have affected their flowering phenology. A special feature of herbarium specimens as sources of flowering phenology data lies in their ability to offer insights into the historical flowering trends (Lang et al., 2019), particularly when paired with expert ecological knowledge of the flora.

One of the predictions of climate change for drylands is an increased probability of drought occurrence and extended dry seasons by the end of the 21st century (Collins et al., 2013). In chapter three of this study, I used rainout shelters to simulate drought and assessed the vegetative growth and phenology, reproductive output (number of flowers and fruits) and flowering phenology responses of the summer annual and leafy vegetable *Cleome gynandra* L. in a semi-arid savanna. In alignment with predictions of an increased occurrence of extreme rainfall events in drylands, chapter four of this study determined the effect extreme drought and flooding on the vegetative and flowering phenology of *C. gynandra* plants grown from seed in the greenhouse. Empirical evidence from the experimental work on the vegetative and flowering phenology of the widely consumed and locally sold leafy vegetable species *Cleome gynandra*, alludes to the potential impacts of climate change on the availability of this valuable resource.

In a world that threatens an even drier climate for drylands, it is critical to determine how the vegetative and flowering phenology of plants might respond to these changes. This dissertation draws data from the literature, natural history collections, field, and greenhouse experiments to study the vegetative and flowering phenology of dryland plants in relation to climate change. Data generated from this study does not only contribute to the phenology literature but may also help mitigate the impacts of climate change in drylands such as through coordinated seed and other propagule conservation.

CHAPTER 1

1 FLOWERING PHENOLOGY IN DRYLAND ECOSYSTEMS: A META-ANALYSIS OF MULTIPLE RESPONSES TO CLIMATE CHANGE

Abstract

Flowering phenology can offer a sensitive and reliable biological indicator of climate change because plants use climatic and other environmental cues to initiate their seasonal production of flowers. Flowering phenology assessments are now widely used to study trends and forecast potential impacts of climate change across ecosystems. However, empirical evidence on flowering phenology trends and responses to climate change from dryland ecosystems remains scarce. I conducted a global meta-analysis compiling 427 species-specific observations from 13 studies to systematically synthesize phenological responses of flowering date to time series, temperature, and precipitation in drylands. The study revealed that dryland plants included in this meta-analysis are advancing their flowering date on average by 2.12 days decade^{-1}. Both temperature and precipitation are important predictors of flowering phenology in drylands, advancing flowering date by 2.83 days °C^{-1} and 2.91 days mm^{-1} respectively. Climate change responses of flowering phenology in drylands varied across taxonomic and functional groups. Grasses are accelerating their flowering onset faster than woody plants and forbs. These findings suggest that warmer and potentially drier conditions in the future will result in earlier

flowering and a lengthened growing season in drylands, which may impact ecosystem structure and function.

Introduction

Phenology, defined as the study of the timing of recurring lifecycle events in living organisms (Willis et al., 2008a), has been a part of human society since ancient times, with records of phenological observations dating back as far as the eighth century BC (Aono & Kazui, 2008; Nord & Lynch, 2009). Hunter-gatherers used phenological cues to guide them about when and where to find food (Nord & Lynch, 2009). Similarly, early (and current) agriculturalists needed to know the appropriate time for sowing seeds that allows adequate time for crop development to maturity and harvesting (Demarée & Rutishauser, 2011). More recently however, phenological observations represent a prime and reliable data source for global change assessments (Cleland et al., 2007; Ibáñez et al., 2010; Menzel et al., 2006).

Flowering phenology, the seasonal timing of flowering, is a critical determinant of reproductive success and fitness (Elzinga et al., 2007; Hegazy et al., 2017), and hence the capacity of plants to sustain viable populations. Optimal timing of flowering increases pollination success and affects the timing of fruit maturity and seed dispersal. Plants that flower too early or too late in the season may therefore risk reproductive failure due to factors such as unfavorable environmental conditions or inadequate pollinator availability

(Elzinga et al., 2007). Since plants rely on climatic (and non-climatic) environmental factors as cues for the timing of flowers, flowering phenology is recognized as a highly sensitive biological indicator of climate change (Chmura et al., 2019; Cleland et al., 2012; Root et al., 2003). Indeed, there is increasing evidence suggesting that globally, many plants are shifting their flowering phenology in response to the on-going anthropogenic change (Ge et al., 2015; Menzel et al., 2006; Parmesan & Yohe, 2003), resulting in ecological consequences such as altered species performance and community interactions (Chmura et al., 2019). Shifts toward earlier flowering dates are referred to as "advanced flowering" in the flowering phenology literature, while shifts toward later flowering dates are termed "delayed flowering" (Calinger et al., 2013a; Mazer et al., 2013). The phrases: "advanced flowering" and "delayed flowering" will be used in this dissertation, within this context.

Studies have shown that most plants have advanced their flowering dates, responding to changes in climate, although some species have delayed their flowering (Chambers et al., 2013; Root et al., 2003). However, the magnitude of the shift in flowering phenology in response to climate change, hereafter 'flowering phenology responsiveness', varies across hemispheres, ecosystems, functional and taxonomic groups. For example, Chambers et al., (2013) noted a much greater mean rate of change in the timing of plant phenological events in the Southern Hemisphere (-11.3 ± 0.8 days decade^{-1}) than in the Northern Hemisphere (-1.1 ± 0.2 to 3.3 ± 0.9 days decade^{-1}), although both hemispheres shifted toward earlier flowering. Menzel et al.(2006) reported in a meta-analysis that leafing, flowering and fruiting phenological records have advanced by 2.5 days decade^{-1}., in Europe. Another meta-analysis from temperate regions in the Northern Hemisphere showed an advance of 3 and 5 days decade^{-1} for spring phenological events (including flowering) of trees and non-trees respectively (Root et al., 2003). Most of the data included in current global and local flowering phenology analyses are sourced predominantly from mesic ecosystems (Menzel et al., 2006; Parmesan & Yohe, 2003; Root et al., 2003). For example, the majority of experimental warming studies included in the meta-analysis by Stuble et al.(2021) were conducted in temperate forests and grasslands, alpine and sub-alpine grasslands, arctic tundra and subarctic wetlands and only 17% of these studies were carried out in drylands. In a review by Willis et al.(2017), which summarized the global status of herbarium-based flowering phenology, only 13% of the studies reviewed were carried out in drylands while 71% of these studies were conducted in tropical and sub-tropical ecosystems. Whereas these studies have contributed to the growing literature on flowering phenology, their disproportional focus on mesic systems limit the extent to which they might be extrapolated to other ecosystems, particularly drylands. Indeed, empirical evidence on flowering phenology responses to climate change from drylands remains scarce as emphasized in recent global meta-analyses on warming experiments (Liu et al., 2021; Stuble et al., 2021).

Arid and semi-arid ecosystems, ('hereafter drylands'), are defined as locations where the aridity index, the ratio of mean annual precipitation to mean annual potential evapotranspiration, is less than 0.65 (Greve et al., 2019; Maestre et al., 2012). Globally, drylands cover about 41% of the land surface and are expected to expand by another 10% by the end of the 21st century (Feng & Fu, 2013; Huang et al., 2016; Prăvălie, 2016). In addition, large increases in potential evapotranspiration are anticipated and the collective effect with rising surface air temperatures are predicted to result in a drier climate over a considerable portion of global drylands (Huang et al., 2017). Soils in drylands are relatively infertile, the vegetation cover is patchy, and nutrient cycling is generally slow, making these ecosystems considerably more sensitive to environmental perturbations than mesic systems where temperatures are cooler, moisture supply is well-balanced and decomposition occurs more rapidly (Huang et al., 2017; Maestre et al., 2012). Furthermore, the flowering of most species in some subtropical environments such as drylands is restricted to frost-free periods which tend to coincide with moisture availability, while plants in some tropical environments may flower all-year round (Ma & Zhou, 2012; Segrestin et al., 2018).

Climate models predict that the mean annual temperature in drylands will increase by 2°C and 4°C for the RCP4.5 and RCP8.5 scenarios, respectively (Huang et al., 2017). An increase in the frequency of extremely warm years is also predicted for this time span (Maestre et al., 2012). Precipitation patterns, however, are predicted to vary from one dryland to another (Pachauri et al., 2015). The mean annual precipitation in most mid-latitude and subtropical dry regions is predicted to decrease by up to 30% under the RCP8.5 scenario (Maestre et al., 2012; Pachauri et al., 2015), but there is also evidence to suggest that precipitation could increase by up to 25% in some drylands, over the twenty-first century (Maestre et al., 2012). Given these variable climate model predictions and the already limiting climatic and soil characteristics of drylands (Maestre et al., 2016; Prăvălie, 2016), climate change impacts on flowering phenology in drylands could vary considerably from those of mesic systems. As the world's largest terrestrial biome, it is pertinent to determine environmental drivers of vegetative and flowering phenology in drylands, including the relative role of temperature, precipitation, and geographic location to better quantify and predict climate change responses. Furthermore, it has been noted in the literature that the role of precipitation on flowering phenology is poorly understood (Matthews & Mazer, 2016; Primack et al., 2004) and has proven difficult to quantify (Chambers et al., 2013; Park et al., 2018; Pearson, 2019b; Peñuelas et al., 2004). Since precipitation is a critical driver of plant activity in drylands (Bertin, 2008), conducting flowering phenology studies in these ecosystems could shed some light on how plants might respond to altered precipitation.

This systematic review incorporates empirical evidence from drylands to explore the flowering phenology sensitivity to climate change, by determining the magnitude and direction of response in flowering date to time series, temperature, and precipitation. Specifically, the review:

1) Assesses the spatial and temporal span of flowering phenology studies in drylands.
2) Synthesizes the magnitude and direction of phenological responsiveness of flowering date to time series, temperature, and precipitation.

3) Compares phenological responsiveness of flowering date to time series, temperature, and precipitation across taxonomic and functional groups.

The review focuses on warm deserts, semi-arid regions and coastal deserts (hereafter warm drylands) but excludes studies conducted in cold or polar deserts (hereafter cold drylands). The cold dryland type varies greatly from the warm dryland types, especially in their latitudinal locations and climate (Laity, 2009). Warm drylands are generally located in the tropical and sub-tropical latitudes, between 30° north and south of the equator and are characterized by low and unpredictable mean annual precipitation of less than 500 mm, intense solar radiation and maximum summer temperatures of between 35 °C to over 40 °C, and cool winters with minimum temperature ranging from -4 °C to 10 °C (Laity, 2009; Peguero-Pina et al., 2020). In contrast, cold drylands occur at higher latitudes and are characterized by prevailing low temperatures between -2 to 4 °C in the winter and 21-26° C in the summer while the mean annual precipitation ranges between 150-260 mm, in addition to large amounts of winter snowfall (Laity, 2009). Furthermore, it has been shown that warm and cold drylands are responding variably to climate change. Warm drylands have experienced an increasing temperature trend with greater magnitude in summer than in winter; but in cold drylands, temperature has increased less in the summer than during the winter, for the period 1955-2005 (Mamtimin et al., 2011).

Materials and Methods

Data Extraction

I conducted a systematic search of peer-reviewed studies carried out in drylands on flowering phenology in SCOPUS (http://www.scopus.com) in March 2022. I combined search keywords (Table 1) using Boolean operators (“AND” and “OR”). Acknowledging that flowering phenology is a multivariate trait that is measurable in various ways e.g., flowering onset, duration and end of flowering (Munguía-Rosas et al., 2011), I intentionally included a broad spectrum of flowering phenology descriptors in my literature search. The literature search was not limited by publication year or journal. This search returned 720 studies published from 1976 to 2021.

Table 1. The Key Search Words Used in SCOPUS.

The ecosystem descriptor and flowering phenology descriptor terms were combined using the Boolean operator “AND”. The “OR” operator was used to include all possible options within either of the descriptor categories. Quotation marks were used to search for loose or approximate phrases. An asterisk (*) was placed before or after a key search word to include related terms while curly brackets were used to specify exact phrases.

Flowering phenology descriptor (primary)	“flowering phenology” OR “reproductive phenology” OR “flowering onset” OR “phenological response*” OR “phenological tim*” OR “phenological shift*”
	AND

Flowering phenology descriptors (secondary)	{earl* flowering} OR {late flowering} OR {peak flowering} OR {first flowering date} OR {flowering date} OR {day of flowering} OR {date of first flower} OR {day of year} OR {day of first flower} OR {days to flowering} OR {days to bolting} OR {number of flower*} OR {number of open flower*} OR {advanc* flowering} OR {delay* flowering} OR {phenophase} OR {herbarium phenolog*} OR {herbarium specimen*} OR {herbarium record*} OR {shift}* OR {reproductive output}

Of the 720 results from the keyword search in SCOPUS, 37% (n=265) of the articles were rejected because they focused on phenological aspects outside scope of this study (which is, flowering phenology responses), covering topics on the seasonal patterns and synchrony in flowering phenology, relationships between ecological trait measurements (e.g., flower abundance, biomass production, competition, population performance and phenological plasticity) and flowering phenology, relationships between phenology and other environmental factors such as elevation and latitude. A further sixteen percent of the 720 studies (n=116) comprised phenological studies conducted in ecosystems other than drylands, predominantly tropical, humid subtropical and deciduous forests, alpine, alpine meadows and sub-alpine communities, arctic and sub-arctic environments or cold drylands and were also subsequently excluded from this meta-analysis. Nearly a quarter of the 720 studies (n=165), were either conducted on animal phenology or plant-animal interactions. About an eighth of the studies (n=96) assessed other ecological characteristics such as warming effects on population dynamics, chlorophyll degradation, carbon accumulation and nectar production and the remaining 6% of studies (n=44) were excluded from the meta-analysis because they were based on modeling, remote sensing, or machine learning techniques.

Only studies (n=43) that used regression techniques to quantify change in the flowering date of plants through time and in response to changes in environmental conditions were retained for full-text analysis, to determine suitability for inclusion in the meta-analysis. A quarter of these 43 studies (n=11) were excluded from the meta-analysis because they used statistical analyses other than regression to quantify changes in flowering date such as by comparing mean differences in flowering date between periods. An additional 19% of the 43 studies (n=8) were excluded as they were meta-analyses (e.g., Ge et al., 2015; Liu et al., 2021; Stuble et al., 2021). Two studies not in English, were excluded from analysis (Chen et al., 2016; Li et al., 2014). The reference lists of all qualifying papers were also screened to find other publications for inclusion in this meta-analysis. From the papers retained for the meta-analysis, flowering phenology response data were extracted for each species, hereafter ‘species-specific responses’. The final dataset comprised 427 species-specific responses from 13 studies, that quantified change in flowering date with time, temperature and precipitation as predictors using regression analysis and conducted predominantly in warm drylands (Figure 1 and Table A1, Appendix A). Each study was classified based on study type (1) herbarium phenology (or other historical collections such as photographs), (2) field observations, (3) field experiments, (4) and greenhouse or lab-based studies; and was further profiled based on geographic location and study duration. Finally, the species-specific responses were classified and analyzed for trends at plant family and functional group levels. The need for the consideration of species-specific and other plant characteristics in phenological sampling has been emphasized as an important precursor for accurate climate change forecasting (Munson & Long, 2017;

Wolkovich et al., 2012). Because the literature search criteria were fairly narrow, no limits were applied on study duration. The duration of studies included in this analysis ranged from 4 years (Rafferty & Nabity, 2017) to 118 years (Munson & Long, 2017), averaging at 58 years (57.69±12.13).

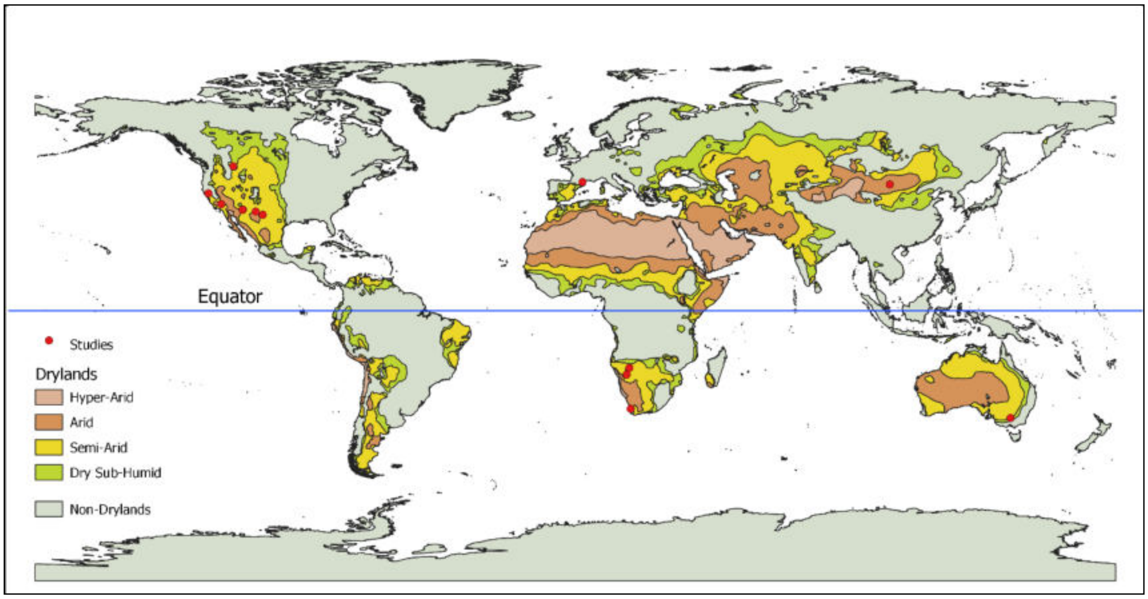


Figure 1. The Distribution of Studies (red dots) Included in this Meta-Analysis Across Drylands of the World.

The base world map was created with land shapefile data from Natural Earth www.naturalearthdata.com while the drylands map was assembled with data sourced from the UNCCD Global Drylands Dataset (datadownload.unep-wcmc.org/datasets) (Miles et al., 2006; Sorensen, 2007).

Statistical Analysis

I used species-specific regression coefficients were used to quantify change in flowering date as predicted by time series, precipitation and temperature as the effect size of interest, analysed here as rate data (Higgins et al., 2019). Flowering phenology shifts over time series were quantified as the number of days per decade (hereafter days decade^{-1}) by which flowering has shifted (Dose & Menzel, 2004), whereas the slopes of the relationships between flowering date and temperature or precipitation were considered as the number of days flowering per 1 degree °C or per 1 mm change, respectively. All analyses were carried out in R version 4.1.0 (R Core Team, 2021), using metafor (Viechtbauer, 2010) to compute the mixed-effects models, for funnel-plot and forest plot analysis, to calculate the overall effect sizes, Confidence Intervals (CI) and sampling variation; and weightr (Coburn et al., 2019) to test for publication bias.

The effect size or outcome measures (and the corresponding sampling variances) were calculated using the escalc() function in metafor based on the log transformed incidence rate outcome measure (Viechtbauer, 2010), specifying xi, as the regression coefficients of shifts in flowering date and ti, as the sample sizes underlying each species-specific response. The corresponding sampling variances were based on the matched sample size data i.e., the number of individuals monitored per species. Random-effects models were then fitted to the log transformed incidence rate outcome measure data, using the rma function in metafor to compute summary effects or overall effect sizes (Viechtbauer, 2010). The summary effect size and the total amount of study heterogeneity (τ^2), was computed using the restricted maximum likelihood ratio estimator (Allen, 2009; Quintana, 2015; Viechtbauer & Viechtbauer, 2015), assuming that the range of true effects follows a normal distribution. The analysis also reports two additional measures of heterogeneity, Q-test for heterogeneity and the I^2 statistic, a percentage-based measure of variability across studies in a meta-analysis where 30% to 60%, 50% to 90% and 75% to 100% are regarded as moderate, substantial and considerable heterogeneity respectively while 0% to 40% may be classified as negligible heterogeneity (Higgins et al., 2019).

To study flowering phenology responses to time series, temperature, and precipitation separate random-effects models were built The overall responses to these factors were also assessed across the plant families for which data could be obtained (Asteraceae, Poaceae, Proteaceae, Fabaceae, Euphorbiaceae, Boraginaceae, Rosaceae, Brassicaceae, Scrophulariaceae, Amaryllidaceae, Nyctaginaceae and Polygonaceae), plant functional groups (trees, shrubs, grasses, and forbs) and study types (herbarium phenology and field observation phenology). Because there were no dryland warming studies found during the literature search from which to extract flowering phenology response data, random effects models were also developed to track phenology responses to temperature and precipitation, distinguishing how these climatic variables were defined or considered in the different studies. For example, studies in which precipitation was defined as a mean seasonal variable (Kwembeya, 2021; Kwembeya & Pazvakawambwa, 2019) were included in a separate model from those that considered total monthly (Crimmins et al., 2011; Love & Mazer, 2021) or mean monthly values (Daru et al., 2019). Similarly, temperature was either expressed as mean annual temperature (n = 16) for the year of flowering (Love & Mazer, 2021; Munson & Long, 2017) or mean monthly temperature (n = 54) for the month of flowering (Crimmins et al., 2011; Daru et al., 2019; Mazer et al., 2015) and these were included in separate models. In total, 43 random effects models were compiled in this meta-analysis and evaluated for significance at alpha level = 0.05 (Table A1, Appendix A). Evidence for small study bias (Viechtbauer & Viechtbauer, 2015) was assessed using concurrent funnel plot analysis and Egger's regression tests. Publication bias in the three main random effects models built to synthesize the overall response of flowering phenology for dryland plants to time series (n = 277), temperature (n =71) and precipitation (n = 148) was tested by using the Likelihood Ratio Test in the weightr package (Coburn et al., 2019).

Results

The responses of flowering date to time series, temperature and precipitation show considerable variation, in their respective categories, with notable outliers in the data (Figure 2). A comparison using an unpaired Wilcoxon rank sum test with continuity correction showed a significant difference between the advanced responses (median = -3.75, n = 173) and delayed responses (median = 3.09, n = 104) for time series (W = 10446, P = 0.025; Figure 3A). T-test comparison between flowering phenology advances and delays for temperature responses was not significant (t = -0.51, N=71, P = 0.61; Figure 3B). Similarly, an unpaired Wilcoxon rank sum test showed that advanced flowering responses to precipitation did not vary from delayed flowering responses (W = 1430.5, N = 148, P = 0.32; Figure 3C). Of the 427 species-specific flowering phenology responses, 65% (n = 277) were time series, while 35% (n =148) and 17% (n =71) were precipitation and temperature responses, respectively. Sixty-two percent (n = 173) of the time series responses advanced their flowering date while 38% (n = 104) delayed it. For responses to temperature, 55% (n = 39) advanced their flowering date and 45% (n = 32) delayed it. Eighty-two percent (82%, n = 121) of flowering responses to precipitation were advanced while 18% (n = 27) were delayed.

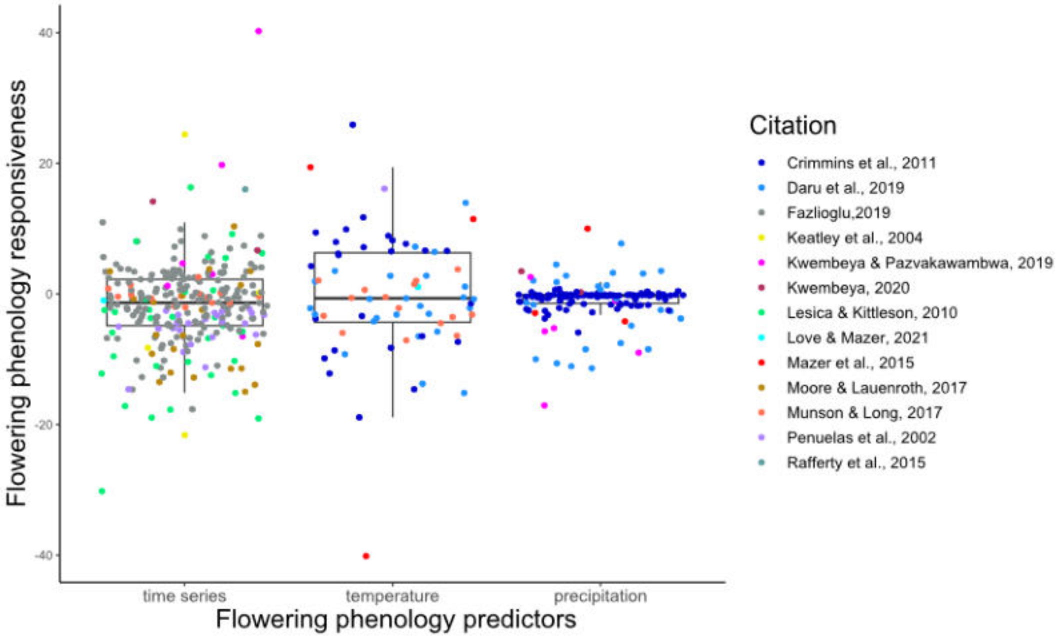


Figure 2. Boxplots of Phenological Responsiveness of Flowering Date to Time Series (days decade^{-1}), Temperature (days °C^{-1}) and Precipitation (days mm^{-1}) Showing the Distribution of the Data Points.

The dots represent the species-specific responses, and the colors indicate the studies from which the data were obtained.

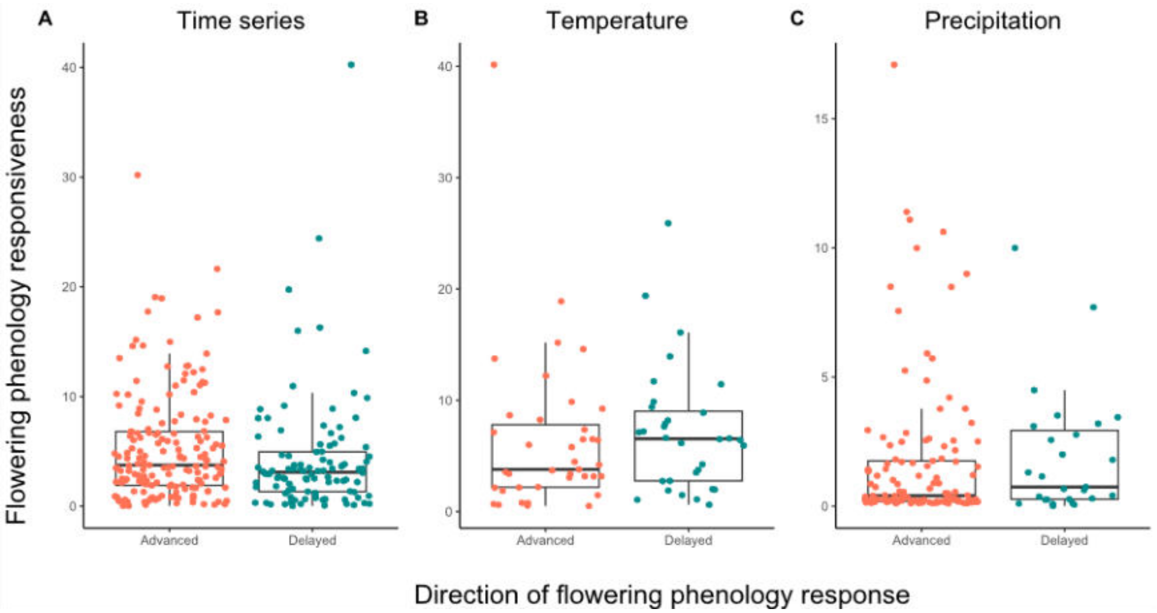


Figure 3. Boxplots of Advanced and Delayed Flowering Phenology Responses to Time Series (days decade^{-1}), Temperature (days °C^{-1}) and Precipitation (days mm^{-1}) Showing the Distribution of the Data Points.

The dots represent species-specific flowering phenology responses, while the orange and green colors denote advanced and delayed responses respectively.

Flowering Phenology Responses to Time Series

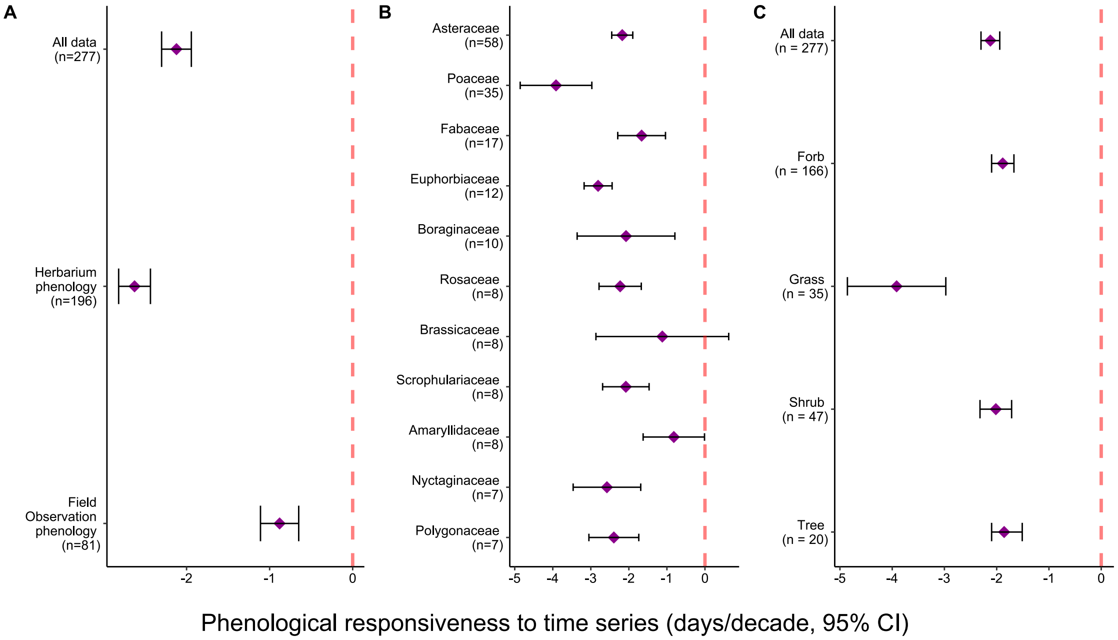


Figure 4. Flowering Phenology Responses to Time Series for (A) All Data, (B) Families and (C) Functional Groups.

The purple diamonds represent the overall effect size, the error bars are the 95% confidence intervals, and n = sample size of the species-specific responses included in the respective random effects models. The vertical dashed line represents the line of null effect. As an interpretation rule, confidence intervals that cross the line of null effect indicate a non-significant effect size, as in the case of Brassicaceae. Confidence intervals on either side of the line of null effect represent significant advanced responses (negative values) or significant delayed responses (positive values).

Synthesis of the 277 species-specific responses of flowering date to time series from all 13 studies revealed that on average, plants in drylands are advancing their flowering phenology by approximately 2 days decade^{-1} (effect size = -2.12, Q = 2521.65, df =276, P < 0.0001, Figure 4A), although some species have delayed their flowering date. When assessed taxonomically flowering phenology responses to time series ranged from advanced flowering of 30.2 days decade^{-1} in *Alyssum desertorum* (Brassicaceae) to delayed flowering of 40.2 days decade^{-1} in *Crinum stuhlmannii* subsp. *delagoense*

(Amaryllidaceae). Although the summary effects of flowering date response to time series of both the herbarium-derived and field observation phenology studies were both negative and different from zero, the value for herbarium phenology (effect size = -2.63, Q = 1245.68, df = 195, $P < 0.0001$, Figure 4A) was higher than that of field observation phenology estimate (effect size = -0.88, Q = 562.76, df = 80, $P < 0.0001$, Figure 4A).

Phenological responsiveness of flowering date to time series also varied across plant families ranging from advances of approximately 4 days decade^{-1} in Poaceae (effect size = -3.91, Q = 500.79, df = 34, $P < 0.0001$, Figure 3B) to less than one day decade^{-1} in Amaryllidaceae (effect size = -0.82, Q = 79.70, df = 7, P = 0.047, Figure 4B). Brassicaceae was the only family assessed in this study that did not show any significant change in flowering date response to time series (effect size = -1.12, Q = 82.73, df = 7, P = 0.208, Figure 4B).

When assessed by growth form, grasses were the functional group with the greatest flowering date response to time series of nearly -4 days decade^{-1} to time series (effect size = -3.91, Q = 500.79, df = 34, $P < 0.0001$, Figure 4C), consistent with the family-level outcome for Poaceae. Forbs, shrubs and trees showed similar summary effects of flowering date responses to time series, approximately -2 days decade^{-1} (forbs: effect size = -1.88, Q = 1600.88, df = 165, $P < 0.0001$; shrubs: effect size = -2.02, Q = 186.36, df = 46, $P < 0.0001$, and trees: effect size = -1.86, Q = 68.76, df = 19, $P < 0.0001$, Figure 4C).

Flowering Phenology Responses to Temperature

On average plants have advanced their flowering date by nearly 3 days °C^{-1} in response to rising temperatures (effect size = -2.83, Q = 1335.80, df = 70, P < 0.0001, Figure 5A). The summary effect of flowering date responses to temperature was -4.22 days °C^{-1} for herbarium-derived observations and -0.95 days °C^{-1} for field observation phenology (Figure 5A).

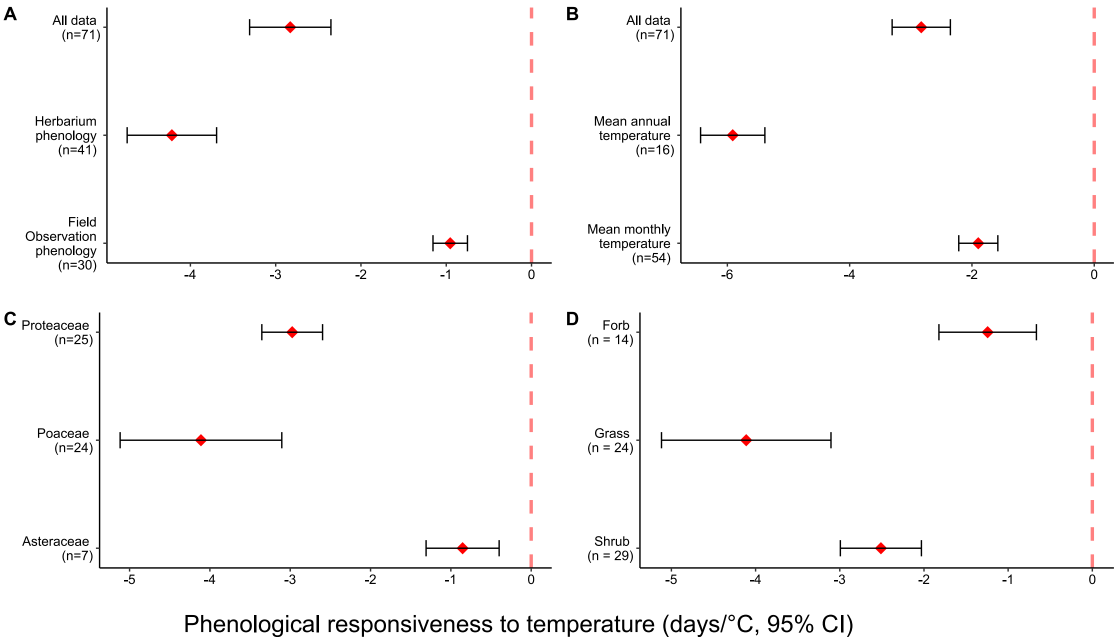


Figure 5. Overall Flowering Phenology Responsiveness to Temperature for (A) All Data & Study Type, (B) Temperature Measures, (C) Plant Families, and (D) Functional Groups.

The red diamonds represent the overall effect size, the error bars are the 95% confidence intervals, and n = sample size of the species-specific responses included in the respective random effects models. The vertical dashed line represents the line of null effect. As an interpretation rule, confidence intervals that cross the line of null effect indicate a non-significant effect size. Confidence intervals on either side of the line of null effect represent significant advanced responses (negative values) or significant delayed responses (positive values).

Flowering date response to temperature was -5.91 days °C^{-1} when temperature was defined as a mean annual value and -1.89 days °C^{-1} when it was considered as a mean monthly value (Figure 5B). Flowering date responses to temperature have advanced by 1, 3 and 4 days °C^{-1} in the families Asteraceae, Proteaceae and Poaceae respectively (Figure 5C). Temperature advanced flowering date for the functional groups evaluated in this study (Figure 5D). Seventeen percent (71 out of 427 observations) of the species-specific flowering phenology observations in this dataset assessed phenological responsiveness to temperature (Appendix A, Table A1).

Flowering Phenology Responses to Precipitation

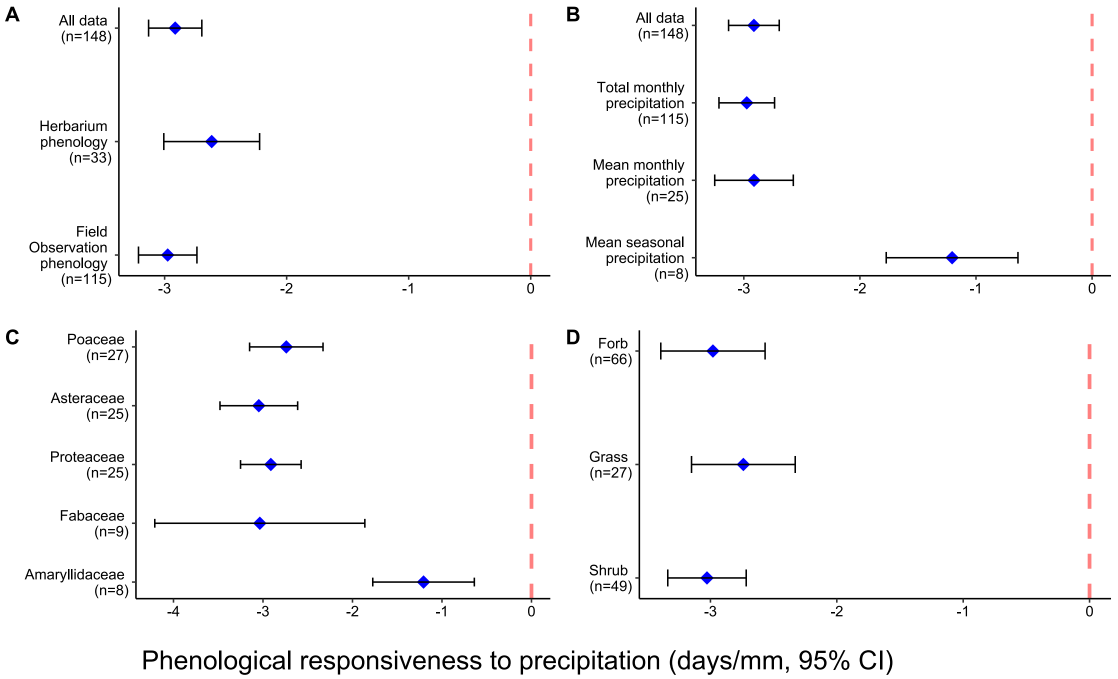


Figure 6. Overall Flowering Phenology Responsiveness to Precipitation for (A) All Data and Study Types, (B) Precipitation Measures, (C) Plant Families, and (D) Functional Groups.

The blue diamonds represent the overall effect size, the error bars are the 95% confidence intervals and n = sample size of the species-specific responses. The vertical dashed line represents the line of null effect. As an interpretation rule, confidence intervals that cross the line of null effect indicate a non-significant effect size. Confidence intervals on either side of the line of null effect represent significant advanced responses (negative values) or significant delayed responses (positive values).

Thirty-five percent (n=148) of observations in this meta-analysis evaluated precipitation effects on the timing of flowering and revealed that plants in drylands have advanced their flowering dates by 3 days mm^{-1} in response to changes in precipitation (effect size = -2.91, Q = 302.35, df = 147, P < 0.0001, Figure 6A). This overall effect size is computed from a wide variation of species-specific flowering phenology responses to precipitation, ranging from delays of 10 days mm^{-1} in *Baccharis pilularis* (Asteraceae) (Mazer et al., 2015) to advances of 17.1 days mm^{-1} in *Crinum paludosum* (Amaryllidaceae)

(Kwembeya & Pazvakawambwa, 2019). Contrary to time series and temperature responses, flowering responses to precipitation showed similarity between the two study types (Herbarium phenology: effect size = -2.61, Q = 186.63, df = 32, $P < 0.0001$ and Field observation phenology: effect size = -2.97, Q = 87.77, df = 114, $P < 0.0001$, Figure 6A). All five families assessed responded to changes in precipitation by advancing their flowering date, with the greatest response of -3.05 days mm^{-1} (Figure 6C) in Asteraceae and the least response magnitude of -1.21 days mm^{-1} observed in Amaryllidaceae of (Figure 6C).

The overall effect size of flowering phenology was comparable when precipitation was defined as a monthly total (effect size = -2.97, Q = 87.77, df = 114, $P < 0.0001$) or a monthly mean in the month of flowering (effect size = -2.91, Q = 66.86, df = 24, $P < 0.0001$, Figure 6B). However, when precipitation was defined as mean seasonal precipitation, the summary effect differed by nearly two-fold (effect size = -1.21, Q = 22.63, df = 7, $P < 0.0001$, Figure 6B). Unlike flowering date responses to temperature, responses of flowering date to precipitation were similar across the different functional groups, although grasses showed the least response-(forbs: effect size = -2.98, Q = 157.92, df =65, $P < 0.0001$; grasses: effect size = -2.74, Q = 16.04, df = 26, $P < 0.0001$ and shrubs: effect size = -3.03, Q = 90.49, df = 48, $P < 0.0001$, Figure 6D).

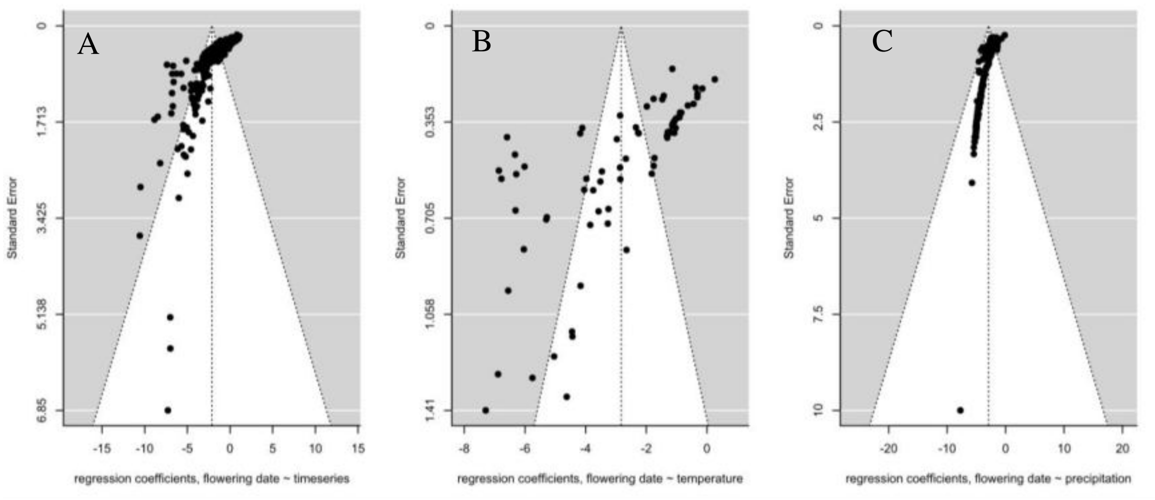


Figure 7. Funnel plots (A-C) Illustrate the Distribution of Flowering Phenology Responses to Time Series, Temperature and Precipitation.

The flowering phenology responses are distributed around the summary effect (the vertical line in the center of each plot) and the standard error of the summary effect plotted on the vertical axis.

Small Study Bias, Moderator Variables and Publication Bias

Visual inspection of the three funnel plots computed for summary effect sizes of flowering phenology responses to time series, temperature and precipitation shows asymmetry in the distribution of individual species responses to these predictors (Figure 7). The plot asymmetry was confirmed with Egger's regression test (time series: $P < 0.0001$, temperature: $P < 0.0001$ and precipitation: $P < 0.0001$). The moderating effect of study type was significant for all three flowering phenology responses to time series ($Q_{M(1)} = 111.4$, $P < 0.0001$), temperature ($Q_{M(1)} = 103.99$, $P < 0.0001$) and precipitation ($Q_{M(1)} = 7.98$, $P = 0.0047$). Furthermore, moderator analysis revealed that study duration affected the overall heterogeneity in the flowering phenology responses to time series ($Q_{M(1)} = 171.82$, $P < 0.0001$) and temperature ($Q_{M(1)} = 145.51$, $P = 0.046$) but not to precipitation ($Q_{M(1)} = 0.68$, $P = 0.41$). The likelihood ratio test did not find evidence of publication bias for flowering responses to time series ($\chi^2_{(1)} = 2.41$, $P = 0.12$), temperature ($\chi^2_{(1)} = 0.18$, $P = 0.67$) and precipitation ($\chi^2_{(1)} = 0.21$, $P = 0.65$).

Discussion

This meta-analysis provides a synthesis of dryland flowering phenology responses to time, temperature, and precipitation. Regardless of the predictor variable, i.e., time series, temperature or precipitation, the overall flowering phenology summary effects sizes were all negative, indicating a stronger influence of advanced flowering responses in dryland plants. This advanced flowering trend was also apparent across plant families and functional groups. Forty-two of 43 random effects models computed in this meta-analysis were significant, suggesting that the species-specific flowering phenology responses differed from each other. The fact that the magnitude of change in flowering date was greater for advanced than delayed responses to time series supports the overall earlier flowering trend reflected in the summary effects. The lack of statistical significance when advanced and delayed flowering phenology responses to temperature were compared could be due to small sample sizes (Advanced: n =39, Delayed: n = 32). No experimental warming studies with flowering phenology data were found, despite a few recent global meta-analyses on warming experiments (Liu et al., 2021; Stuble et al., 2021). This suggests the lack of warming experiments in drylands is not surprising considering that most drylands are located in developing countries and financial resources of establishing and maintaining warming experiments could be very limited.

Flowering Phenology Responses to Time Series

Our meta-analysis showed that, overall, dryland plants advanced their flowering date by 2.12 days decade^{-1}. This outcome suggests that these plants hold potential to adjust their growth and developmental processes to track favorable environmental conditions (Elzinga et al., 2007; Segrestin et al., 2018). However, phenologically responsive species could also be at a disadvantage if their shifting flowering phenology coincides with unfavorable biotic (e.g., activity of potential pollinators) and environmental conditions (Elzinga et al., 2007; Mazer et al., 2013). Considering the overall flowering phenology response to time series of -2.12 days decade^{-1}, shifts of about -20 days in 100 years could be expected. This could be detrimental to the reproductive success of the plants, particularly in the highly responsive species such as *Alyssum desertorum* which advanced its flowering date by 30 days decade^{-1} (Lesica & Kittelson, 2010) and *Crinum stuhlmannii* subsp. *delagoense* with the flowering date delayed by 40 days decade^{-1} (Kwembeya & Pazvakawambwa, 2019). Assuming linear responses of flowering phenology to time series, these trends could seriously off-set the flowering time and compromise the reproductive success of these species, potentially impacting ecosystem structure and function of drylands in the future.

The apparent earlier flowering in response to time series of -2.12 days decade^{-1} reported here for dryland plants demonstrates congruence with global estimates of -2.3 days decade^{-1} (Parmesan & Yohe, 2003) and regional trends from recent and previous meta-analyses, particularly the advanced flowering of 3.7, 2.5 and 3.1 days decade^{-1} reported for the Qinghai–Tibetan region in China (Jiang et al., 2021), Europe (Menzel et al., 2006) and the Northern Hemisphere (Parmesan, 2007), respectively. However, the overall summary effect obtained in this present meta-analysis falls far behind the estimated change in flowering date for the Southern Hemisphere, -5.6 days decade^{-1} (Chambers et al., 2013) and the global synthesis of -4.6 days decade^{-1} (Root et al., 2003). Additionally, 62% of the flowering phenology responses to time series advanced their flowering date and only 38% delayed it, although the magnitude of response varied among species. These differential responses are probably due to spatial and climatic variability since the studies included in this meta-analysis were conducted in global drylands, with different aridity indices, climate trends and other environmental characteristics. Additionally, plant species naturally show diverse biological responses to environmental change (Ma & Zhou, 2012).

I showed in this meta-analysis that families and functional groups respond differentially to time series. Of the 11 plant families evaluated here, flowering phenology responses to time series in Brassicaceae did not show significant shifts. In a community level comparative study, Davis et al., (2010) noted a phylogenetic signal in flowering time tracking (defined in their study as the correlation between the annual first flowering day and seasonal temperature variation) among similar clades, allowing them to identify and classify clades within families as good or poor flowering time trackers. Davis et al., (2010) found that flowering time tracking in the family Brassicaceae (represented in their study by the widely studied species *Arabidopsis thaliana* and *Brassica rapa*) is phylogenetically conserved, particularly the *FLOWERING LOCUS C* (*FLC*) genes that regulate flowering time response to temperature. Based on datasets from two geographically isolated locations, Massachusetts, USA and Oxfordshire, UK, these widely diverged Brassicaceae species exhibited identical flowering time tracking abilities (Davis et al., 2010). This phylogenetic conservatism may explain the lack of true variation in the time series flowering response found in this study for the family Brassicaceae. Unfortunately, no temperature response data were available for this plant family for comparison in this study.

Grasses (Family Poaceae) showed the greatest magnitude of flowering phenology response to time series of -3.91 days decade^{-1} compared to all 11 plant families assessed here (Figure 3B). This accelerated flowering in Poaceae is problematic, particularly given the economic importance of this family to which major crops e.g., maize, millet, rice, wheat and barley belong, and if negatively affected by climate change can have devastating impacts on crop production (Lizaso et al., 2018; Sandmeier & Dajoz, 2000; Volis, 2009). Similar findings were documented in China where herbaceous wind-pollinated plants also showed the greatest magnitude of flowering response of -4.1 days decade^{-1} (Mo et al., 2017). Although grasses are wind-pollinated, and do not depend on animal pollinators for sexual reproduction, synchronization of their flowering phenology might still be limited by resource availability and the state of abiotic conditions in drylands (Moore & Lauenroth, 2017). Drylands are characterized by strong seasonality with clearly defined wet periods to which the greatest plant production is restricted, followed by long periods of dry conditions, when plants senesce and/or become quiescent (Maestre et al., 2021; Santos Neves et al., 2017). A recent study conducted in the Chihuahuan Desert revealed that changes in precipitation patterns are shifting the timing of grass green-up and senescence (Currier & Sala, 2022). Specifically, it was found that drought conditions tending to advance the green-up phenology of grasses while increased precipitation tended to delay, possibly affecting the length of the growing season (Currier & Sala, 2022). Shifts in the flowering phenology of wind-pollinated plants could therefore result in a contracted or expanded growing season, which could cost or benefit the affected species (Munson & Long, 2017). In a herbarium-based phenology study, Munson & Long (2017) showed that C3 grasses responded by flowering earlier while C4 grasses delayed their flowering in response to climate warming, determined in that study as mean annual temperature (Munson & Long, 2017).

This synthesis also revealed variable responses in the magnitude of change in flowering date of dryland plants across functional groups (Figure 3C). The magnitude of response in the flowering date to time series for dryland plants at the functional group level in this present study (forbs: -1.88, grasses: -3.91, and shrubs: -2.02 days decade^{-1}) is greater than that of Northern Hemisphere plants, where both herbaceous plants (forbs and grasses) and shrubs showed a -1.1 and -1.1 days decade^{-1} (Parmesan, 2007). The exception was for Northern Hemisphere trees which advanced flowering date faster (Parmesan, 2007) than dryland trees (-3.3 and -1.86 days decade^{-1}, respectively). In drylands, the flowering phenology of forbs and grasses is seasonally restricted to the growth period (Crimmins et al., 2011; Munson & Long, 2017). Generally, annuals and C3 plants tend to flower earlier than perennials and C4 plants (Munson & Long, 2017). In temperate climates, daylength and temperature are important predictors of grass flowering phenology. Annual and some perennial grasses require long days to flower, while most perennial grasses require low temperatures or short-days, followed by transition to long days for the initiation of flowering (Tooke & Battey, 2010). The greater magnitude of response in tree flowering phenology reported by Parmesan (2007) could be because higher latitudes in the Northern Hemisphere have showed a stronger warming trend than in the lower latitudes such as the tropical and subtropical zones where most warm drylands are located (Collins et al., 2013). Additionally, tree flowering phenology in drylands is influenced by various environmental variables, although precipitation is commonly regarded to be most important in these systems (Bowers & Dimmitt, 1994; Crimmins et al., 2011). Indeed, Seghieri et al., (2012) showed that the flowering phenology of different tree species in the Sahel are strongly predicted by air temperature (*Vachellia flava*, *Vachellia seyal*, *Vachellia tortilis* subsp. *raddiana*, and *Balanites aegyptiaca*), daylength (*Leptadenia pyrotechnica*, and *Senegalia senegal*), and cumulative rainfall (*Combretum glutinosum*). In another study conducted in the Kalahari Desert in Botswana, only one of three tree species, *Vachellia luederitzii*, produced flowers and fruits at the peak of the rainy season and the timing of these phenophases were significantly correlated with both total monthly rainfall and relative humidity (Sekhwela & Yates, 2007). Meanwhile, *Vachellia erioloba*, and *Senegalia mellifera* produced flowers and fruit well before the onset of the rain season (Sekhwela & Yates, 2007); probably because they are reliant on deeper soil horizon for stored water reserves (Peguero-Pina et al., 2020), demonstrating non-dependence of these phenophases on current season rains in these species, in this ecosystem.

Flowering Phenology Responses to Temperature

Plants in warm drylands assessed in this meta-analysis have advanced their flowering date by 2.83 days °C^{-1} in response to temperature, suggesting that warmer conditions will accelerate reproductive onset in these ecosystems, consistent with global trends (Parmesan & Yohe, 2003; Root et al., 2003; Stuble et al., 2021). This summary effect response is, however, below the estimates of flowering phenology responsiveness to temperature in continental Europe (-4.6 days °C^{-1}) (Menzel et al., 2006), China (-4.93 days °C^{-1}) (Ma & Zhou, 2012) and the Northern Hemisphere (-4.6 days °C^{-1}) (Wolkovich et al., 2012). I suggest two hypotheses for the lower phenological sensitivity of flowering to temperature in drylands. First, the flowering phenology data included in Menzel et al., (2006), Ma & Zhou, (2012) and Wolkovich et al., (2012) are predominately sourced from the Northern Hemisphere, a part of the world with greater climate warming than the Southern Hemisphere (Collins et al., 2013; Pachauri et al., 2015). The annual mean temperature in the Northern Hemisphere is warmer than the Southern Hemisphere by

1.24 ± 0.16 °C (Kang et al., 2015), mainly due to the northward cross-equatorial ocean heat transport and the larger greenhouse effect which is prominent in the northern latitudes, although other factors such as a seasonal variations and the proportion of ocean to land in the two hemispheres have also been suggested to contribute to the temperature differences (Feulner et al., 2013; Kang et al., 2015). Globally, the ocean transports large proportions of energy across the equator northward of about 0.56 ± 0.09 PW on average annually, particularly across the Atlantic resulting in a warmer Northern Hemisphere (Kang et al., 2015). Furthermore, Kang et.al., (2015) showed that the greenhouse trapping effect on annual mean temperature is generally larger over the land than over the ocean which contributes to increased warming in the Northern Hemisphere since the fraction of land is greater than the ocean, compared to the Southern Hemisphere (Kang et al., 2015). Second, flowering phenology in the temperate Northern Hemisphere is highly sensitive to temperature (Bertin, 2008; Körner & Basler, 2010; Parmesan, 2007), probably because temperature variations in this hemisphere tend to be more pronounced than in the subtropical regions. For example, while the larger proportion of land to ocean ratio in the Northern Hemisphere warms boreal summers, it also results in extremely cold winters (Kang et al., 2015), exposing the plants to large seasonal fluctuations in temperature. Comparatively, warm drylands assessed in this study are located in the subtropical latitudes of the world, mainly between 30° north and south of the equator, variations in temperature are less dramatic and precipitation is more variable (McGinnies, 1979; Peguero-Pina et al., 2020). Consequently, flowering phenology is often driven by precipitation (Bertin, 2008; Crimmins et al., 2011) although temperature and the interaction effects of these two climatic variables have also been shown to be important predictors of flowering time in these ecosystems (Lesica & Kittelson, 2010; Matthews & Mazer, 2016).

Shifts in flowering phenology can either be beneficial or detrimental to plants (Mohan et al., 2019) depending on several factors including their general characterization as early, mid-season or late flowering species (Moore & Lauenroth, 2017), life history and photosynthetic pathway (Munson & Long, 2017). Because the onset of flowering generally marks the beginning of the growing season, some studies have shown that earlier flowering onset typically extends the growing season, potentially benefiting the plants (Menzel & Fabian, 1999; Schwartz & Reiter, 2000). However, a lengthened growing season due to warming may not necessarily translate into longer reproductive phases (Liu et al., 2021) or fitness, although consequent extension of flowering duration has been reported in some studies (Valencia et al., 2016). For example, Moore & Lauenroth, (2017) showed that the early-flowering species in the semi-arid Central Plains Experimental Range, Colorado, bloomed earlier and stopped flowering earlier in response to warmer spring temperatures. In fact, earlier flowering has been shown to alter reproductive fitness and influence ecological interactions of coexisting plant and animal species (Arfin Khan et al., 2018; Valencia et al., 2016). Earlier flowering onset reduced the production of flowers and fruits for multiple plant species (Valencia et al., 2016) and resulted in mismatched emergence of bee pollinators for the red-listed perennial spring plant species *Pulsatilla vulgaris* in the grasslands of Wurzburg, Germany (Kehrberger & Holzschuh, 2019b). Mismatches in plant-pollinator interactions reduce the opportunity for sexual reproduction and are disadvantageous because natural selection tends to favor self-fertilization in these scenarios as a mechanism of reproductive assurance (Etterson & Mazer, 2016; Wright et al., 2013). Although the overall outcome of flowering phenology shift in drylands is indicative of earlier flowering trend, it is worth noting that a considerable number of the species-specific responses to warming (45%, n=32) were delayed or late flowering responses. Plants that delay their flowering in response to warming (such as C4 plants) are usually well adapted to warm environments and are able to photosynthesize more efficiently under these conditions, giving them a competitive advantage to grow larger, delay their flowering time and possibly reproduce more over the long-term (Fazlioglu, 2019; Sherry et al., 2007). This is the case in the drylands of southwestern USA region, where high temperatures and associated water stress in the early summer have selected late-season C4 grasses to delay reproduction until monsoon precipitation triggers floral development (Munson & Long, 2017). However, it is important to note that this benefit of a longer growing time and delayed flowering observed in C4 plants under warming conditions could be countered and negatively affected by rising atmospheric CO2 (Munson & Long, 2017; Thuiller et al., 2006). In non-monsoon drylands, limiting water resources associated with the end of season (Maestre et al., 2021) will negatively impact reproductive success in late flowering species as moisture becomes limiting toward the end of the growing season. In some instances, delayed flowering may also result in a shorter flowering duration and reduced reproductive fitness. Indeed, Rafferty et al., (2016) showed that delayed flowering in the C3 Sonoran desert shrub *Arctostaphylos pungens*, was concomitant with a compressed flowering season, low-weighing fruits, a reduced number of fruits produced per plant and lower seed count per fruit. Later flowering onset could therefore affect fruit dispersal patterns and phenological relationships with herbivores (Pearson, 2019b).

Climate models predict that global drylands will experience a warming of 2 and 4 °C and a 100 percent increase in the occurrence of extreme warm years by the end 21st century, respectively, according to the Representative Concentration Pathway (RCP) 4.5 and RCP8.5 scenarios (Huang et al., 2017; Pachauri et al., 2015). In Namibia, the driest country in sub-Saharan Africa, temperatures may increase by 1°C to 3.5°C in summer and 1°C to 4°C in winter for the period 2046 – 2065 (Dirkx et al., 2008). Based on the flowering phenology response to warming of -2.83 days $°C^{-1}$ in this present study, a dramatic shift in flowering date of up to -11.32 days may be anticipated for plants in that country over this time period of only 19 years, at the maximum predicted temperature increase of 4 °C. The random effects models in this meta-analysis also detected significant variation in the magnitude of phenological response to temperature across taxonomic groups. One interesting finding from this synthesis is the detection of phenological responsiveness to temperature in the largest family of flowering plants, Asteraceae, which has been suggested to have weaker climate change sensitivity compared to other groups (Davis et al., 2010; Fazlioglu, 2019). The greatest magnitude of flowering phenology responses to temperature of -4.11 days $°C^{-1}$ was found in Poaceae, which could result in earlier flowering of up to 16 days for this plant group by the end of the 21st century, under the RCP8.5 predictions of 4 °C warming. The composition and structure of grass-dominated biomes such as deserts, grasslands and savannas could therefore change under warm future conditions. Differences among functional groups in drylands flowering phenology response to temperature also contrasts with similar phenological responsiveness among trees: -4 days °C^{-1}, shrubs: -4.1 days °C^{-1}, and herbaceous plants: -4.8 days °C^{-1} from different ecosystems in China (Mo et al., 2017). This outcome suggests that different functional groups in drylands will respond variably to climate warming compared to other ecosystems.

Flowering phenology is most responsive to temperature in the months immediately prior to flowering, commonly up to four months before phenological onset (Fitter & Fitter, 2002; Pearson, 2019b; Primack et al., 2004; Tooke & Battey, 2010), although the number of months may vary depending on plant and site characteristics such as growth forms and ecosystem type. An important aspect to consider in the study of the reproductive phenology of perennial plants is the environmental conditions of the seasons prior to their present-day phenology. For example, Mazer et al., (2015) showed that the onset of its reproductive (and vegetative) phenophases of *B. pilularis* was strongly correlated with conditions of the preceding winter months even though although the species flowers in late summer (Mazer et al., 2015). Warmer temperatures have resulted in mixed flowering phenology responses in dryland woody plants. A two-year experimental study of the role warming on two dominant shrub species in a Mediterranean shrubland in Spain found that one species *Globularia alypum* increased its flowering effort (measured in that study as the number of plants with functional flowers) in winter and decreased it in the autumn, during the first year (Llorens & Peñuelas, 2005). Furthermore, warming delayed the flowering onset of *G. alypum* in the first year and shortened the duration of flowering in the autumn of both years. Meanwhile, warming did not affect the flowering phenology of the second species *Erica multiflora* (Llorens & Peñuelas, 2005). The authors of this work suggested that the delay in autumn flowering onset and shortened flowering duration in the warmed plots was probably related to the reduction of soil moisture by the warming treatment in the first year, as this effect was not observed in the second year (Llorens & Peñuelas, 2005). In a short-term (2011-2014) field observation study conducted in National Parks around California, Mazer et al., (2015) also found highly variable effects of winter and spring temperature on the flowering phenology across four woody species. For *Baccharis pilularis* high December (winter) minimum temperature advanced flowering, but higher minimum January (winter) temperature Tmin delayed it. Meanwhile, warm December and January conditions resulted in a delayed flowering response on *Quercus lobata*. High minimum temperature during spring (March) delayed flowering in *Eriogonum fasciculatum* while there was no significant effect of monthly minimum temperature on the flowering date of *Sambucus nigra*. The delayed flowering response to warmer winter conditions in these species could be due to ineffective vernalization cue because insufficient chilling over the winter, would fail to promote earlier flowering in the spring (Mazer et al., 2015). Furthermore, the delayed flowering response to warmer winters is uncommon in temperate zone systems where earlier flowering is often the outcome of rising winter and spring temperatures (Cleland et al., 2007; Menzel et al., 2006). Delayed flowering responses to temperature as noted in drylands suggests that climate warming effects on flowering phenology may vary considerably between water-limited and temperature-driven ecosystems. Additionally, the interaction effects between temperature and precipitation commonly affected flowering phenology in this water-limited ecosystem (Mazer et al., 2015). A two-year microcosm warming impact study conducted at the Climate Change Outdoor Laboratory in the semi-arid Mediterranean ecosystem in Spain, focusing on grasses, nonnitrogen-fixing forbs, and nitrogen-fixing legumes; also alluded the advanced the onset of flowering, a lengthened flowering duration and overall reduction in flower production to the interaction effects of warming and soil moisture (Valencia et al., 2016). The works of Valencia et al.,(2016), Mazer et al., (2015) and Llorens & Peñuelas (2005) emphasize the need to consider the interaction effects of temperature, soil moisture and precipitation in dryland flowering phenology research.

Flowering Phenology Responses to Precipitation

The relationship between flowering time and precipitation in drylands is not well understood or documented. Yet, precipitation is often regarded an important driver of flowering phenology in drylands (Crimmins et al., 2011; Jiang, 2021; Lesica & Kittelson, 2010). This meta-analysis is one of a few efforts to synthesize the magnitude of flowering date response to precipitation for drylands, and will complement the work of Jiang (2021) who demonstrated important interaction effects of temperature and (cumulative preseason) precipitation on flowering phenology of herbaceous plants in the Qinghai–Tibetan Plateau in China. Huang et al., (2020) also discussed and emphasized the important role of precipitation in drylands flowering phenology, and showed that increasing preseason precipitation advanced the spring phenology of the herbaceous plants. However, first flowering date was clumped together with other spring phenophases, specifically, bud burst date, first leaf date and date of 50% leaf unfolding, collectively considered as spring phenology and the study covered a range of grassland types across China (Huang et al., 2020). While these studies undoubtedly shone much-needed light on the specific role of precipitation in dryland flowering phenology, they are limited by spatial extent. In this present study, I draw data from across global drylands and reveal that overall, plants have advanced by 2.91 days mm^{-1} in response to increasing precipitation in these systems. This summary effect however encompasses a large and variable range individual responses (Figure 3C), and in view of the mixed effects of precipitation on the flowering phenology across drylands, must be interpreted with caution. Some authors have reported no effect of increased precipitation on flowering phenology (Sherry et al., 2007), others have shown advanced flowering phenology responses to increasing precipitation (Crimmins et al., 2011) and in some cases enhanced moisture inputs delayed flowering (Matthews & Mazer, 2016; Moore & Lauenroth, 2017). In some studies, decreased precipitation delayed flowering onset (Llorens & Peñuelas, 2005; Zhou et al., 2019), resulted in earlier flowering (Lesica & Kittelson, 2010) and completely suppressed it in some drylands (Moore & Lauenroth, 2017). It remains pertinent to acknowledge that precipitation in drylands is naturally highly variable and patchy, both spatially and temporally (Maestre et al., 2012; Noy-Meir, 1973; Schwinning & Sala, 2004), which could account for the diverse flowering phenology responses to precipitation observed in these ecosystems. The large spatial scales of some the studies included in this meta-analysis, for example Munson & Long (2017) which included data from 23 ecoregions across the south-western

USA and Kwembeya & Pazvakawambwa (2019) which has derived data from 9 of 14 regions in Namibia, further necessitate the cautionary interpretation of the overall effect size of flowering date response to precipitation reported here. Accordingly, it is important that future dryland flowering phenology studies focusing on precipitation responses must consider the effects of spatial heterogeneity.

From a global change perspective, in contrast to temperature, which generally shows a warming trend, future changes in the precipitation patterns of drylands show greater variability (Collins et al., 2013). Precipitation is expected to increase in some locations, decrease in others and remain unchanged in certain regions (Collins et al., 2013; Daramola & Xu, 2022). In the subtropics where most global warm drylands are located, decreases of up to 30% or more in precipitation amounts and increased aridity are projected (Collins et al., 2013). A recent analysis based on four decades of climatic data in drylands (1979-2018), Daramola & Xu, (2022) revealed that drylands have experienced an overall precipitation decrease about 0.074 mm^{-1} $month^{-1}$ $year^{-1}$; although changes in precipitation varied greatly across regions. Significant decreases in precipitation were noted over expansive areas of South America dryland as well as parts of east Africa and most of central North America across seasons (Daramola & Xu, 2022). However, precipitation has increased in the drylands of southern Asia, southern Africa, Australia, northern Africa and the central and northeastern parts of North America (Daramola & Xu, 2022). In view of these diverse projected changes in precipitation characteristics for different drylands and the variable response spectrum of species, it is challenging to make accurate predictions on the flowering phenology in these systems.

The role of precipitation in flowering phenology in drylands is also often confounded by other environmental factors, particularly temperature, potential evapotranspiration, topography, elevation, solar radiation and soil moisture (Crimmins et al., 2011; Huang et al., 2020; Mazer et al., 2015; Moore & Lauenroth, 2017). The interaction effects between temperature and precipitation on flowering phenology responses in drylands are of particular importance and may vary from those in other ecosystems, especially with known climate change impacts on the relationship among these two variables. Globally, there is a notable positive relationship between changes in precipitation and temperature has been documented for non-dryland areas such that warmer years have tended to be wetter years (Collins et al., 2013; Daramola & Xu, 2022; Hulme, 1996). However, this relationship does not hold true for drylands where a rather negative correlation between precipitation and temperature, such that warmer years have tended to be drier and vice versa (Daramola & Xu, 2022; Hulme, 1996).

This present meta-analysis has revealed striking similarity in the overall response of flowering date with an earlier flowering trend to both temperature (-2.83 days $°C^{-1}$) and precipitation change (-2.91 days mm^{-1}). I can infer from these findings that both precipitation and temperature are important predictors of flowering phenology in drylands and could exert significant interaction effects on the reproductive phenology of plants in these ecosystems. Indeed, flowering phenology studies in drylands have shown that changes in precipitation can alter temperature effects on flowering phenology and vice versa. This was demonstrated in the Qinghai Tibetan Plateau where Jiang et al.(2021) found that a positive relationship between flowering date and cumulative pre-season precipitation for early-flowering time series suggesting that increasing precipitation delayed flowering. However, the delayed flowering response was attributed to decreasing temperature rather than to variation in precipitation, because higher precipitation in the study area was associated with lower temperatures resulting from increased cloud cover and reduced solar radiation. This hypothesis was supported by a negative relationship between precipitation and average temperature (Jiang, 2021). Matthews & Mazer (2016) also found that warmer spring minimum temperature advanced flowering date in *Trillium ovatum*, but its advancing effect was stronger where precipitation was higher. Similarly, high precipitation was associated with later flowering, but the delaying effect of increased precipitation was greater with lower minimum temperature (Matthews & Mazer, 2016). The authors suggested that the species' ability to track minimum temperatures under wetter conditions is probably enhanced, while the potential for reproductive failure is reduced, hence a greater magnitude response of earlier flowering. On the contrary, the delaying effect of high precipitation was enhanced under low minimum temperatures because precipitation could freeze under cooler conditions, limiting the plants' ability to initiate growth and reproduction (Matthews & Mazer, 2016).

Precipitation effects on flowering phenology in drylands also varies with flowering season and the various taxonomic and functional groups. In the Sonoran Desert, herbaceous perennials flowered significantly earlier than woody species and, in some instances, earlier than herbaceous annuals (Crimmins et al., 2011). For most herbaceous perennials in this study area, summer represents the second period of flowering, the first being springtime, following winter rains. By the summer, these plants have already invested energy in vegetative (and reproductive) growth, giving them competitive advantage to break dormancy, resume growth, and flower again. In contrast, summer annuals must germinate, grow and build-up the necessary biomass before they can produce flowers, resulting in a flowering onset lag in annual plants (Crimmins et al., 2011).

In my study, the plant families Poaceae, Asteraceae, Proteaceae, and Fabaceae each responded similarly to precipitation increase by advancing their flowering date with a magnitude of approximately -2.74, -3.05, -2.91 and -3.04 days mm^{-1} respectively. Trends toward earlier flowering in forage plant families Gramineae (Poaceae), Leguminosae (Fabaceae) and Cyperaceae have also been shown in a recent meta-analysis across China's desert steppes (Huang et al., 2020). As the largest plant family, Asteraceae also comprises numerous weedy species such as *Galinsoga parviflora* known to compete effectively with low-growing (short height) crops such as wheat, onion, cabbage, garlic, and tomato (Damalas, 2008). *Chromolaena odorata* (Asteraceae) is another example of a globally renowned trouble weed plant that forms dense thickets depriving other vegetation of ecosystem resources and causing economic and ecological losses particularly through habitat loss and transformation (Uyi & Igbinosa, 2010). Advanced flowering responses to precipitation in Asteraceae could enhance the competitive potential of this family, shifting water use and availability in dryland croplands. Similarly, earlier onset of flowering in response to increasing precipitation shown in the grass family Poaceae may alter the composition of grasslands and rangelands in drylands which may impact beef production, which is a major industry in these ecosystems (Maestre et al., 2012). Furthermore, shifts in the flowering phenology of Proteaceae in response to changing precipitation could also have significant impacts for commercial cut flower industry, where Proteas are highly valued globally (Louw et al., 2015). The bulb-forming plants in the family Amaryllidaceae showed the weakest, yet significant response to precipitation according to the random effects model. Amaryllidaceae is a family of geophytes, plants that are adapted to survive extreme environments because they have a capacity to store large quantities of water, starches and protein compounds in their subterranean organs (Kamenetsky et al., 2005). This survival strategy could explain the weak flowering phenology responses in this plant family.

The summary effects of the flowering responses differed according to measures of precipitation as a predictor variable, which in this meta-analysis were either as mean seasonal, mean monthly and total monthly variables (Figure 5D). Naturally, mean seasonal precipitation, considered over a number of months is expected to differ considerably from total or mean monthly amounts; more so in drylands where precipitation tends to be highly variable, both temporally and spatially. Similarity in the summary effect values when precipitation was defined as total monthly and mean monthly values suggests there may be a strong correlation between these variables. Studies have shown that most plants tend to be responsive to climate conditions during the month of and up to four months immediately preceding flowering (Menzel et al., 2006; Pearson, 2019b). However, responsiveness to climatic conditions beyond the months immediately prior to flowering has been found in some plants, particularly woody plants (Seghieri et al., 2012; Sekhwela & Yates, 2007). Only a few flowering phenology studies test the effect of a multitude of climatic variables on flowering phenology (Matthews & Mazer, 2016; Seghieri et al., 2012) to account for the diverse biological responses to environmental change that different plants may display. Most studies tend to test for the effect of a predetermined, commonly temperature (Jones & Daehler, 2018; Root et al., 2003).

The long-term field-observation study (1984-2009) conducted by Crimmins et al., (2011) in the Santa Catalina Mountains in the Sonoran Desert shone much-needed light on the role of precipitation in dryland flowering phenology, particularly where elevation and monsoon rains are also important ecological characteristics. The region is characterized by a bimodal rainfall pattern where rain is distributed about equally across two rainy seasons, one in the winter, mainly December to March, and the other during the summer monsoon when rains fall from July through September (Crimmins et al., 2010). Additionally, this region is also characterized by an elevation-driven soil moisture gradient with greater and more consistent soil moisture at higher elevations (Crimmins et al., 2010). Indeed, Crimmins et al., (2011) found evidence to suggest that plants at higher elevations could experience greater flowering phenology responses in future due to greater sensitivity of mountain-top mesic plants to water stress. However, the physical and climatic conditions in the Santa Catalina mountains near Tucson, Arizona (Crimmins et al., 2011) may not necessarily be representative of all warm global drylands, therefore interpretation of the results from the overall effect size of flowering phenology responses to precipitation should take this caveat into account.

Small Study Bias, Moderator Variables and Publication Bias

Asymmetrical arrangement of points in the funnel plots (Figure 6) and the corresponding Egger's regression tests suggest the presence of small study bias. Despite this confirmation, it is important to note that asymmetry in funnel plots could also account for alternative sources of bias, such as study quality, location bias (Quintana, 2015). This is the case in this meta-analysis where both study type (herbarium phenology or field observation phenology) and study duration showed significant moderator effects. A significant moderator effect of study duration in the time series and temperature responses suggests that some of the heterogeneity noted in these two models is due to the time span of the studies. No moderating effects of study duration was apparent in the precipitation response model probably because most observations were drawn from Crimmins et al., (2011), reflecting the same study span.

Flowering phenology summary effects derived from field observations differed from those computed with herbarium phenology data for time series, temperature, and precipitation responses (Figures 4A, 5A and 6A); as confirmed with significant moderator analysis outcome for study type. This should be expected because herbarium-based phenology involves a reconstruction of flowering dates from specimen collection dates and the phenological status of the plants at the time of collection. Through this process, precise details on flowering dates in the field cannot be determined and are therefore derived as mere estimations. Despite these limitations, herbarium-based phenology remains an inexpensive, widely available, accessible, and reliable method for studying shifts in the flowering phenology of plants due to climate change. Additionally, herbarium phenology data offer longer time-spans and coverage of larger geographic regions (Jones & Daehler, 2018; Lavoie & Lachance, 2006; Willis et al., 2017). Comparatively, regular monitoring in field observation studies guarantees a more precise tracing of exact flowering dates, therefore yielding estimates with higher accuracy. However, the establishment of permanent monitoring field sites can be a costly operation requiring dedicated financial and human resources for long-term upkeep and maintenance.

There was no evidence of publication bias noted in the random effects models of flowering responses to time series, temperature, and precipitation, probably because the effect size data were based on individual species responses from each study, rather than as composite values of each representing a unique study as per traditional meta-analysis practice.

Conclusions

Dryland plants are responding to time series, temperature, and precipitation by advancing their flowering dates overall, albeit wide variation in the magnitude of response across species. The greater phenological sensitivity in earlier than later flowering responses evident from time series comparisons could drive apart existing relationships among species in drylands. A warming earth as projected globally could result in increased earlier flowering responses in drylands. However, flowering responses to precipitation may be more variable and challenging to predict given its high temporal and spatial variability in drylands, the non-uniform global change inferred patterns as evident from existing data and climate models, and the limited flowering phenology data available to study relationships between precipitation characteristics and flowering. The interaction effects of temperature and precipitation on flowering phenology responses in drylands should be studied closely as both environmental variables are important predictors of flowering time in these systems. This is also critical for drylands because, while increasing temperatures are linked to wetter conditions in non-drylands, warming is associated with drier conditions in drylands which may result in different flowering phenology responses when compared with other ecosystems.

Differential flowering responses across plant families and functional groups may change the species composition, structure, and function of dryland ecosystems. This may be more so for grasslands and rangelands in drylands since grasses showed the largest phenological responsiveness to time series and temperature, which may have implications for the livelihoods that these ecosystems support, especially given that livestock production is a major land-use. Earlier flowering is known to result in extensions of the growing season, particularly if flowering end dates remain unchanged or are delayed. Extended growing season does not necessarily end in positive net growth and reproductive output. Instead, lengthened growing seasons could affect use and availability of ecological resources through altered ecosystem function and interactions. In addition, shifts in flowering response can potentially disrupt the reproductive events of different species, and ecological interactions within and across ecosystems e.g., plant-pollinator and disperser relationships. Pollinators play a significant role in the diversity and continued survival of natural communities and in crop yields, by transferring gamete containing pollen and ensuring sexual reproduction in seed plants (Memmott et al., 2007; Ollerton et al., 2011). For animal-pollinated plants, which constitute about 88% of the global angiosperm diversity (Ollerton et al., 2011), shifting flowering time poses the risk of mismatch with the active time of their respective pollinators which could result in reproductive failure (Cleland et al., 2007; Elzinga et al., 2007; Peñuelas et al., 2002). Mismatched ecological interactions do not only affect interacting species, as their impacts may also trickle to other biotic and non-biotic relationships e.g., trophic interactions; implying that phenological shifts may indeed exert prodigious effects on the structure and functioning of ecosystems. Furthermore, reproductive disruptions due to shifts in flowering time could seriously impact livelihoods and food security in drylands, where a third of the world’s human population reside, surviving principally through agro-pastoralism i.e., the integration of crop and livestock production as the main source of livelihoods (UNCCD, 2016).

The combination of the variable species responses, inherent and global change-induced variability in dryland climate does not only make for complex future flowering responses but also emphasize the uncertainties surrounding our ability to predict species flowering responses. Acknowledging that flowering phenology responses to climate change are not limited to temporal assessments, precipitation, and temperature, I recommend that future studies should incorporate other factors such as photoperiod, soil moisture, elevation, latitude, and biotic interactions.

CHAPTER 2

2 FLOWERING PHENOLOGY FROM HERBARIUM SPECIMENS COLLECTED ACROSS NAMIBIAN DRYLANDS

Abstract

The climate is changing and affecting plant responses in global ecosystems and more so in drylands. I conducted a herbarium-based flowering phenology study across Namibian drylands to determine flowering phenology trends through time and their sensitivity to climate change. I analyzed 1707 specimen records of 26 herbaceous species, spanning six families (Acanthaceae, Asteraceae, Cleomeceae, Lamiaceae, Scrophulariaceae and Zygophyllaceae). I paired each record with the mean monthly temperature and precipitation of the two successive months prior to flowering and used linear mixed effects models to assess phenological sensitivity to temperature and precipitation. I found that three species (*Geigeria ornativa*, *Cleome gynandra* and *Cleome oxyphylla*) significantly delayed their flowering dates over time (7.7 d decade^{-1}, 26 d decade^{-1}, and 8.2 d decade^{-1}, respectively). All six families significantly advanced their flowering dates in response to warmer temperatures while four out of six advanced their flowering phenology with increasing precipitation. Temperature was the single most important predictor of flowering phenology of herbaceous plants in these drylands, yielding the lowest AIC values in 76% of the species and phenophases-specific models. Plants in the hyper-arid to arid regions showed lower phenological sensitivity to temperature (-9 d °C^{-}

^{1}) than those in the arid to semi-arid regions (-17 d °C^{-1}), probably resulting from adaptations to the more variable temperatures. Meanwhile, serotinous plants showed greater sensitivity to both temperature and precipitation than non-serotinous plants. Most notably, this study demonstrated the relative influence of temperature and precipitation on the flowering phenology of herbaceous plants in multiple families across dryland gradient, laying an important foundation for predicting future changes in flowering phenology and consequently the structure and functioning of drylands in the driest country in sub-Saharan Africa and elsewhere.

Introduction

As the earth continues to undergo environmental changes, the adaptations of plants to their native environments are tested and challenged, presenting the need for re-adaptation to cope with the subsequent novel environmental circumstances (Chmura et al., 2019; MacGillivray et al., 2010). In many plant species, flowering phenology or the timing of flowering is a life cycle event, that occurs only at selected times of year or when a precise combination of environmental conditions is met (Chmura et al., 2019). Flowering phenology is particularly sensitive to seasonal climate cycles as natural selection favors reproductive timing to occur when key environmental conditions such as temperature, light and water availability are optimal (Chuine, 2010). Accordingly, flowering phenology as a functional trait makes sexual reproductive timing particularly vulnerable to the effect of climate change, given the close relationship between seasonal flowering and climatic conditions, hence an important subject in global change research (Chambers et al., 2013; Chmura et al., 2019). Flowering phenology or reproductive timing is not only a critical determinant of reproductive success for plants but also affects the nature of symbiotic relationships between plants and their pollinators, seed dispersers and predators, herbivores and competitors (Elzinga et al., 2007; Thomson, 1978).

While field observations of flowering phenology are preferred for determining phenological responses to climate change, such data are scarce. Only a few long-term datasets are available worldwide. Notable examples include (1) phenological observations of the flowering dates of cherry trees (*Prunus* spp.) in Japan (A.D. 794–2005), documented and kept as diaries by emperors, aristocrats, politicians, monks, and merchants (Aono & Kazui, 2008); (2) the Marsham phenological records (1736-1745) from Marsham family estates, from Norwich, Norfolk in the United Kingdom (Sparks & Carey, 1995), and (3) the Henry David Thoreau (1852-1858), Alfred Hosmer (1878–1903), Pennie Logemann (1963-1993), Abraham Miller-Rushing – Richard Primack (2004-2006) datasets from Concord, Massachusetts, USA (Miller-Rushing & Primack, 2008). These observations-based datasets are not only scarce, they are also geographically restricted to the Northern Hemisphere with no known equivalent long-term datasets in the Southern Hemisphere (MacGillivray et al., 2010). In contrast, herbarium collections represent an accessible, cost-effective and largely untapped resource of long-term records covering vast spatial scales from which flowering phenology data can be mined and used for global change studies (Jones & Daehler, 2018;

Lavoie, 2013). Herbarium collections provide both phylogenetic and geographic diversity toward phenological investigations making it possible to study multiple lineages across biomes (Lang et al., 2019; Willis et al., 2017). With many collections dating back several decades or even centuries, a special feature of natural history collections is that specimens offer a unique and rare view into the past, allowing for the reconstruction of historical flowering phenology and comparison to modern day phenological records and climate change data (Willis et al., 2017). For these reasons, herbarium specimens should be explored and prioritized as phenological data sources for flowering phenology (Lang et al., 2019). Because herbarium specimens were mainly collected for taxonomic research and documentation of local floras, botanists would generally set out to conduct collection expeditions during the flowering seasons of the geographic regions or taxa of interest. Specimens with reproductive structures have been thus historically the main target criteria for a botanical collector because flowers and fruit aid in the identification and taxonomic description of various flora (Jones & Daehler, 2018; Lavoie, 2013). These qualities make herbarium specimens ideal for phenological studies because collection dates typically target flowering dates. Accordingly, specimen collection dates have been used in herbarium phenology studies as proxies of flowering dates (Calinger et al., 2013a; Primack et al., 2004), with the assumption that the flowering dates reflect the true flowering season of the species under study.

In addition to flowering dates, the meticulous cataloguing systems of herbarium collections allow for additional ecological and geographic information to be obtained from archived specimens (de Beurs et al., 2013; Willis et al., 2017). Each archived specimen is usually accompanied by a label, providing information on the locality, collection date, collector, global position system (GPS), abundance, habitat, and other details. Furthermore, the physical specimens also provide a wealth of information on the health condition, life history, morphology, and most importantly, the phenological status of the plant at the time of collection (Willis et al., 2017). Generally, specimens can be classified to be in the early, peak or late stages of flowering phenology, depending on the proportion of flower buds, open flowers and matured flowers (de Beurs et al., 2013). Previous studies have established that herbarium specimens at peak flowering provide a reliable estimate of the peak flowering date, a convenient measure of flowering time which is relatively independent of population size (Primack and Miller-Rushing 2009).

The use of herbarium specimens to study flowering phenology shifts in the context of climate change is a relatively new field of research; a study published by Primack et al., (2004) was the first to report herbarium-derived flowering phenology trends (Jones & Daehler, 2018). The Primack et al.(2004) study became the prototype for the assessment of flowering phenology shifts over time and relationships between flowering dates and climatic and other environmental variables using herbarium specimens. The main steps outlined in this process include proxying flowering dates from specimen collection dates, most commonly as Julian dates, obtaining and pairing long-term climatic data from an independent source with the flowering dates. A Julian date is a value between 1 and 365 corresponding to the day of year when the specimen was collected based on the Gregorian calendar (de Beurs et al., 2013; Jones & Daehler, 2018). Regression techniques, most commonly linear regression, are then applied to the data to quantify relationships between flowering dates and climatic variables, and with time series, defined as the year of specimen collection (Jones & Daehler, 2018; Primack et al., 2004). Despite the valuable potential of herbarium specimens as a reliable source of phenological data (Jones & Daehler, 2018; Willis et al., 2017), their use remains unevenly employed. Most studies that have used herbarium specimens for flowering phenology assessments are concentrated in temperate latitudes such as the eastern Himalayas, southern Australia, northern Europe and North America (Jones & Daehler, 2018; Lavoie, 2013; Willis et al., 2017), reflecting geographic biases. The potential to extend phenological investigation to non-temperate biomes using these biological collections promises to provide comparable data for a broader global comparison.

Intrinsic differences in plant responses in temperate versus tropical environments need to be taken into consideration. For example, in many temperate regions, daylength, and temperature are important predictors of flowering phenology (Tooke & Battey, 2010) and plants have been shown to be particularly responsive to warming spring temperatures, by advancing their flowering dates (Cleland et al., 2012; Körner & Basler, 2010; Tooke & Battey, 2010). In some of these systems, advanced flowering results in lengthened growing seasons, which affects flower abundance between spring and summer (Menzel & Fabian, 1999). In contrast, the mechanisms regulating flowering phenology in subtropical biomes such as warm drylands, are largely unknown and remain an open question for research. In subtropical areas, winter temperatures seldom drop below the 5°C chilling requirement which is an important cue for spring flowering in temperate plants (Song et al., 2021; Vitasse & Basler, 2013). A number of relevant questions therefore arise, including, what are the main drivers of flowering phenology in subtropical regions; what is the role of temperature and precipitation in the flowering phenology of subtropical plants and how might this vary with global change? These questions can be answered by considering flowering phenology data extracted from herbarium specimens. Given their long-term temporal and large spatial scales, herbarium phenology data may also help to address the role of precipitation in the flowering phenology of subtropical systems, particularly drylands, which is another pertinent aspect of flowering phenology where questions remain. While there is evidence suggesting that precipitation is an important determinant of flowering phenology in drylands (Crimmins et al., 2011; Currier & Sala, 2022; Kwembeya & Pazvakawambwa, 2019), phenological sensitivity of flowering to precipitation is complex and non-uniform, as both increasing and decreasing precipitation tend to advance and delay flowering dates. For example, leguminous tree species *Leptolobium dasycarpum* and *Leptolobium elegans* in the dryland Cerrado region in Brazil delayed their flowering date with increasing rainfall (Fava et al., 2019). In Namibia, geophytes in Amaryllidaceae (e.g., *Crinum buphanoides, Crinum stuhlmannii* subsp. *delagoense* and *Crinum paludosum*) advanced their flowering dates (Kwembeya & Pazvakawambwa, 2019) while others such as *Scadoxus multiflorus* subsp. *multiflorus* are delaying their flowering phenology with increasing precipitation (Kwembeya, 2021). These mixed responses probably reflect the natural variability of environmental conditions in drylands as represented by their level of aridity and/or their variable responses to climate change. Drylands vary in their degree of aridity commonly expressed as an aridity index (AI) (Huang et al., 2017). When defined based on the water balance approach, the AI is calculated as the precipitation/potential-evapotranspiration (P/PET) ratio, where PET is the maximum amount of moisture that can be lost to the air from a surface with an unlimited supply of water under a given atmospheric condition. Because PET is generally higher than P in drylands, their AI is usually below 0.65. Drylands therefore range from dry subhumid ($0.50 < AI < 0.65$) to hyper-arid ($AI < 0.05$) (Huang et al., 2017).

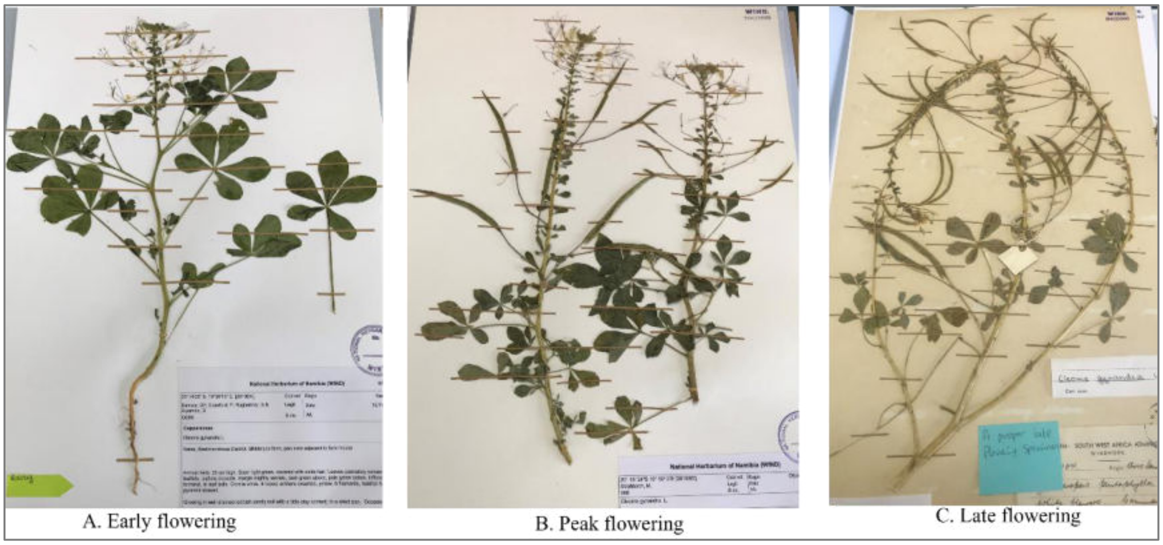
The multiple potential sources of variation in the flowering phenology of dryland ecosystems therefore necessitate further investigation into the flowering phenology trends of different drylands and the environmental factors that regulate these patterns. I conducted this study to explore the potential of herbaceous plants to shift their flowering phenology in response to time series and climate over the last century across a predominantly dryland landscape. I classified my focal species into two seed dispersal functional groups: serotinous and non-serotinous. Serotinous plants, *sensu* Bond (1985), accumulate and retain a canopy seed bank on the plant for one or more years post seed maturation; a key adaptation to temporal heterogeneity of resources in seasonally dry environments (Bond, 1985; Günster, 1994b; Thanos, 2004). This adaptive strategy allows for seed release, germination and establishment to occur only when conditions are favorable, typically when there is sufficient moisture (Thanos, 2004). In this study, I considered species to be non-serotinous if they lacked the seed retention and delayed dispersal strategy of serotinous plants. The results of this study will be useful for predicting the future survival and composition of natural ecosystems in drylands given the climate change expectations of enhanced aridity, warming temperatures and increased variability in precipitation patterns including extreme events. Specifically, I asked the following questions.

1. How does the flowering phenology of herbaceous plant taxa respond to time series, temperature, and precipitation, across Namibian drylands?
2. How does the flowering phenology of serotinous and non-serotinous herbaceous plants respond to time series, temperature, and precipitation?
3. How does the flowering phenology of herbaceous plants from different aridity zones respond to time series, temperature, and precipitation?

Materials and Methods

Herbarium Flowering Phenology Data

I extracted flowering phenology data from herbarium specimens of the selected plant species (Table A1) represented in the National Herbarium of Namibia. Flowering date was proxied from specimen collection date. Rather than adopting the Julian date, flowering date in this study was expressed as the number of days since October 1st, and May 1st, for summer and winter flowering species respectively. The summer growing season in most of Namibia spans from October-April and more than 90% of the rainfall occurs during these months while the cold, dry winter season extends from May to September (Lu et al., 2016). However, it is common for plants to continue flowering throughout May, supported by the occasional showers which mark the end of the growing season, before the arrival of frost events and cold temperatures in June which suspends most plant growth and development especially for herbaceous species (Mendelsohn et al., 2002).



A. Early flowering

B. Peak flowering

C. Late flowering

Figure 8. Representative Specimens of *Cleome gynandra* at Three Different Phenophases. (A) Early flowering, (B) Peak Flowering and (C) Late Flowering.

Specimens were grouped into one of three phenophase classes: early, peak and late flowering, based on the proportional abundance of flower buds, open flowers and mature flowers (fruits) following the guidelines described in Pearson (2019a) and Kwembeya (2021). Specimens with 50%-100% buds and 1%-50% open flowers were considered as early flowering, while those with 1%-25% buds and 75%-100% open flowers or 75%-100% open flowers and 1%-25% fruits were taken to be at peak flowering. Finally, specimens with 25%-50% flowers and 50%-100% fruits were regarded as late flowering (Kwembeya, 2021; Pearson, 2019a) (Figure 8). Sterile or specimens without any reproductive structures (flowers, fruits) were removed from the dataset because their flowering phenology could not be determined. Duplicates (specimens collected by the same or different collector on the same day and at the same location) were included as a single datapoint to prevent non-independence of samples (Calinger et al., 2013b), except if the specimens were collected in different years. Additionally, only species represented by 10 or more specimens were considered for statistical analysis (Calinger et al., 2013b). The number of specimens in my herbarium phenology study ranged from n=17 for *Tribulus pterophorus* to n=164 for *Geigeria ornativa*, and a mean of n= 63 per species.

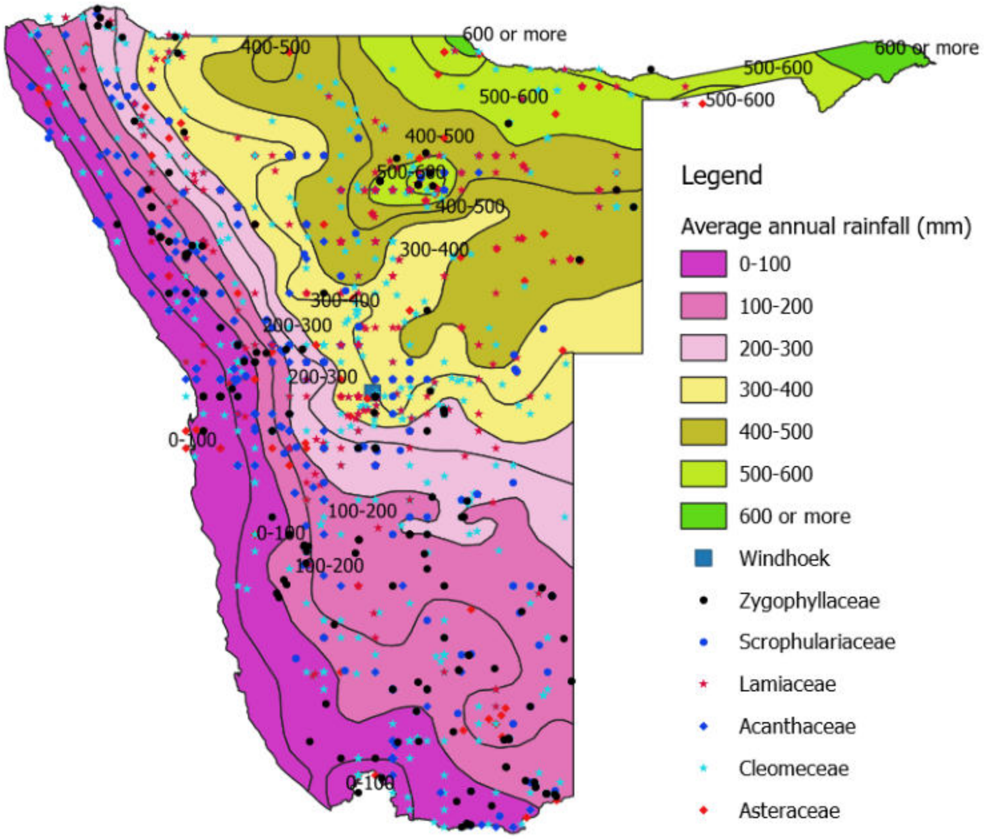


Figure 9. Map of Namibia Showing the Mean Annual Precipitation and the Distribution of Plant Specimens Used in this Study, Categorized by Family.

Study Location

I extracted herbarium flowering phenology data from plant specimens collected within Namibia, the driest country in sub-Saharan Africa (Ministry of Environment & Tourism of Namibia, 2011). Located in south-western Africa where it is backed by the south Atlantic Ocean, Namibia is characterized by a coastal desert (the Namib) to the west and the Kalahari to the east, bordering Botswana. The climate in Namibia characterized by highly variable and unpredictable rainfall, intense solar radiation, high evaporation rates and hot daytime temperatures. Mean monthly minimum temperatures range from less than 2 ^{o}C to about 12 ^{o}C during the coldest months (June-August) of the year while mean monthly maximum temperatures range from 20 ^{o}C to more than 36 ^{o}C during the summer months (October-April) (Mendelsohn et al., 2002). Most of the country receives average annual rainfall below 500 mm with the driest locations in the coastal Namib Desert receiving 25 mm or less per annum (Figure 9). With the exception of the south-western part of the country, most of the rain in Namibia falls in the summer months, typically October-April (Mendelsohn et al., 2002). A notable climatic characteristic in Namibia is the prominent rainfall gradient, which decreases from east to west and north to south (Figure 9) (Mendelsohn et al., 2002). Based on this rainfall gradient, I divided the country into two aridity zones. I defined the hyper-arid to arid zone as the locations that receive $\leq$ 400 mm rainfall and the arid to semi-arid zone as areas in which the mean annual rainfall is $\geq$ 400 mm (Figure 9 and Figure B4). Although 91% of Namibia is characterized as either semi-arid, arid and hyper-arid (White and Nackoney, 2003), the country boasts a rich plant diversity of more than 4500 species, 20% of which are endemic (Klaassen & Kwembeya, 2013). This botanical diversity is preserved in the National Herbarium of Namibia, the natural history collection of plants in Namibia, housing over 100,000 specimens dating back as far as the late 1800s (Klaassen & Kwembeya, 2013). This herbarium collection represents a readily available resource for examining flowering phenology in Namibia and holds potential to contribute to our understanding of how dryland ecosystems might respond to changing climates. In this study, I explored 1768 specimens and extracted herbarium flowering phenology data from 26 species as detailed in section 2.3 and Table B1. However, I excluded data from four of the 14 administrative regions (Omusati, Oshana, Ohangwena and Zambezi), because they were under-represented in the dataset with only 12, 7, 10 and 21 records, respectively. One species, *Cleome luburnifolia* was excluded from analysis because it was represented by less than 10 specimens (n = 8). The final dataset comprised 1707 specimens collected from nine regions across Namibia.

Study Taxa

For this herbarium phenology study, I targeted the plant families Acanthaceae, Asteraceae, Scrophulariaceae, Lamiaceae, Cleomaceae and Zygophyllaceae from across Namibia (Table B1). These plant families were selected because they comprise plant species that are well represented in the Namibian flora and in the National Herbarium of Namibia collection. Additionally, I targeted herbaceous annual and perennial species in these families, particularly those which are collectable as whole specimens for herbarium preservation. Generally, small herbaceous plants [defined here as not exceeding the dimensions of a standard plant press i.e. 40 cm height x 30 cm length (National Herbarium of Namibia, 1994)], hold advantage over woody plants in herbarium phenology studies, because the entire specimen is often preserved, allowing the full phenological status of the plant at time of collection to be determined. In contrast, large herbs and most woody plants are less suited for the extraction of flowering phenology data because only a part of the specimen is collected for herbarium archiving, which may not always be representative of the full phenological status (de Beurs et al., 2013). All species included in this study are indigenous to Namibia (Klaassen & Kwembeya, 2013). I selected the serotinous species *Aptosimum lineare*, *Blepharis grossa*, *Petalidium setosum*, *Petalidium variabile*, *Gerigeria ornativa*, and *Geigeria alata* (Günster, 1994a, 1994b) to evaluate how this group of desert-adapted species may respond to climate change. I also compared serotinous and non-serotinous plant responses and sensitivity to climate change. The non-serotinous group of plants in this study mostly represent taxa from families (Cleomeceae, Lamiaceae, Zygophyllaceae) known for their use in traditional and contemporary medicines, cosmetics and as food plants in many countries and are therefore important for human well-being. For example, the aromatic herbs *Acrotome angustifolia* and *Acrotome inflata* are widely used in Namibia as insect repellents and deterrents where the plants are burnt in huts to keep away unwanted insects, especially mosquitos (Kangombe et al., 2016).

Climatic Variables

To determine the strongest climatic predictors of flowering date in the different taxa, each specimen was paired with climate records the Climatic Research Unit gridded Time Series (CRU TS) version 4 online database corresponding to the date, year, and location of collection since each specimen is also georeferenced. The CRU TS is a global climate dataset derived from the interpolation of monthly climate anomalies from extensive networks of weather station observations (Harris et al., 2020). The data have a resolution of 0.5° latitude by 0.5° longitude grid and features the following climate variables: total monthly rainfall, mean monthly average temperature, vapor pressure, number of wet days, potential evapo-transpiration and number of frost days (Harris et al., 2020). In the current study, I have regressed flowering date as a function of total monthly rainfall and mean monthly average temperature. Since the herbarium collections are dated and georeferenced, I paired each specimen with the total monthly rainfall and mean monthly temperature of the month of collection according to their climate grid as extracted from the Climate Research Unit database, which in my study covered the time period 1913-2018. Each record was paired with climatic variables corresponding to their geographic location, month, and year of collection. In addition, I also paired specimens with averages of total monthly rainfall and mean monthly temperature for the two and three months prior to flowering date, including the month of flowering. For example, if a specimen flowered during October, then I averaged the mean monthly temperature of September and October to obtain its corresponding successive two-month mean monthly temperature value.

Statistical Analysis

Analysis of Flowering Phenology Time Series Trends

To assess trends in flowering phenology over time (days year^{-1}), I applied regression analyses by modeling flowering date as a function of year of specimen collection as the fixed effect in the linear mixed effect models, and region of collection as the random effects. The nine regions of Namibia from which the specimens were collected are shown in Figure B4 (Appendix B). I constructed these models for each species represented by at least 10 specimens (Calinger et al., 2013a), as well as across families at each phenophase (early, peak and late flowering). I also compared flowering phenology time series trends between serotinous and non-serotinous plants and between plants collected from hyper-arid to arid regions and those sourced from arid to semi-arid regions, using the same base structure of linear mixed effects models, although I substituted species for region as a random effect for between aridity zones comparisons.

Analysis Of Phenological Sensitivity of Flowering to Temperature

To explore the sensitivity or responsiveness of flowering timing to temperature, I regressed the flowering date as a function of the mean monthly temperatures of the month of collection, two and three successive months prior to flowering date, including the month of flowering. I selected the mean monthly temperature of the two-successive months prior to flowering as the best-fit temperature because it minimized the Akaike’s Information Criterion (AIC) of all models across species, families, serotiny groups, and aridity zones.

Analysis Of Phenological Sensitivity of Flowering To Precipitation

I followed the same approach as applied for the assessment of phenological sensitivity to temperature to test for phenological responsiveness of flowering date to precipitation. I explored the predictive power of the total precipitation of the month of flowering, two and three successive months before flowering date to identify the precipitation parameters that best explained variation in the flowering dates of summer-flowering species in this study, using linear mixed effects models. Similar to temperature, when the average of the total monthly precipitation of the two successive months of flowering showed the lowest AIC values and therefore higher predictive power across models on flowering date as a response variable, compared to the other precipitation parameters.

Best Fit Model Analysis

For each dataset i.e., 26 species, six families, two seed-dispersal functional groups and two aridity zones, I constructed seven linear mixed effects models at each phenophase to select the best model fitting the data, based on the lowest AIC value. The fixed effects were either (1) year of specimen collection, (2) total precipitation of two successive months before flowering or (3) mean monthly temperature two successive months before flowering (3); or a combination of these predictors as (4) precipitation and temperature, (5) year and temperature and (6) year and precipitation. The full model comprised of (7) all three predictors as fixed effects: year of specimen collection, total precipitation of two successive months before flowering and mean monthly temperature two successive months before flowering. I used the random effects of region of collection across all models except when the data was arranged according to aridity zones, in which case the species were considered as random effects instead since region was accounted for by splitting the data according to aridity levels. The best fit model was chosen if it returned the lowest AIC values. However, if the difference between two competing models was less than two AIC units, the simpler model was selected as the best fit model (Arnold, 2010; Symonds & Moussalli, 2011).

Results

Table 2. Estimates of Flowering Phenology Responsiveness of the Herbaceous Plants to Time Series (Collection Year), Temperature and Precipitation for the Different Phenophases.

* Indicates a significant change in flowering date ($p < 0.05$), the sample size (n) refers to the number of specimens represented by each phenophase, and ‘d’ denotes days.

	Phenophase		
Fixed effects	Early flowering (n = 310)	Peak flowering (n = 772)	Late flowering (n = 625)
Time series (d decade^{-1})	0.28	-0.2	0
Temperature (d °C^{-1})	-9.85 *	-10.62 *	-11.28 *
Precipitation (d mm^{-1})	-0.33 *	-0.52 *	-0.54 *

Flowering Phenology Trends Over Time

Overall, I found no significant response in the time series of early flowering (1926-2018), peak flowering (1913-2018), and late flowering (1924-2018) for the herbaceous forbs assessed in this study (Table 2). However, the flowering dates of these herbaceous plants were responsive to temperature and precipitation across all three phenophases, averaging -11 days per 1°C rise in temperature and -0.5 days per 1 mm increase in precipitation (Table 2).

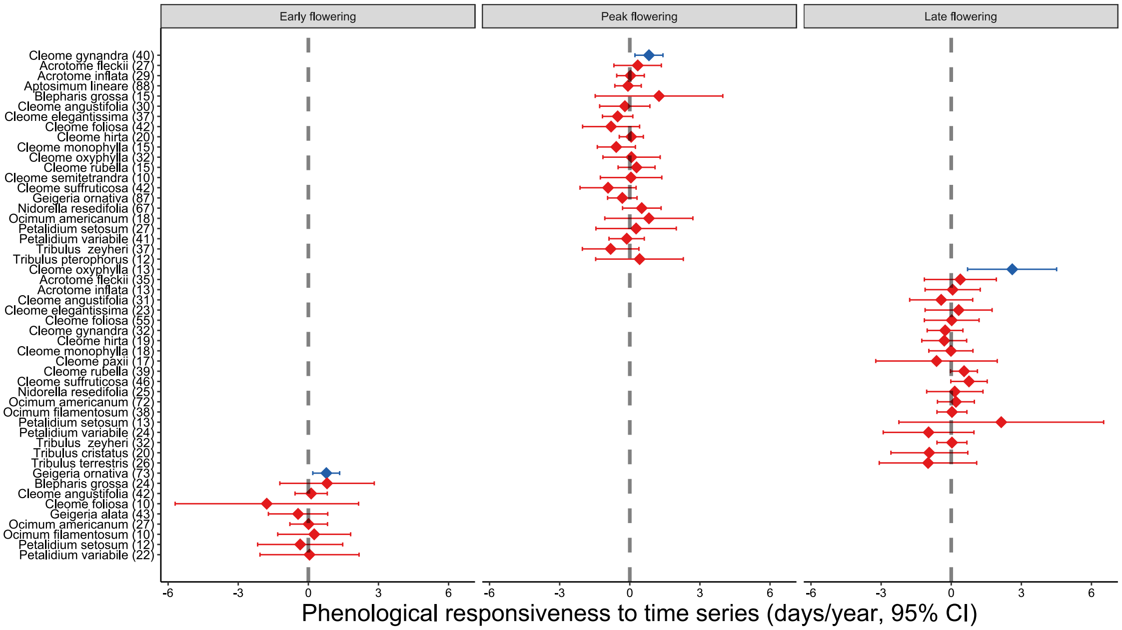


Figure 10. Flowering Phenology Responsiveness to Time Series of the Herbaceous Species at Early Flowering (1925-2018), Peak Flowering (1913-2018) and Late Flowering (1924-2018).

Each horizontal line corresponds to the species-specific flowering date response to time series. The diamond representing the estimates, centered between the lower and upper 95% confidence limits. The blue color represents significant change while the red color represents lack of significant change. The dashed vertical line represents no effect. The number inside parenthesis represents the number of specimens analyzed for each species.

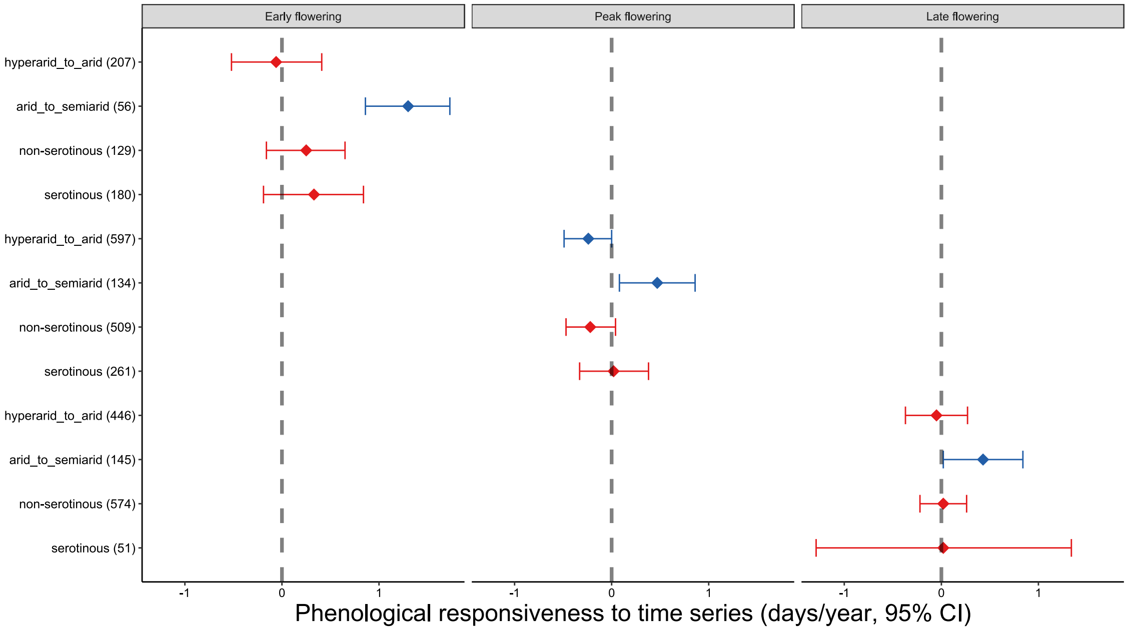


Figure 11. Flowering Phenology Responsiveness to Time Series Between Serotiny, Aridity Zones, And Across Phenophases. Each Horizontal Line Corresponds to The Change in Flowering Date.

The diamonds represent the estimates, centered between the lower and upper 95% confidence limits. The blue color represents significant flowering phenology response while the red color represents lack of a significant flowering phenology response. The dashed vertical line represents no effect. The number inside parenthesis represents the number of specimens analyzed in each dataset.

Of the 26 species assessed in this study, early flowering for *Geigeria ornativa* was delayed by 0.77 days year^{-1} or 7.7 days decade^{-1} (P = 0.01), while *Cleome gynandra* at peak flowering and *Cleome oxyphylla* at late flowering delayed their flowering dates by 0.82 days year^{-1} (P = 0.01) and 2.61 days year^{-1} (P = 0.01) respectively (Figure 10). Family-level analyses did not find any differences in the flowering date response to time series across all phenophases for the six families assessed in this study, although there were trends toward earlier flowering in Zygophyllaceae (P = 0.09) and Cleomeacae (P = 0.08) at early and peak flowering phenophases respectively (Appendix B, Table B3).

Flowering date responses to time series differed between aridity zones. Plants collected in the arid to semi-arid zones significantly delayed their flowering dates by 1.3 d year^{-1} ($P < 0.05$), 0.47 d year^{-1} ($P < 0.05$), and 0.43 d year^{-1} ($P < 0.05$) in the early flowering, peak flowering, and peak flowering phenophases (Figure 11). In contrast, plants collected from the hyper-arid to arid regions advanced their flowering dates by 0.24 d year^{-1} ($P > 0.05$) in the peak flowering phenophase (Figure 11).

Phenological Responsiveness of Flowering to Temperature

Overall, when all species were grouped together, a linear mixed effects model showed that herbaceous plants in these drylands have responded by advancing their flowering date in response to increasing temperature by 11 d °C^{-1} ($P < 0.0001$) across all phenophases. Seven of the nine species assessed at the early flowering phenophase significantly changed their flowering date in response to warming by an average of -12.69 d °C^{-1}, ranging from -7.18 in *Cleome angustifolia* to -19.09 d °C^{-1} in *Petalidium variabile* d °C^{-1}. Similar mean phenological responsiveness to temperature of -11.30 d °C^{-1} was found for 90% of the species assessed at the peak flowering phenophase, ranging from -6.52 d °C^{-1} in *Tribulus zeyhiri* to -22.78 d °C^{-1} in *Blepharis grossa* d °C^{-1} and for 81% of species at late flowering (-11.41 d °C^{-1}), ranging from -7.94 in *Nidorella resedifolia* to -19.09 d °C^{-1} in *Acrotome fleckii* d °C^{-1}) (Figure 12).

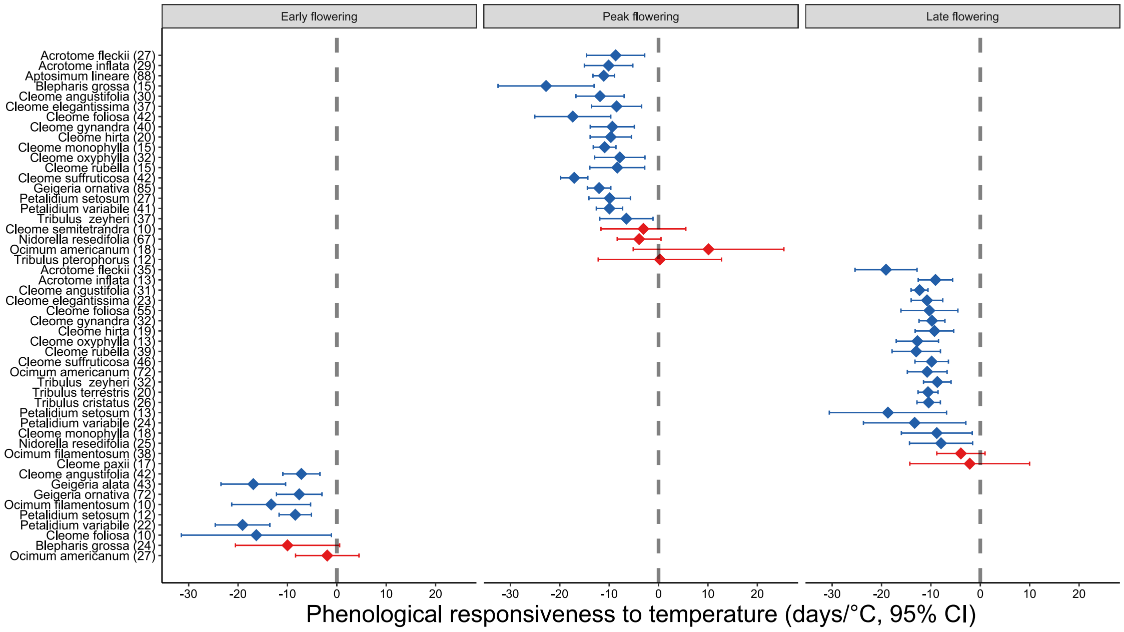


Figure 12. Flowering Phenology Responsiveness to Temperature for Early Flowering, Peak Flowering and Late Flowering Herbaceous Plants.

Each horizontal line corresponds to the species-specific flowering date response to rising temperature. The diamonds represent the estimates, centered between the lower and upper 95% confidence limits. The blue color represents significant flowering phenology response while the red color represents lack of a significant flowering phenology response. The dashed vertical line represents no effect. The number inside parenthesis represents the number of specimens analyzed for each species.

At peak and late flowering phenophases, all six families responded to warming by flowering earlier, ranging from shifts of -4.69 d $°C^{-1}$ ($P = 0.02$) in Zygophyllaceae to -14.98 d $°C^{-1}$ ($P < 0.0001$) in Acanthaceae (Appendix B, Table B3). The response of early flowering to temperature, was also earlier in Acanthaceae (-13.67 d $°C^{-1}$, $P < 0.0001$), Asteraceae (-11.43 d $°C^{-1}$, $P < 0.0001$) and Cleomaceae (-5.08 d $°C^{-1}$, $P < 0.0001$), while Lamiaceae and Zygophyllaceae did not show any responsiveness to increasing temperature.

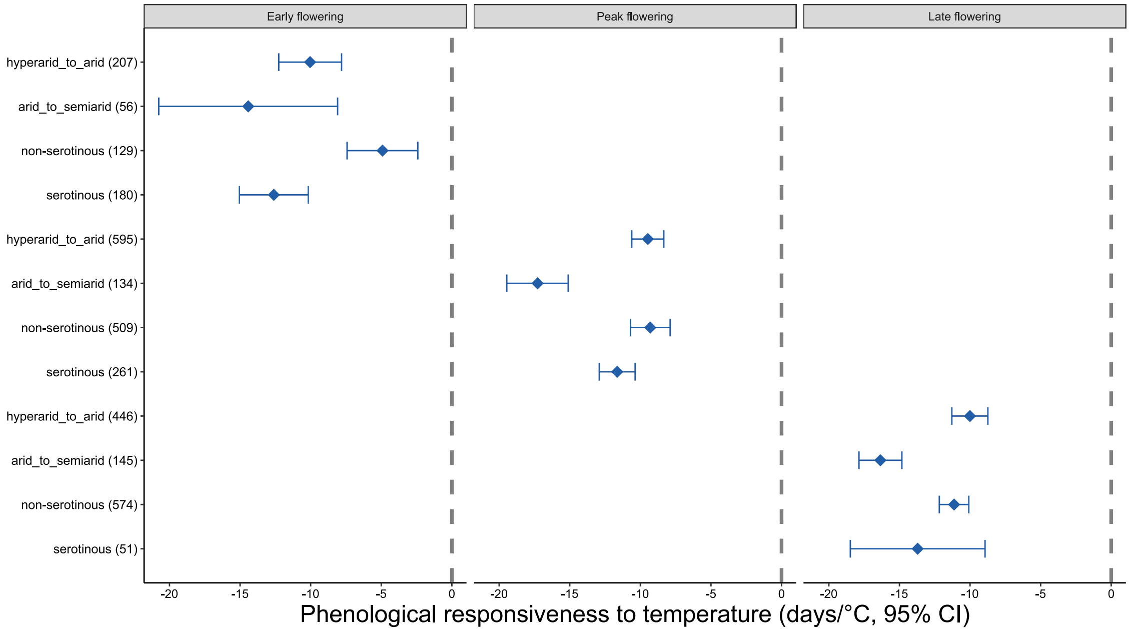


Figure 13. Flowering Phenology Responsiveness to Temperature Between Serotiny, Aridity Zones, and Across Phenophases.

Each horizontal line corresponds to the species-specific flowering date response to rising temperature. The diamonds represent the estimates, centered between the lower and upper 95% confidence limits. The blue color represents significant flowering phenology response while the red color represents lack of a significant flowering phenology response. The dashed vertical line represents no effect. The number inside parenthesis represents the number of specimens analyzed in each dataset.

The flowering phenology of serotinous plants at early, peak and late flowering phenophases responded similarly to warming by an average of -12.61 d $°C^{-1}$ ($P < 0.0001$), -11.64 d $°C^{-1}$ ($P < 0.0001$) and -13.7 d $°C^{-1}$ ($P < 0.0001$) respectively. However, the magnitude of response to increasing temperature for non-serotinous plants at early flowering (-4.91 d $°C^{-1}$, $P < 0.0001$) was about half that of responses at peak (-9.3 d $°C^{-1}$, $P < 0.0001$) and late (-11.13 d $°C^{-1}$, $P < 0.0001$) flowering phenophases. Plants from arid to semi-arid zones showed a greater mean phenological responsiveness to temperature of -16.02 d $°C^{-1}$ ($P < 0.0001$), nearly twice as much as those collected in the hyper-arid to arid regions which changed their flowering dates by -9.84 d $°C^{-1}$ ($P < 0.0001$) across all three phenophases (Figure 13).

Phenological Responsiveness of Flowering To Precipitation

The flowering phenology responsiveness to precipitation was determined as -0.33 d mm^{-1} ($P < 0.0001$), -0.52 d mm^{-1} ($P < 0.0001$) and -0.54 d mm^{-1} ($P < 0.0001$) for early, peak and late flowering phenophases respectively (Table 2). However, flowering phenology sensitivity to precipitation varied across species, families, seed dispersal groups and aridity zones. Higher total precipitation in the two months prior to flowering advanced the peak flowering dates of 48% of the 21 species by -0.6 d mm^{-1} and late flowering dates of two-thirds of the 20 species by an average of -0.35 d mm^{-1} (Figure 14). Only two out of nine species, *Geigeria alata* and *Ocimum filamentosum* in the early flowering phenophase changed their flowering date in response to increasing precipitation by -0.79 d mm^{-1} and -0.46 d mm^{-1} respectively (Figure 14).

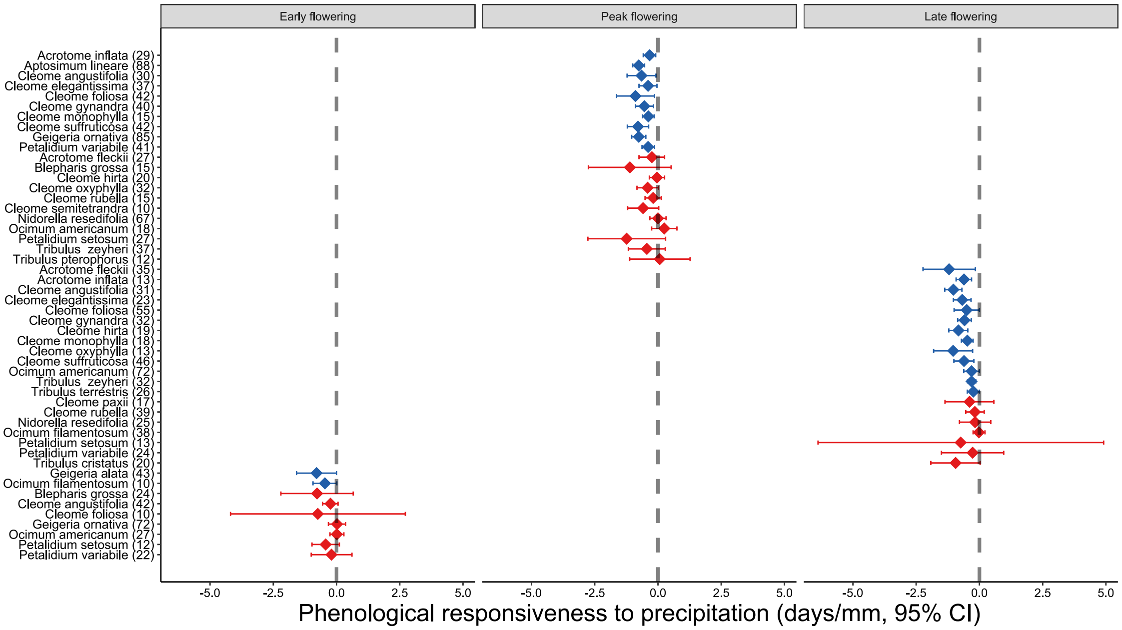


Figure 14. Flowering Phenology Responsiveness to Precipitation for Early Flowering, Peak Flowering and Late Flowering Herbaceous Plants.

Each horizontal line corresponds to the species-specific flowering date response to increasing precipitation. The diamonds represent the estimates, centered between the lower and upper 95% confidence limits. The blue color represents significant flowering phenology response while the red color represents lack of a significant flowering phenology response. The dashed vertical line represents no effect. The number inside parenthesis represents the number of specimens analyzed for each species.

Across families, the early flowering of Acanthaceae (-0.64 d mm^{-1}, $P = 0.01$) was nearly twice as responsive to precipitation than Asteraceae (-0.37 d mm^{-1}, $P = 0.02$) and Zygophyllaceae (-0.33 d mm^{-1}, $P < 0.0001$) while Lamiaceae ($P = 0.52$) and Cleomeceae ($P = 0.15$) did not show any responsiveness to precipitation. At peak flowering, phenological responsiveness to precipitation ranged between -0.49 d mm^{-1} ($P < 0.0001$) in Asteraceae and -0.76 d mm^{-1} ($P < 0.0001$) in Scrophulariaceae. Cleomeceae showed the largest magnitude of response to precipitation (-0.61 d mm^{-1}, $P < 0.0001$) for the late flowering phenophase.

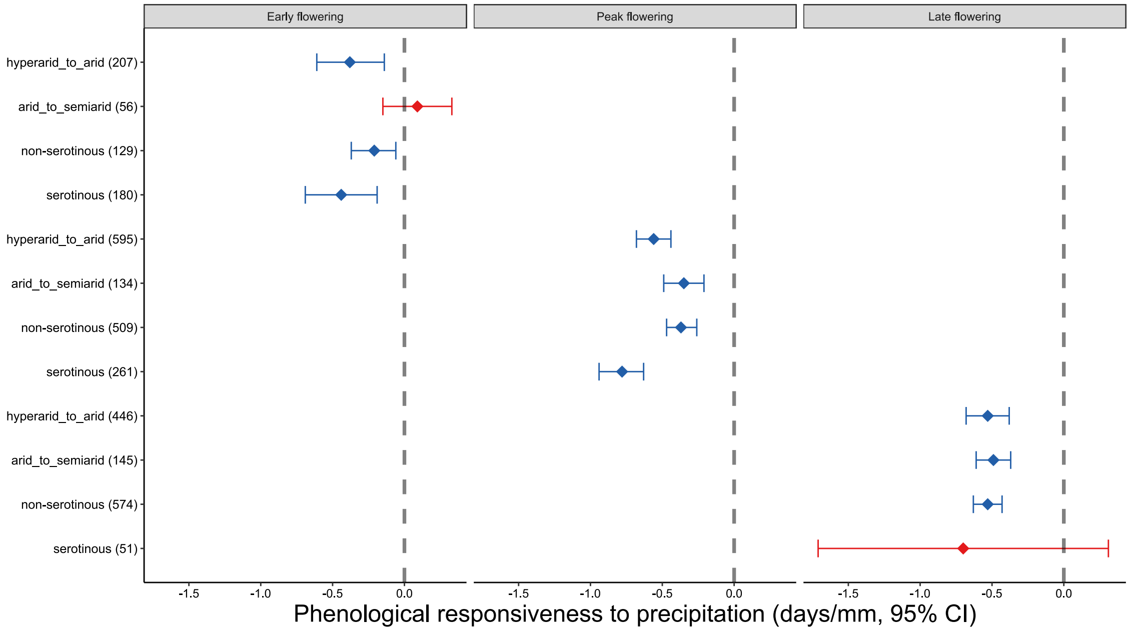


Figure 15. Flowering Phenology Responsiveness to Precipitation Between Serotiny, Aridity Zones, and Across Phenophases.

Each horizontal line corresponds to the species-specific flowering date response to increasing precipitation. The diamonds represent the estimates, centered between the lower and upper 95% confidence limits. The blue color represents significant flowering phenology response while the red color represents lack of a significant flowering phenology response. The dashed vertical line represents no effect. The number inside parenthesis represents the number of specimens analyzed in each dataset.

Serotinous plants were on average twice as responsive to precipitation (-0.44 d mm^{-1}, $P < 0.0001$) than non-serotinous plants (-0.21 d mm^{-1}, $P = 0.01$) for the early flowering phenophase. There was a similar pattern for the peak flowering phenophase for serotinous plants (-0.78 d mm^{-1}, $P < 0.0001$) and non-serotinous plants (-0.37 d mm^{-1}, $P < 0.0001$). The early, peak, and late flowering dates of plants collected in the hyper-arid to arid regions has advanced with increasing precipitation by 0.38 d mm^{-1} ($P < 0.0001$), 0.56 d mm^{-1} ($P < 0.0001$), and 0.53 d mm^{-1} ($P < 0.0001$) respectively. Comparatively, the early flowering dates of plants collected from arid to semi-arid zones was not responsive to precipitation ($P = 0.45$), while the peak, and late flowering dates advanced by 0.35 d mm^{-1} ($P < 0.0001$), and 0.49 d mm^{-1} ($P < 0.0001$) respectively (Figure 15). Furthermore, peak flowering of the plants collected from hyper-arid to arid regions was more responsive to precipitation (-0.56 d mm^{-1}, $P < 0.0001$) than those from arid to semi-arid zones (-0.35 d mm^{-1}, $P < 0.001$) (Figure 15).

Best Fit Model of Flowering Date Response

The multiple model comparison results revealed that mean temperature of the two months before flowering as an important predictor of flowering date across phenophases of the dryland species assessed in this study. All best fit models included temperature, either as a single predictor or in combination with total precipitation of the two months before flowering and/or collection year. Mean monthly temperature of the two months prior to flowering date was the single best predictor of flowering date in 76% of the 50 species and phenophase-specific models. During early and peak flowering, the interaction between collection year and temperature best explained variation in the flowering date of serotinous plants. At the late flowering phenophase, all three predictors, collection year, temperature and precipitation were included in the best fit flowering phenology model for serotinous plants. For non-serotinous plants, collection year and temperature best predicted flowering date during early and late flowering stages while temperature alone best explained variation in the peak flowering date. In the arid to semi-arid regions, models comprising year of collection and mean monthly temperature best explained variation in flowering date at the onset, peak and end of flowering. In the hyper-arid to arid regions, however, the best fit model varied across phenophases with temperature as the single most important predictor at the onset of flowering, while precipitation and temperature interacted with each other to influence peak flowering as year of collection and temperature best predicted flowering date during the late flowering phenophase. models (Appendix B, Tables B2 and B3).

Discussion

Flowering Phenology Trends Over Time

Only 3 of 26 species showed significant change in flowering phenology for the 105 y study duration, ranging from 1926-2018 (for early flowering), 1913-2018 (for peak flowering), to 1924-2018 (for late flowering) herbarium records, and all responded by delaying their flowering dates. This delayed flowering response is consistent with other dryland studies (Kwembeya, 2021; Rafferty et al., 2016; Song et al., 2021). Delayed flowering responses have been shown to shorten the flowering season in some species resulting in reduced reproductive output of flowers, fruits and seeds (Rafferty et al., 2016). In addition, delayed flowering phenology may also decrease resources available for pollinators, seed predators and dispersers (Rafferty et al., 2016; Takkis et al., 2018). Other studies have found that flowering later in the season risks increased competition for pollinators as floral resources become limited and the number of pollinators tends to increase (Kehrberger & Holzschuh, 2019a; Takkis et al., 2018). While it may seem logical that an increase in pollinator numbers toward the end of the flowering season might increase pollination opportunities for plants flowering during that time; fewer flowers may also lead to reduced pollinator activity and visitation rates (Kehrberger & Holzschuh, 2019a). However, there is also a possibility that plants flowering later in the season have the advantage of growing their vegetative structures for longer periods before they bloom and reproduce (Munson & Long, 2017).

However, I recommend cautious interpretation of these results in this herbarium phenology study particularly because the specimens were sourced from large geographic scales encompassing high geological, topographical, and climatological diversity in Namibia. Namibia is characterized by distinct dry and cold winters and warm to hot rainy summers where rainfall is not only unpredictable but also highly variable in time, space and pulse size which could account for variable vegetation responses. Precipitation in drylands can be highly localized with high inter- and intra- annual variation (Daramola & Xu, 2022), a pattern that is quite apparent and has been observed across Namibian drylands (Mendelsohn et al., 2002). In addition to this inherent variability in drylands characteristics, climate change is further enhancing precipitation and temperature extremes in these systems. For example, Spear et al., (2018) have noted an overall decline in annual average rainfall, with the largest decreases in the late summer (March to May), and an increased inter-annual rainfall variability with more frequent extreme events i.e., heavy storm events and more intense droughts since the 1970. However, in the hyper-arid and hot central Namib Desert, the total rainfall has remained the same over a 17-year period (1998-2015), while the frequency of storm events has declined (Lu et al., 2016). Similar to precipitation, inter- and intra- annual and inter-seasonal variation in temperature have characterized drylands over the past century (Daramola & Xu, 2022), further imposing high variability in flowering phenology responses across spatial scales. Using the reanalysis dataset, ERA5, a product of the European Centre for Medium-Range Weather Forecasts, Daramola & Xu (2022) showed temperature in global drylands increased at the rate of 0.032 °C year-1 or by 1.28 °C over the studied 40-year period (1979-2018). Their study also showed that aridity zones are warming at different rates and temporal patterns with the highest overall warming rate observed in the hyper-arid areas (Daramola & Xu, 2022). The hyper-arid areas warmed at a faster rate from 1979-1998 than during the next two decades from 1999-2018. Meanwhile there was a continuous temperature increase in the semiarid and dry subhumid zones from the first to the last decade (Daramola & Xu, 2022). These variable patterns in temperature changes across aridity zones in drylands could also result in complex and non-uniform responses and potentially masking temporal trends in flowering phenology.

Furthermore, there were gaps in the collection years in the dataset, similar to other herbarium phenology studies (Kwembeya, 2021). Previous studies have recommended using time series with at least 15 years to ensure an accurate estimates when assessing flowering phenology across different regions (Menzel et al., 2006). In this study, 8 out of 50 species-specific datasets of the time series were less than 15 years and most had unequal intervals in-between (Appendix B, Figures B1-B3). Thus, some of the data series I used may be insufficient for detecting significant changes in flowering phenology. The lack of significant shifts in flowering date in other species could therefore have been masked by the inherent high variation in the dataset or that there is no change in flowering phenology in response to time series.

Phenological Responsiveness of Flowering to Temperature

Temperature was by far the most important predictor of flowering date of the summer annual and perennial forbs assessed in this study, particularly because it is included in all best fit models, either by itself in a simple model (76% of species and phenophase-specific models), or together with year of specimen collection year and/or precipitation (24 % of species and phenophase-specific models). The results show that herbaceous plants from across Namibia are advancing their flowering dates in response to warming (Figures 12 and 13), although the magnitude of response varied substantially among species and families as well as between seed dispersal functional types and aridity zones. Variability in flowering phenology could also be due to spatial variation in climatic and non-climatic properties such as precipitation, frost, latitude, elevation, local topography, soil and underlying geology across the wide geographic landscapes from which the plants were collected. The overwhelming earlier flowering response to temperature is consistent with the findings from other studies. In a global meta-analysis, Parmesan & Yohe (2003) found that 87% of plant species advanced their flowering phenology in response to increasing spring temperatures. Across Europe, spring and summer leaf unfolding and flowering has advanced by an overall mean of 4.6 d $°C^{-1}$ in response to rising temperature in 78% of records (Menzel et al., 2006).

It is often suggested that plant phenology in temperate systems is sensitive to temperature whereas plants in arid and tropical ecosystems tend to be most responsive to precipitation (Bertin, 2008; Chmura et al., 2019; Cleland et al., 2007). I showed in this study that the flowering phenology of herbaceous plants in drylands is highly sensitive to temperature, responding by shifting their flowering date by an average of -12 d $°C^{-1}$, while sensitivity to precipitation averaged at -0.6 d mm^{-1} across phenophases. Since the summer months (October-April) comprise the main growing season in Namibia when most rains fall, the combination of moisture availability and warming temperatures probably represent conditions favorable for accelerated growth, development and completion of the life cycle of the herbaceous plants hence the advanced flowering response (Ma & Zhou, 2012; Stuble et al., 2021). To test this hypothesis future flowering phenology studies should specifically assess interaction effects of temperature and precipitation on flowering dates.

Some studies have suggested that phenologically responsive species may be able to gain ecological benefits from this ability to track climate (Cleland et al., 2012; Munson & Long, 2017). In a meta-analysis of experimental warming studies, Cleland et al., (2012) found that species that advanced their phenology with warming also increased their performance including biomass production, percent cover, and number of flowers, while those that failed to advance their phenology showed reduced performance with warming. A recent experimental study also showed that advanced flowering phenology in response to warming resulted in increased reproductive investment with plants producing more flowers (Schuchardt et al., 2021). However, when warming was combined with low precipitation, reproductive investment either remained the same or declined with advanced flowering dates (Schuchardt et al., 2021).

Changes in flowering phenology as a result of climate warming may result in a multitude of ecological consequences including the potential for mismatched timing of animal pollinator activity, the availability of nectar and other floral rewards (Kehrberger & Holzschuh, 2019a; Rafferty et al., 2016). For example, exposure to high experimental temperatures reduced the flower number and both the nectar quantity and sugar content in flowers of six native Mediterranean species (Takkis et al., 2018), which in turn may affect the pollinator populations. Shifts in flowering phenology may also drive apart the ecological interactions of co-occurring species, further impacting pollination dynamics. For example, pollinator visits in the spring flowering forb *Pulsatilla vulgaris* decreased with the increasing number of co-flowering plants (Kehrberger & Holzschuh, 2019a).

In addition, warming has the potential to influence plant available moisture through increased evapotranspiration (Ma & Zhou, 2012), especially in drylands, where precipitation is generally low, highly variable and unpredictable (Maestre et al., 2016).

Taken together, these studies demonstrate that while potential benefits associated with advanced flowering phenology responses may occur, such gains are not straightforward and could vary from one ecosystem to another.

Phenological Responsiveness of Flowering to Precipitation

The results indicate that precipitation is an important predictor of flowering date in herbaceous plants. In this study, increasing precipitation advanced flowering date, consistent with previous studies in drylands. For example, Crimmins et al., (2011) found in a 30-year field observation study that the wettest years also had the earliest flowering dates while flowering occurred later in drier years. A herbarium phenology study conducted in Namibia also found that the flowering date of *Crinum* lillies advanced with increasing precipitation (Kwembeya & Pazvakawambwa, 2019). However, other flowering phenology studies have however found opposite trends to my study, where increasing precipitation resulted in plants delaying their flowering (Kwembeya, 2021; Song et al., 2021). Higher precipitation delayed the flowering date of summer flowering plants in a subtropical ecosystem in south China (Song et al., 2021). In another summer flowering species, *Scadoxus multiflorus* subsp. *multiflorus*, sampled predominantly across dryland ecosystems, flowering date was also delayed in response to higher precipitation (Kwembeya, 2021).

Because the growth, development, and completion of the life cycle of herbaceous annuals and facultative perennials (which constituted 24 out of 26 species) is generally constrained to the growing season in the study area, I expected the flowering phenology of these species to show high dependency on the summer growing season precipitation. To my surprise, all species showed greater magnitude of flowering phenology response to temperature (about -12 d per 1°C) than to precipitation (about -0.6 d mm^{-1}). These results show that the flowering phenology of herbaceous plants in this study was impacted by both precipitation and temperature. It is worth noting that the significant advanced flowering in response to higher precipitation does not imply that precipitation over study area has changed during the data collection period, but rather that wet years were associated with earlier flowering.

The shift toward advanced flowering with increasing precipitation observed in herbaceous plants in this study suggests that accelerated development as a strategy to reach reproductive maturity quickly while the conditions remain conducive. Consequently, the plants could favor reproduction over vegetative growth, especially for annuals as these plants are typically monocarpic i.e., they reproduce only once during their lifetime and die (Tooke & Battey, 2010). Accelerated development can negatively affect seed production and quality (Kigel et al., 2011; Seleiman et al., 2021) and may therefore result in a reduced soil seed bank. Advanced flowering may also indicate potential for opportunistic responses to extreme rain events (Huang et al., 2020), since vegetation activity in drylands tends to follow precipitation pulses (Noy-Meir, 1973).

This is likely the case in this study since there is an increased possibility for intense precipitation storms with climate change in drylands. A recent rainfall trend analysis showed an increase in extreme precipitation such as storm events in the peak rainfall months in the late summer, although there was no significant change in total rainfall amount across four sites located along a rainfall gradient in Namibia (Lu et al., 2016).

The herbarium-based phenology assessments showed that the peak flowering of the plants collected from hyper-arid to arid regions was more responsive to precipitation (-0.56 d mm-1, $P < 0.0001$) than those from arid to semi-arid zones (-0.35 d mm-1, $P < 0.001$).

Interestingly, plants from the hyper-arid to arid zone showed greater sensitivity to precipitation than those from the arid to semi-arid zone suggesting that future changes in precipitation patterns will affect plants in drier regions more than those in wet regions. This outcome also suggests that the extent of aridity probably influences flowering phenology, therefore, variable phenological responses must be anticipated across the aridity gradient in drylands. Furthermore, this result could probably be explained by the higher variability in precipitation patterns in the more arid regions as demonstrated by Lu et al., (2016) in their study which found evidence of decreasing rainfall frequency at the driest site, located at the Gobabeb Namib Research Institute, in the hyper-arid and hot central Namib desert compared to the semi-arid site in Windhoek (Lu et al., 2016). In this present study, I examined the relationship between flowering date and average total monthly precipitation in the two months prior to flowering. It is however important to acknowledge that in drylands, other precipitation characteristics such as frequency, season and timing also strongly influence flowering phenology (Beatley, 1974; Crimmins et al., 2011).

The flowering phenology of serotinous plants was more sensitive to precipitation than that of non-serotinous plants. Serotinous plants accumulate and retain a canopy seed bank on the plant for one or more years post seed maturation (Günster, 1994a; Thanos, 2004). Seed retention is thus a key adaptation of plants in seasonally dry environments, promoting seed release, germination and establishment to occur only when conditions are favorable, typically after sufficient rains or following a fire event (Thanos, 2004). The greater sensitivity of serotinous plants to precipitation therefore suggests that this group could be more vulnerable to the effects of climate change than the non-serotinous group, particularly with fluctuations in precipitation characteristics.

The fact that some species (e.g., 11 of 21 species at peak flowering) did not show any phenological sensitivity to precipitation suggests that other environmental factors such as temperature, latitude, elevation, and soil type may further affect the flowering phenology of plants in these dryland ecosystems including through potential interaction with precipitation. Other climatic factors such as fog, which is an important source of moisture for plants in the hyper-arid regions of Namibia, though not considered here, could also play an important role in the flowering phenology of these herbaceous plants.

Best Fit Model of Flowering Date Response

Temperature emerged as the most important environmental driver and predictor of flowering phenology in the summer flowering herbaceous plants assessed from these dryland ecosystems. The best fit models were those that included temperature in a simple model (76% of species and phenophase-specific models) or together with precipitation and/or year of specimen collection in a complex model (24% of species and phenophase-specific models). Summer flowering was therefore most sensitive to mean temperature in successive two-months preceding flowering including the month of flowering. This outcome is surprising because most studies have shown that the flowering phenology in water-limited ecosystems is controlled more by precipitation than by temperature (Crimmins et al., 2011; Jiang, 2021). Given that all herbaceous flora from across Namibian drylands as assessed in this chapter, have responded to increasing temperatures by advancing their flowering dates, this is inconsistent with the findings in chapter 1 where it is shown in the meta-analysis that when multiple types of drylands from across the world were considered, both advanced and delayed responses were apparent. This suggests that flowering phenology responses may differ with scale. However, an overall estimate of flowering phenology temperature sensitivity, determined here as -11 d $°C^{-1}$, is more than two-fold greater than that estimated for herbaceous plants from across different ecosystems in China (-4.8 d $°C^{-1}$; Mo et al.,(2017) and the temperature sensitivity of wild plants in a global synthesis (-4.6 d $°C^{-1}$; Wolkovich et al., 2012). At flowering phenology shifts of -11 d $°C^{-1}$, this response is also more than three times the mean response of flowering date to increasing temperature, determined for global drylands of -2.83 d $°C^{-1}$ (as shown in chapter 1). This outcome suggests that herbaceous plants in drylands will respond variably to climate warming (compared to other ecosystems), potentially changing the composition, structure, and function of these herbaceous-dominated systems.

Herbaceous plants are an important component of vegetation in drylands, where they account for sizable proportions of species diversity and perform key ecological functions including primary productivity, carbon storage and habitat provision for other organisms (Cowling et al., 1994). Herbaceous vegetation is also important for stabilizing soil and preventing erosion in drylands (White & Nackoney, 2003), a role that is even more important under changing climates in drylands where the probability of extreme precipitation events such as rain storms is expected to increase (Daramola & Xu, 2022).

Flowering phenology sensitivity to rising temperature varied considerably across species, families, functional groups, and aridity zones which might potentially change the ecological interactions between species within their environments and across their distribution ranges. Data from various global climatic circulation models, such as the South African Long-Term Adaptation Scenarios (LTAS), suggest that the mean annual temperatures across Namibia are estimated to increase by 2-5 °C over the period 1960–2010 (Spear et al., 2018). The Coupled Model Intercomparison Project - Phase 5 (CMIP5) also shows similar projections with temperatures over Namibia expected to increase between 2.5 and 3.3°C by 2050 and between 3.3 and 5.8°C by the end of the

21st century (Spear et al., 2018). These changes in temperature could result in dramatic flowering phenology responses in the future especially in serotinous plants such as *Petalidium setosum*, *Petalidium variabile* and *Geigeria ornativa*, which appear to have greater sensitivity to temperature than non-serotinous plants. Furthermore, flowering phenology responses may be more pronounced in arid to semi-arid regions where collective shifts in flowering date have advanced by a mean of up to 17 d $°C^{-1}$ in peak flowering species compared to more modest changes in the hyper-arid to arid regions (9 d $°C^{-1}$).

Rising temperatures may change the availability of medicinal and food resources for the local population in Namibia. This could be the case with plants such as the widely used mosquito repellant *Acrotome inflata* and the leafy vegetable *Cleome gynandra* (Kangombe et al., 2016) which have advanced their peak flowering dates by 10 and 9 d $°C^{-1}$ respectively. At this pace, the peak flowering dates of these plants could occur about 18-20 days earlier if temperatures rise by 2 °C, which could affect their socio-ecological impacts through altered competition with co-occurring plants, symbiotic interactions with herbivores and pollinators and availability of food and medicines for the local people.

Conclusions

I showed in this chapter that the flowering phenology responses of herbaceous plants collected across Namibian drylands, to climate change varied across taxa, aridity zones and seed dispersal functional types. The results showed that herbaceous plants across Namibian drylands are responding to climate warming at a faster rate (of advanced flowering) compared to those reported from other studies in similar or other ecosystems (Menzel et al., 2006; Parmesan & Yohe, 2003). Plants in arid to semi-arid regions showed higher phenological sensitivity to temperature than those in the hyper-arid to arid zones. Meanwhile, serotinous plants showed greater sensitivity to both temperature and precipitation than non-serotinous plants. These variable responses are indicative of divergent flowering phenology across taxa, functional groups and regions with climate change which may result in disrupted ecological interactions and processes such as pollination, predation, and competition. I also showed that both temperature and precipitation are important environmental drivers of flowering phenology in these dryland ecosystems. However, temperature was the single most important predictor of flowering date in the majority of models and a greater proportion of taxa showed phenological sensitivity to temperature compared to precipitation. While other studies have reported mixed flowering phenology responses to precipitation, I showed here that herbaceous plants across Namibian drylands are predominantly advancing their flowering dates with increasing precipitation.

However, I acknowledge that these findings may be limited by the regional differences in other environmental characteristics such as elevation and humidity that were not considered in this analysis, the variable climate change patterns and the fact that flowering dates were proxied from specimen collection dates. Despite these limitations, the value of biological collections as sources of large and long-term datasets of phenological information across multiple taxa and regions is unmatched and should be appreciated and promoted in scientific studies. Future studies should include other functional types and particularly graminoids, an important plant group for livestock production which is a major land use and economic activity in drylands.

CHAPTER 3

3 VEGETATIVE GROWTH, REPRODUCTIVE OUTPUT AND PHENOLOGICAL RESPONSES OF *CLEOME GYNANDRA* L. TO DROUGHT IN A SEMI-ARID DRYLAND SAVANNA

Abstract

Flowering phenology studies are critical to predict probable species reproductive responses in a climatically changing earth and to forecast potential ecosystem and socio-economic consequences. In this study, I tested how the summer annual *Cleome gynandra* L. (Cleomaceae), an important food and medicinal plant, responds to drought. I quantified above-ground vegetative growth and flowering phenology responses to 0% (control), 20%, 40% and 60% drought treatment using rainout shelters in a dryland savanna ecosystem. Linear mixed-effects models revealed that drought treatment did not affect phenotypic plastic responses of stem height, leaf length and number of leaves produced by *C. gynandra* across the drought treatments. However, the mean dates for peak leaf length and peak number of leaves were advanced by six and 10 days, respectively, in response to drought, suggesting vegetative phenology sensitivity to declining moisture. The mean peak flowering date of *C. gynandra* was also advanced by seven days, demonstrating a drought-escaping strategy through accelerated reproductive development. The first flowering date, flowering end date and flowering duration were

not responsive to drought treatment. The advancement of both the vegetative and flowering phenology of *C. gynandra* in response to drought suggests that this important food, medicinal and cash crop could be affected by future climate conditions. Further studies on natural replenishment of seed banks under climate change will be important to understanding the future availability of this socio-economically important wild plant.

Introduction

Vegetative phenology, defined as the observation of recurring, seasonal life cycle events in the non-reproductive phases of plant development, and includes leaf-out (green-up), post fruit leafing and leaf coloring (Liu et al., 2021; Polgar & Primack, 2011). Vegetative phenology affects the length of the growing season. A lengthened growing season allows for more time investment into the vegetative development of the plants, which has also been shown to boost the reproductive output (Liu et al., 2021). Vegetative phenology may therefore affect the rate of photosynthesis and/or biomass production, with implications for ecosystem processes such as carbon and water cycling, and plant-animal relationships (Polgar & Primack, 2011). In some plants, such as some tree species, vegetative phenology may occur before and after the reproductive phase (Liu et al., 2021). In annuals however, the vegetative phase is restricted to the time between germination and flowering onset, as plants tend to die after the reproductive stage (Howell et al., 2020; Tooke & Battey, 2010). Understanding vegetative phenology is essential for assessing the impact of climate change on plant life cycles, as shifts in these events can have ecological and environmental consequences.

Flowering phenology, the timing of flowering in angiosperms, is an important ecological phenomenon which signifies the developmental transition from the vegetative growth state to reproductive state in plants in response to the environment (Hegazy et al., 2017; Reekie & Bazzaz, 1987). In seasonal environments, flowering phenology has generally evolved to occur when environmental (biotic and abiotic) conditions favor increased reproductive fitness, although this may vary across life histories (Chmura et al., 2019; Cleland et al., 2007; Godoy et al., 2009). Indeed, the timing of flowering may determine the magnitude of mutualistic, competitive and antagonistic interactions between plants and their pollinators, seed dispersers, competitors, herbivores and seed predators (Matthews & Mazer, 2016), with corresponding ecological consequences for plant fitness and ecosystem structure and function. A study by Memmott et al.(2007) has shown that shifts in flowering timing deprived some 17-50% of pollinators of their floral food supply. Competing plant species can indirectly benefit and affect each other's reproductive success because they vary in their ability to attract and maintain pollinators (Thomson 1978). At the ecosystem level, the timing and duration of flowering may influence the acquisition and availability of water and soil nutrients, potentially affecting species interactions (Baumann et al., 2017; Zhang et al., 2007).

Since plants generally rely on climatic cues for flowering onset (Cleland et al., 2012), climate change will impact flowering phenology, including the length of the reproductive period and output. As major primary producers and initiators of energy flow in terrestrial ecosystems, climate change impacts on plant reproductive timing and fitness may have profound and lasting effects on ecosystems. Investigative studies into flowering phenology responses to changing climates are therefore urgently needed to understand and predict any subsequent impacts on plant reproductive timing mechanisms, especially as the earth continues to undergo global environmental change. Drylands, the world's largest terrestrial biome, covering about 41% of land surface (Huang et al., 2017) are particularly understudied and lacking in flowering phenology data (Browning et al., 2018; Primack et al., 2004). Yet drylands are home to about 38% of the global human population, who are predominantly dependent on the land for their livelihoods, mostly through livestock and crop production (Chan et al., 2012; Huang et al., 2017; Maestre et al., 2012). Drylands are also important for terrestrial carbon storage and account for approximately 40% of the global net primary productivity (Huang et al., 2017; Poulter et al., 2014). At the same time, drylands are eminently sensitive to climate change-induced degradation, especially given their highly infertile soils (Huang et al., 2017; Maestre et al., 2012). However, little is known about the flowering phenology responses and potential impacts on the long-term survival of plants in drylands under climate change scenarios.

For drylands (arid to semi-arid ecosystems), rising mean surface temperatures of more than 3°C and an increase in the incidence of extremely warm years by the end of the twenty-first century is predicted (Collins et al., 2013; Pachauri et al., 2015). Climate models further predict that drylands will experience water cycle changes with some locations likely to become drier and others wetter. Precipitation in drylands will not only change by amount but also in temporal and spatial distribution (Collins et al., 2013; Pachauri et al., 2015). Drylands will experience intensified surface drying, with an increased probability of drought occurrence and extended dry seasons by the end of the 21st century (Collins et al., 2013). Another climate change expectation for drylands is the emerging trend of warmer years tending to be drier, which distinguishes these ecosystems from non-drylands, particularly mesic systems where warmer temperatures have been associated with higher precipitation (Collins et al., 2013; Daramola & Xu, 2022). Yet, the ecological effects and consequences of such climate changes on species are much less well understood especially in drylands where environmental conditions are naturally highly variable and ecological research data is scantily available.

Most plants where phenology has been studied across various ecosystems have advanced their flowering dates in response to increasing temperature, which is also demonstrated in Chapters 1 and 2 of this dissertation. For example, long-term phenological datasets from Concord, Massachusetts, USA (1852-2007) and from the genus *Protea* in South Africa (1900-2011) have found flowering dates have advanced by 3.1 and 5 days per 1 °C increase in temperature, respectively (Daru et al., 2019; Miller-Rushing & Primack, 2008). Comparatively, flowering onset in China has advanced by up to 2.3 days decade^{-1} (1963–2013), ostensibly driven by increases in temperature (Mo et al., 2017). However, the relationship between flowering phenology and precipitation is potentially complex and poorly studied (Bertin, 2008; Browning et al., 2018; Primack et al., 2004). For example, Lesica & Kittelson (2010) showed an overall advanced first flowering date of 12 days for every 1 mm decline in precipitation in 24 of 32 species. However, the same study found a significant delay in the first flowering date with increasing precipitation in one species, *Hydrophyllum capitatum*. In contrast, increasing annual precipitation advanced the flowering date of C4 grasses by 9.2 days mm^{-1} and delayed that of C3 grasses by 5.6 days mm^{-1} (Munson & Long, 2017). In the Santa Catalina Mountains in southern Arizona, USA (1984-2009), Crimmins et al., (2011) found that the onset of flowering has advanced by about 0.69 days per 1 mm increase in precipitation. These mixed flowering phenology responses suggest that plants in drylands may respond differently to the same stressors, emphasizing the need for further investigation toward understanding the likely impacts of global change in these systems.

Cleome gynandra L. is an important green leafy vegetable that is consumed in many countries as a stew or side dish, providing nourishment as a rich source of protein, vitamins A and C and minerals such as calcium, iron and magnesium (Chweya & Mnzava, 1997; Kwarteng et al., 2018; Oshingi et al., 2019). In some countries, this leafy vegetable is the only available relish for extended periods and therefore plays a significant role in household food security during drought (Chweya & Mnzava, 1997).

This is the case in northern Namibia, where large-scale harvesting and preservation of *C. gynandra* is a strategy for rural communities to survive the many dry months of the year until the next summer rains. *Cleome gynandra* is also used as a traditional medicinal plant in some African countries to treat ailments such as headaches, stomach aches and even diabetes (Chweya & Mnzava, 1997; Kwarteng et al., 2018; Oshingi et al., 2019). Furthermore, extracts of *C. gynandra* have shown remarkable antioxidant properties, particularly radical-scavenging activity with an inhibition percentage of 92.8%, that is higher than that of the standard antioxidant, ascorbic acid (Kwarteng et al., 2018).

Despite the importance of this valuable species, there is little information on the potential impacts of climate change on the vegetative growth, reproductive phenology, and output of *Cleome gynandra* hence its long-term survival. In my herbarium phenology study (chapter 2), *Cleome gynandra* was one of the only three species, alongside *Geigeria ornativa* and *Cleome oxyphylla* that showed significant responsiveness of flowering date, with all species responding by delaying their flowering dates. *Cleome gynandra* delayed its flowering date by 0.82 d year^{-1} or 8.2 d decade^{-1}, between 1913 and 2018.

To determine the probable vegetative, flowering, and fruiting phenology responses of *Cleome gynandra* under drought conditions, I used rainout shelters to simulate drought and monitored the vegetative growth and phenology, reproductive output (number of flowers and fruits) and reproductive phenology responses of the summer annual and leafy vegetable *Cleome gynandra* L. in a semi-arid savanna dryland ecosystem. I monitored and measured the stem height, leaf length and counted the number of leaves of each of sample plants. For each vegetative growth trait, I also determined peak phenology (i.e., dates of peak stem height, leaf length and number of leaves) defined as the date on which each trait reached the maximum value for every plant. *Cleome gynandra* produces a terminal, raceme-type inflorescence bearing many conspicuous flowers, each arising from a small trifoliate but sessile bract (Mishra et al., 2011; Oshingi et al., 2019). The showy and easily distinguishable flowers also make *C. gynandra* an ideal candidate species for flowering phenology studies. In this chapter, I defined reproductive output as the number of flowers, fruits and inflorescences produced by each plant (Rafferty et al., 2016; Schuchardt et al., 2021).

Flowering phenology was determined as first flowering date, peak flowering date, flowering end date and flowering duration. The first flowering date was defined as the date on which the first open flower was observed while peak flowering date was defined as the date that the maximum number of flowers were recorded for each individual that reached the reproductive stage. Peak fruiting date was defined as the date on which each individual obtained their maximum number of fruits. Flowering end date was defined as the last date on which an open flower was observed on each individual, while flowering duration was defined as the number of days from the first flowering date to the flowering end date. Phenology measurements were based on Julian calendar dates because the experiment started after the first day of the year, on 14 January 2022.

My first prediction for this study was that exposure to drought conditions would advance the vegetative, flowering, and fruiting phenology, and shorten the reproductive period of

C. gynandra because it will respond by rapidly completing its lifecycle as moisture becomes limited. Secondly, I predicted that a shortened reproductive duration due to drought treatment would result in reduced reproductive output (number of flowers per plant and number of fruits per plant) of *C. gynandra*.

Materials and Methods

Study Site

Fieldwork was conducted from January to April 2022 at the University of Namibia, Neudamm Campus located about 30 km east of Windhoek (17.25E, 22.52S, 1748 m above sea level) (Figure 16). The climate in the central highland savanna is semi-arid, characterized by hot and rainy summers (October-April) with mean minimum and maximum temperatures of 16 ± 0.7 °C and 29 ± 1.1 °C, respectively (Namibia Meteorological Service, 2020). Summer is followed by a cold, dry winter (May-September), with mean minimum and maximum temperatures of 9 ± 0.8 and 23.77 ± 0.76 °C, respectively. The mean annual temperature is 23 °C (1960-2015 from the Windhoek Meteorological Station; Namibia Meteorological Service, 2020). Precipitation is received principally as rainfall and varies greatly in space and time. Rainfall is unimodal, occurring in the summer months from October to April and peaking from January through March with approximately 80% of the total annual rainfall received during this time. Mean annual precipitation is 385 ± 163.6 mm (Namibia Meteorological Service, 2020). Woody vegetation at the site is dominated by *Catophractes alexandrii*, *Tarchonanthus camphoratus*, and *Senegalia melifera*, with *Ziziphus mucronata*, *Vachellia erioloba*, *Vachellia karoo*, *Senegalia hereroensis*, *Searsia marlothii* and *Lycium* sp. occurring occasionally. In the herbaceous layer, abundant grasses such as *Eragrostis rigidior*, *Eragrostis lehmanniana, Urochloa brachyura*, *Melinis repens*, *Schmidtia kalahariensis* and *Anthephora pubescens* are complemented by a mosaic of annual and perennial forbs such as *Geigeria ornativa*, *Aptosimum spinescens*, *Tribulus zeyheri*, *Talinum arnotii*, *Otoptera burchelii*, *Chascanum pinnatfidum*, *Commelina benghalensis* and *Ocimum americanum.*

Topographically, the landscape is undulating with the common Khomas Hochland hills and river valleys. The soils are generally shallow, scattered with quarzitic pebbles that reportedly improve soil moisture levels (Joubert et al., 2008). The common soils in the highland savanna of Namibia are the lithic leptosols (Joubert et al., 2008), and eutric regosols (Mendelsohn et al., 2002).

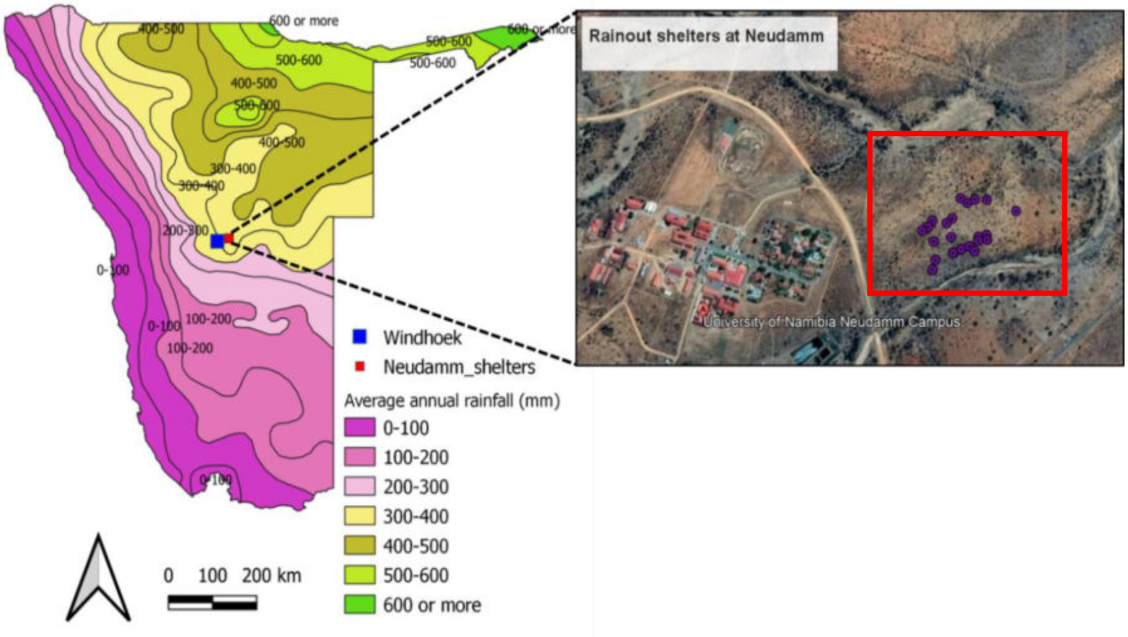


Figure 16. Rainfall Distribution in Namibia.

Notably, rainfall decreases progressively from east to west and north to south, exhibiting a remarkably sharp gradient. The location of the experimental site in the semi-arid highland savanna ecosystem at the University of Namibia, Neudamm campus is indicated by the red square. The inset figure shows the rainout shelters (purple circles inside the red square) at the site. Satellite map: Google.com

Shelter Design and Rainfall Exclusion Treatments

Rainout shelters are experimental structures with transparent roofing material that intercepts known amounts of rainfall for plant-climate studies (Figure 17), while allowing photosynthesis to continue with minimum disturbance to the microclimate (Fay et al., 2000; Gherardi & Sala, 2013). The shelters used in this study are modeled after the rainfall manipulation system design by Yahdjian & Sala (2002) and Gherardi & Sala (2013). However, my rainout shelters are simplified in that they were designed to simulate drought only and are therefore without the complimentary rainfall harvesting and addition elements specified in Yahdjian & Sala (2002) and Gherardi & Sala (2013). Furthermore, unlike the shelters in Gherardi & Sala (2013), the plots in this study were not lined with waterproof lining around the edges to regulate and control surface and sub-surface water movement.

I used fixed location rainout shelters, measuring 4 m x 4 m. The outer frame of shelters was constructed with square metal poles and formed the main support structure for the roofs. Shelter legs were 1.2 m on the west side and 0.8 m on the east side, giving the shelter a tilted orientation with a 5.7° angle. The 20 cm wide roof covers or shingles, made from a double layer of 100-micron clear plastic sheet, were mounted on narrow ropes using plastic zip ties creating a trough shape necessary to facilitate rainfall exclusion from the plot (Figure 17; Appendix C).

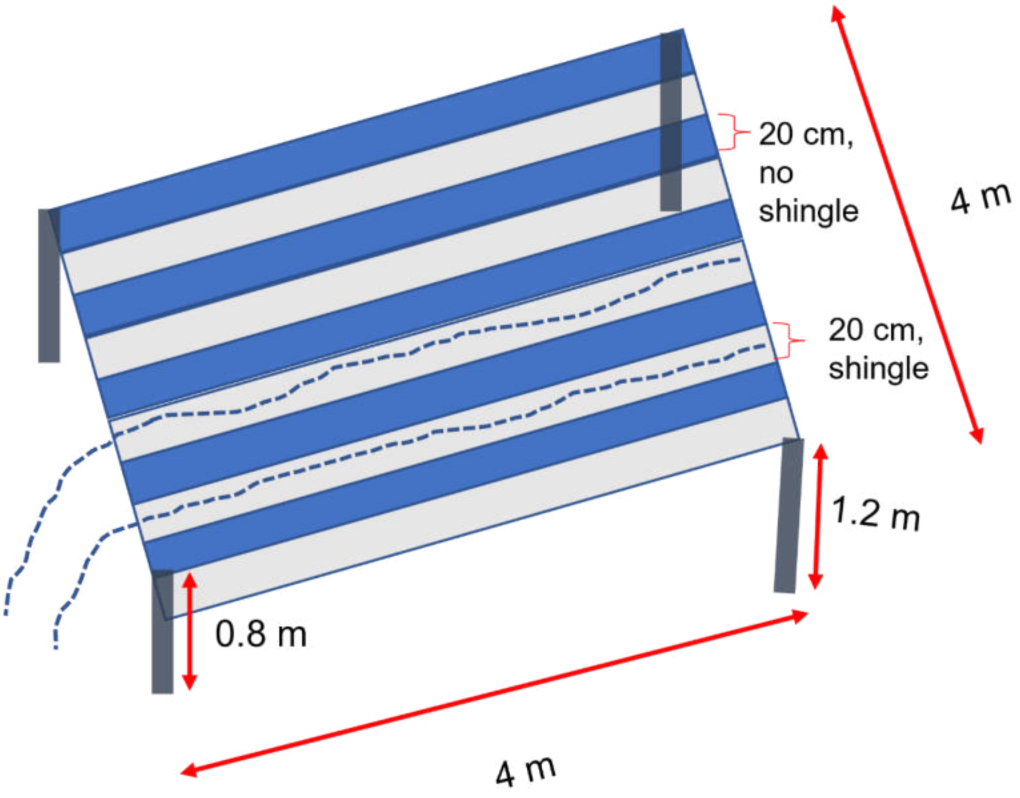


Figure 17. An Overview of the Rainout Shelters Used in this Study to Simulate Drought.

The solid blue bars represent uncovered portions that allow rainfall to reach the soil beneath the shelters while the solid white bars represent the plastic shingles that intercept or exclude rainfall. The dashed blue line represents intercepted rainfall which is excluded from the plot. In this illustration, the 1:1 ratio of covered to uncovered 20 cm spaces simulates a 50% drought treatment (equivalent to 50% rainfall interception).

The shelters simulated four drought treatments by excluding 0% (the control), 20%, 40% and 60% of rainfall (treatments hereafter referred to as D0, D20, D40, and D60, respectively). The D20, D40 and D60 shelters were covered with four, eight and twelve plastic shingles, respectively while the D0 plots were uncovered. The shingles were arranged at as equal intervals as possible to intercept these rainfall proportions (Figure C1, Appendix C). There were five replicate plots for each of the four treatments, totaling 20 rainout shelters. The shelters are permanently mounted at their locations, with a mean distancce of 27 m between them within a perimimeter of approximately 900 m. Plant composition data were collected from each plot. The data organized into a species by plot matrix, reflecting presence or absence of each species in the plots. The matrix was then subjected to multivariate classification to summarize the data into clusters of plots based on the similarity of species composition (Kent, 2011), which facilitated the assignment of treatments to the plots. In this study, botanically similar plots were assigned to different drought treatments to ensure that each treatment was represented across the various microenvironments found at the site. The assignment of co-located plots to the same drought treatments was avoided when possible.

Figure 18. *Cleome gynandra* at the Neudamm Field Site During the Experiment.

Seeding of the Shelters

Cleome gynandra seeds were collected at Onyaanya village, 35 km east of Ondangwa in the Oshikoto region of Namibia, during April 2021 and stored at room temperature for use in this experiment. The area under each shelter was tilled manually to approximately 10 cm, using a hand-held hoe to clear the plot of any existing vegetation, and to loosen and homogenize the soil substrate prior to seeding. I maintained a 50 cm buffer zone from all four directions to the inside of shelters during seeding to minimize edge effects. Plots were seeded on 14 January 2022 by following a systematic procedure of three rows and eight seeding locations per row totaling 24 seeding locations for each shelter. The rows and seeding locations were spaced 30 cm apart. At each seeding location, a small depression of approximately 5 cm width and 2 cm depth was made by hand. Approximately 40 seeds were placed in the depression and covered with a thin layer of soil.

Plant Sampling and Measurements

Cleome gynandra plants (Figure 18) were monitored from germination to senescence from 14 January to 14 April 2022. All plots were monitored every three to four days. Each individual present was sampled on monitoring days for vegetative traits: stem height, length of the three largest leaves, and total number of leaves; and reproductive traits: the number of inflorescences, flowers, and fruits. A total of 226 plants were monitored during the experiment.

Soil and Climate Measurements

Soil samples were collected by taking three replicate cores from the top 10 cm of the soil on 22 February 2020. Samples were collected at 1.5, 3 and 4.5 m along a transect line running from the southwestern corner to the northeastern corner of each shelter. The three samples taken from each shelter were pooled, air dried and then passed through a 2 mm sieve prior to further analysis. The soil samples were analyzed for particle size composition at the Namibia Ministry of Agriculture, Water and Rural Development Soil Laboratory in Windhoek. The soil sample was dispersed with sodium hexametaphosphate or sodium carbonate, allowing the determination of silt and clay particles by pipette method. The proportion of sand particles was determined by sieving to retain >53 micron fraction (Miller & Miller, 1987; Rowell, 2000). Soil texture was therefore determined by matching the processed samples to the Soil Texture Triangle, using the United States Department of Agriculture classification system (Kettler et al., 2001).

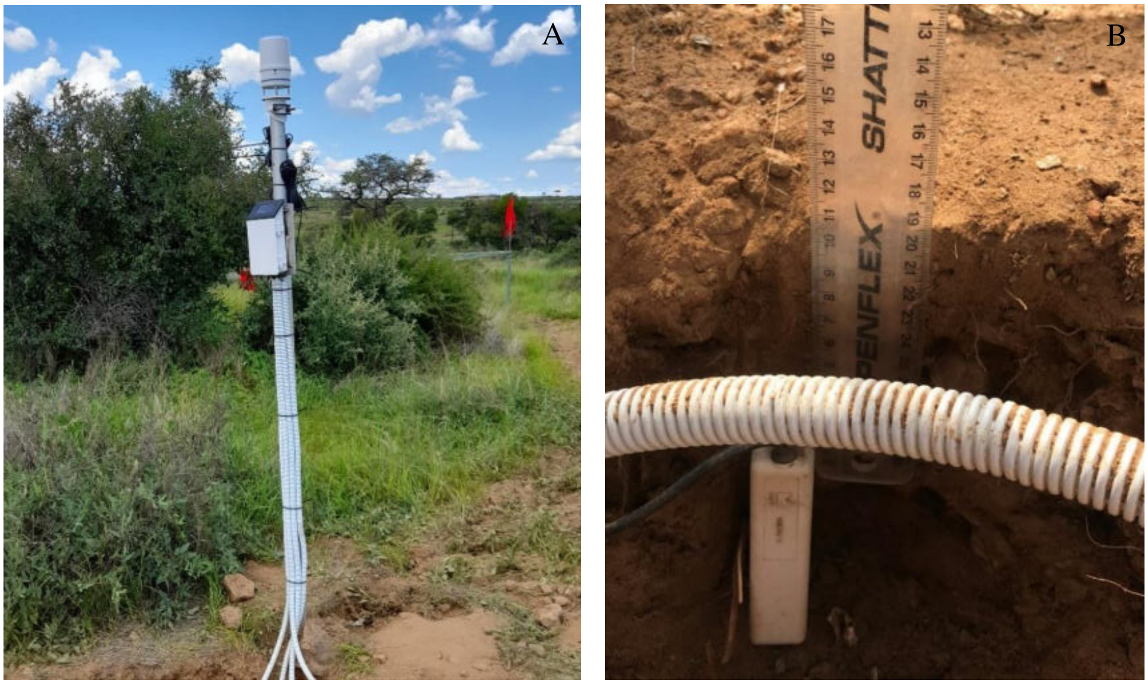


Figure 19. The atmospheric and soil climatic instruments installed at the Neudamm field site.

(A) The ATMOS 41 weather station is a 12-in-1 automated weather station compact device to measure atmospheric conditions; and (B) the TEROS 11 soil moisture and temperature probe. The probe is 5 cm long with three sensors and is installed at 10-15 cm soil depth.

An automated weather station (ATMOS 41, METER, Pullman, WA, USA) was installed on 27 February 2022 (Figure 19A). The weather station measured solar radiation, precipitation, lightning activity, lightning distance, wind direction, wind speed, wind gust speed, air temperature, vapor pressure, atmospheric pressure, maximum precipitation rate, relative humidity sensor temperature, and vapor pressure deficit. A soil temperature and moisture probe (TEROS 11, METER, Pullman, WA, USA) was installed at a depth of 10-15 cm at the center of one plot from each of the four drought treatments (Figure 19B). A fifth soil sensor was installed at an ambient location. By the time the weather station was installed, 95% of the growing season rain had already fallen, thus rainfall data were obtained from the Neudamm Campus and Farm Management Office (500 m from study site), where they are collected daily using a manual rain gauge.

Statistical Analyses

All data were analyzed in R version 4.2.1 (R Core Team, 2021). Data analysis of plant response variables in this experiment was based on the individuals that flowered. The distribution of plant response data was explored visually using histograms and summarized through descriptive statistics. Data were tested for normality using a Shapiro-Wilk test and heteroscedasticity using Levene's Tests. Response variable data were log10-transformed to meet normality assumptions.

To test the fixed effect of drought treatment (as a factor variable) while accounting for differences among plots as a random effect, I constructed linear mixed effects models with random intercepts and fixed slopes for each response variable using restricted maximum-likelihood, for a total of 13 models (Table C1, Appendix C). I used the lme4 (Bates et al., 2014) and sjplot (Lüdecke, 2021) packages to construct the linear mixed effects models, test for model significance, and to extract model coefficient estimates, and their respective p-values in each model. For continuous response variables, I used the Gaussian error distribution with the identity-link function. For count response variables, e.g., number of flowers, number of leaves, I used generalized linear mixed effects models with Poisson error distribution and log-link function. The choice of a random intercept term for the random effect of plot accounted for variation in germination dates, considering that plants germinated on different dates. I could not account for differences in individual plant growth and development because simultaneous inclusion of varying intercepts and slopes of the random effect resulted in computational problems which interfered with model convergence.

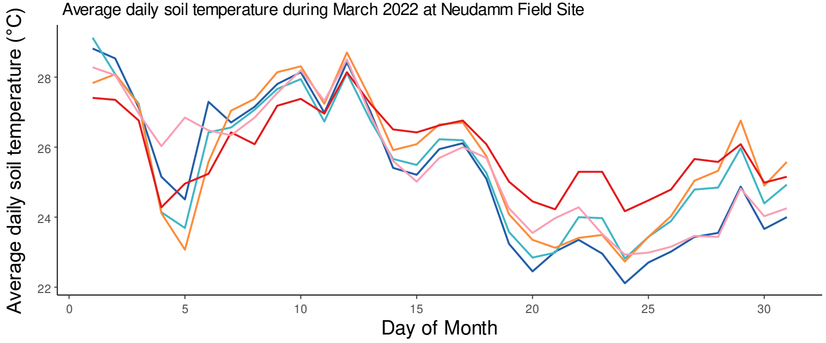
For each model, the marginal R^2 was calculated to show the proportion of variation explained by the fixed effects of drought while the conditional R^2 was determined to account for the random effects of the plots. The marginal R^2 is interpreted as the amount of variance explained by the fixed effects only, while the conditional R^2 represents the variation explained by the entire model i.e., both fixed and random effects (Nakagawa & Schielzeth, 2013). The sjplot package was used for plotting random effects and to obtain marginal R^2 and conditional R^2 and while ggplot2 was used for all other graphical presentations.

Results

Soil and Climate Characteristics

Growing season precipitation (1 October 2021 to 30 April 2022) was 504 mm. The total precipitation over the course of the experiment (14 January 2022 – 14 April 2022) was 497 mm. Implementation of the drought experiment using rainout shelters intercepted and reduced the total precipitation to approximately 497, 398, 298 and 199 mm in the D0, D20, D40 and D60 experimental plots, respectively. The mean soil moisture was 0.086, 0.072, and 0.062 $m^3 m^{-3}$ in the instrumented D0, D20, and D60 respectively from 01 March 2022 to 30 April 2022. Due to an installation error, soil moisture measurements under the D40 shelter were insufficient for further assessment. Following a rainfall event of about 16 mm on 20 March 2022, moisture levels increased sharply under all four shelters (Figure 20B). Although soil moisture and temperature data were only collected from a single plot for each treatment, there was sequentially less moisture in the plots with increasing drought treatment (Figure 20B). The mean soil temperature in the D0, D20, D40, D60 and the ambient plot were 25.4± 0.081, 25.7± 0.082, 25.8± 0.077, 26± 0.074, and 25.6±0.075 °C respectively, over the period 01 March 2022 to 30 April 2022 (Figure 20A). The mean air temperature from 01 March 2022 to 30 April 2022, the duration of the study for which temperature data are available, at the site was 17.23 °C with a minimum of 5.1 °C and a maximum of 29.4 °C. The mean vapor pressure deficit was 0.92 kPa, with a minimum of 0 kPa and a maximum of 3.21 kPa.

Soils at the Neudamm Field Site are predominantly loamy sands and occasionally sands. The mean percentage of sand in the soils was 84 ± 0.8 %, while mean silt and clay content were 11 ± 0.8 % and 5 ± 0.4 %, respectively. Analysis of Variance showed that soil particle size was not different (sand, P = 0.37; silt, P = 0.43; clay, P = 0.50) among drought treatments. Similarly, the levels of soil chemical properties (phosphorus, P = 0.86; potassium, P = 0.58; magnesium, P = 0.55; calcium, P = 0.96; pH, P = 0.92; organic matter, P = 0.95; electrical conductivity, P = 0.84) did not differ across the four drought treatments.


(A)
Average daily soil temperature during March 2022 at Neudamm Field Site

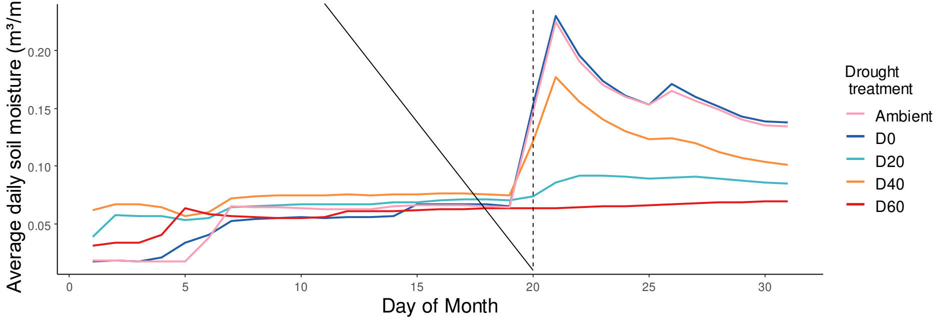

(B)
Average daily soil moisture during March 2022 at Neudamm Field Site

Figure 20. Mean Daily Soil Climatic Properties at the Neudamm Field Site During March 2022, Showing (A) Soil Temperature and (B) Soil Moisture.

Means were calculated by taking the mean of the 15-minute interval records of soil temperature and moisture over each 24-hour cycle. The dashed vertical line represents a 16 mm rainfall event on 20 March 2022.

Vegetative Growth Indicators and Phenology

Germination of at least one *C. gynandra* individual was recorded in all 20 plots, however, plant establishment to flowering varied considerably among plots. A total of 226 plants were monitored over the growing season and 121 individuals from 19 plots flowered. One D0 (control) plot, located on a steep slope, did not yield any plants that reached maturity and was therefore excluded from analyses.

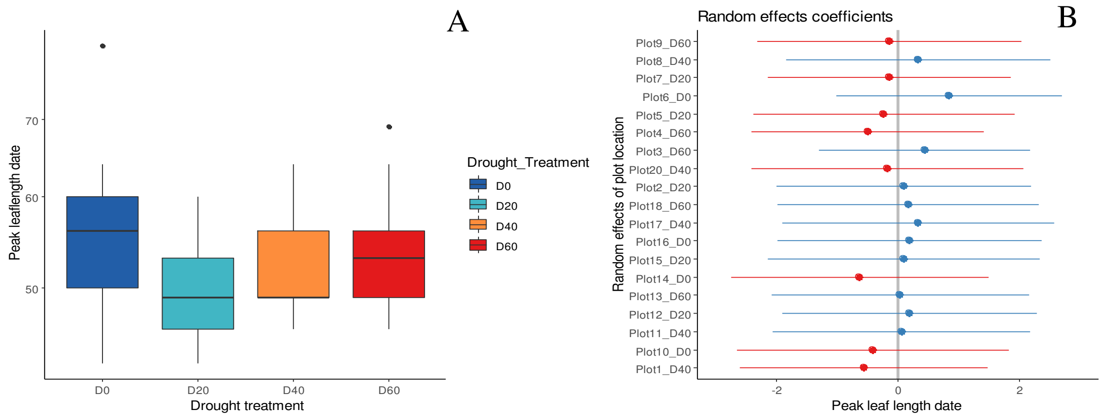


Figure 21. Response of Peak Leaf Length Date of *Cleome gynandra* to Drought Treatment.

(A) The distribution of fixed effects and (B) and the random effects of plot in a linear mixed effects model. The red horizontal lines represent advanced responses and the blue denote delayed responses.

Table 3. Results from the Linear Mixed Effects Model of the Fixed Effects of Drought Treatment on Peak Leaf Length Date of *C. gynandra*.

The CI is the 95% confidence intervals of fixed effects coefficients.

	Peak leaf length date		
Predictors	*Estimates*	*CI*	*p*

(Intercept)	57.56	54.51 – 60.61	<0.001
Drought Treatment [D20]	-7.84	-12.00 – -3.67	<0.001
Drought Treatment [D40]	-5.45	-10.02 – -0.87	0.020
Drought Treatment [D60]	-4.42	-8.23 – -0.61	0.023
Random Effects			
σ^2	46.14		
$\tau_{00\ \text{Plot\_No}}$	1.34		
ICC	0.03		
$N_{\text{Plot\_No}}$	19		
Observations	121		
Marginal R^2 / Conditional R^2	0.129 / 0.153		

Drought treatment did not affect *C. gynandra* maximum stem height ($P = 0.45$) or maximum leaf length ($P = 0.46$). There were also no significant fixed effects of drought treatment on the maximum number of leaves of *C. gynandra*. However, vegetative phenology i.e., peak leaf length date and peak number of leaves date ($P < 0.001$ and $P = 0.020$, respectively) advanced in response to drought treatment (Figures 21 and 22, Table 3 and Table 4). Peak leaf length date advanced by eight days ($P = 0.001$), five days ($P = 0.02$) and four days ($P = 0.023$) in response to 20%, 40% and 60% summer drought respectively. Similarly, the date of peak number of leaves was accelerated by 12 days ($P = 0.007$), eight days ($P = 0.103$), and eight days ($P = 0.075$) in response to 20%, 40% and 60% rainfall reduction, respectively. The fixed effects of drought accounted for 12.9% of variance in the peak leaf length date model alongside the conditional R^2 of 15.3%. The marginal R^2 and the conditional R^2 in the date of peak number of leaves model were determined as 13.5% and 31.7%, respectively. Date of peak stem height of *C. gynandra* showed a general advancing trend in response to the drought treatment (P = 0.065).

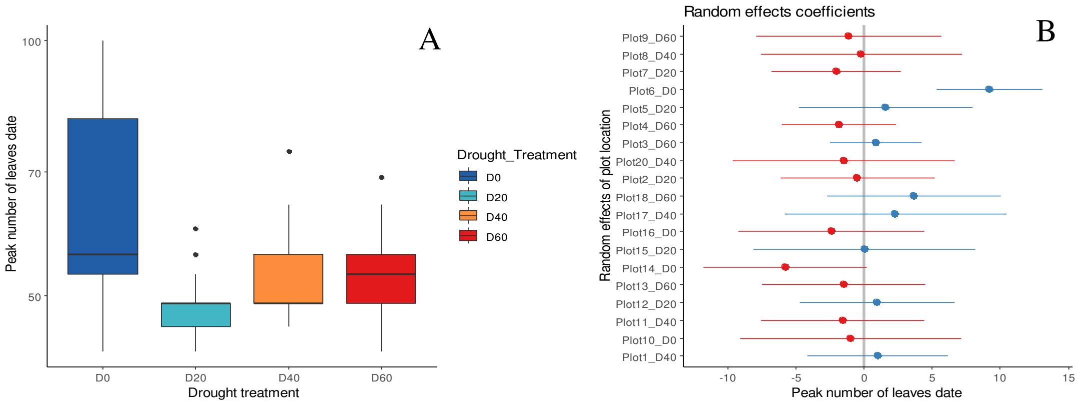


Figure 22. Response of Peak Number of Leaves Date of *Cleome gynandra* to Drought Treatment.

(A) The distribution of fixed effects and (B) The random effects of plot in a linear mixed effects model. The red horizontal lines represent advanced responses and the blue denote delayed responses.

Table 4. Results from the Linear Mixed Effects Model of the Fixed Effects of Drought Treatment on Peak Number of Leaves Date of *C. gynandra*.

The CI is the 95% Confidence Intervals of Fixed Effects Coefficients.

	Peak number of leaves date		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	60.75	54.28 – 67.22	<0.001
Drought Treatment [D20]	-11.80	-20.39 – -3.21	0.007
Drought Treatment [D40]	-7.61	-16.78 – 1.57	0.103
Drought Treatment [D60]	-7.53	-15.83 – 0.76	0.075
Random Effects			
σ^2	81.66		

$\tau_{00\ \text{Plot\_No}}$	21.86
ICC	0.21
N $_{\text{Plot\_No}}$	19
Observations	120
Marginal R^2 / Conditional R^2	0.135 / 0.317

Flowering and Fruiting Phenology

The first flowering date of *C. gynandra* did not differ across drought treatments (P = 0.47). However, there was a significant fixed effect on the peak flowering date (P = 0.026, Figure 23, Table 5). Both the 20% and 60% drought treatments advanced the peak flowering date by 7 days (P = 0.04), and 7 days (P = 0.025), respectively. The fixed effects in the peak flowering date model explained 11% of the variation, while the conditional variance was 23%. Linear mixed effects models indicate that the drought treatment did not affect flowering end date (P = 0.50) or flowering duration (P = 0.95). There was no significant change in the peak fruiting date of *C. gynandra* across the drought gradient (P = 0.27).

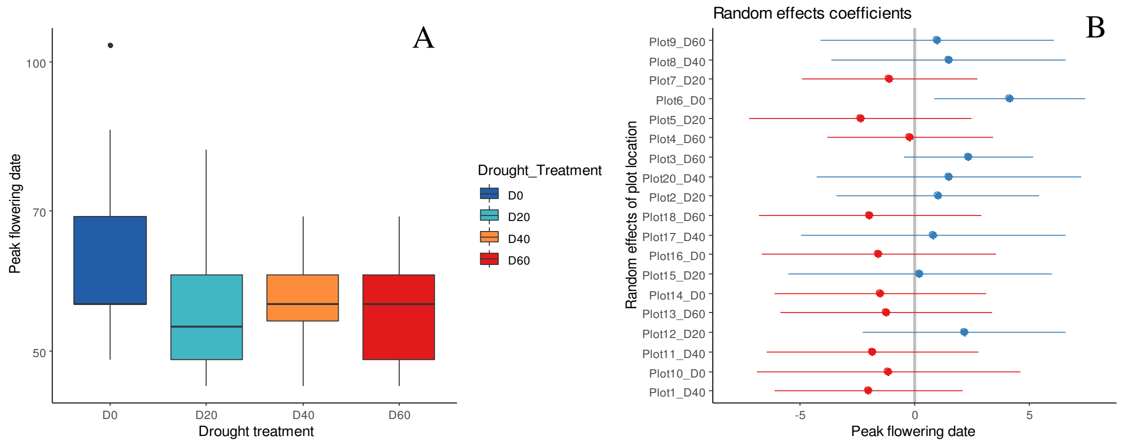


Figure 23. Response of Peak Flowering Date of *Cleome gynandra* to Drought Treatment.

(A) The distribution of fixed effects and (B) the random effects of plot in a linear mixed effects model. the red horizontal lines represent advanced responses and the blue denote delayed responses.

Table 5. Results from the Linear Mixed Effects Model of the Fixed Effects of Drought Treatment on Peak Flowering Date of *C. gynandra*.

The CI is the 95% confidence intervals of fixed effects coefficients.

	Peak flowering date		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	61.11	56.20 – 66.02	<0.001
Drought Treatment [D20]	-6.86	-13.38 – -0.33	0.040
Drought Treatment [D40]	-3.03	-10.00 – 3.93	0.390
Drought Treatment [D60]	-7.16	-13.42 – -0.90	0.025
Random Effects			
σ^2	62.26		
τ_{00} Plot_No	10.01		
ICC	0.14		
N Plot_No	19		
Observations	118		
Marginal R^2 / Conditional R^2	0.107 / 0.230		

Reproductive Output

The maximum number of flowers on *C. gynandra* plants ranged from 1 to 246 while the maximum number of fruits on an individual plant ranged from 1 to 210. The linear mixed effects model showed a trend toward a decrease in the number of flowers produced by *C. gynandra* across the D0, D20, D40, and D60 drought gradient (P = 0.067). Correspondingly, there was generally a decline in the number of fruits of *C. gynandra* in response to the drought (P = 0.08).

Discussion

Vegetative Growth Indicators and Phenology

The advanced vegetative phenology response to drought shown by *C. gynandra* in this dryland savanna is suggestive of the classical escape mechanisms, particularly rapid development, early maturity and contraction of the life cycle, observed in herbaceous annuals to cope with conditions of moisture deficit (Seleiman et al., 2021). By hastening their vegetative development, plants are able to flower quickly, set seed and complete their life cycle to escape the detrimental effects of drought (Seleiman et al., 2021). However, accelerated vegetative development may deprive the plants of the time to grow to their full potential prior to reproduction (Franks et al., 2007). Accelerated vegetative phenology and a shorter growing period could also disrupt the ecological relationships of *C. gynandra* such as with competitors and any herbivores that depend on these plants for their survival. For example, some large herbivores, particularly those in the mammalian families Equidae (e.g., horses and zebras) and Bovidae (e.g., cattle, bison and African buffalo), forage on *C. gynandra* leaves while insect pests (e.g., pentatomids, *Acrosternum gramineum* and *Agonoscelis nubilis*; locusts, *Schistocera gregaria*; and flea beetles, *Phyllotreta mashonana*) are also known to consume this plant (Chweya & Mnzava, 1997). Considering that *C. gynandra* is an important human food plant, harvested for its nutritious leaves, young shoots and flowers (Chweya & Mnzava, 1997; Kwarteng et al., 2018), a shorter growing period and advanced vegetative phenology under drought conditions may result in limited crop harvesting time, which may in turn affect the total harvestable quantities in a given season. It is therefore possible that the limited time in which the resource will be available under drought conditions could impact food security systems in areas where people depend on this leafy vegetable as an important food supplement and may also threaten both livelihoods and the cultural attachment and relationship with communities in northern Namibia and elsewhere.

Drought treatment advanced the vegetative phenology of *Cleome gynandra* but did not affect the growth traits (stem height, leaf length, and number of leaves). The hypothesis that drought treatment will stunt plant growth resulting in shorter stem height and leaf length and lower leaf numbers was not supported. The results are partially similar to those of a field study that manipulated watering regimes in the Sonoran Desert for two winter annuals. That study demonstrated varying species-specific responses of vegetative growth to drought, with *Stylocline micropoides* showing significantly less leaf area expansion and a reduced relative leaf number increase in the low water treatment, while

Pectocarya recurvata showed no response (Angert et al., 2010). These results are similar to a greenhouse study that showed that leaf size in a drought-escaping annual, *Polygonum persicaria* was not affected under drought conditions and the plants responded instead by allocating more biomass to root and reproduction tissue (Heschel et al., 2004). The lack of vegetative growth response to drought treatment of *C. gynandra* is probably due to a combination of the use of C4 photosynthesis (Voznesenskaya et al., 2018), which would both afford the plant competitive advantage to cope by accelerating its growth under limited water conditions. Plants that use C4 photosynthesis have increased water-use efficiency because they decrease photorespiration by spatially separating the initial carbon fixation process and its subsequent conversion into sugars during the Calvin cycle, through evolution of the Kranz anatomy (Voznesenskaya et al., 2018). C4 plants therefore have the capacity to maintain high internal CO_2 levels for optimum functioning of Rubisco as the carboxylating enzyme in the Calvin cycle (Majeran & van Wijk, 2009; Voznesenskaya et al., 2018). The leaves of *Cleome gynandra*, show remarkable circadian rhythmic movements, in response to the position of the sun, which probably enhances its light harvesting abilities and further contributing to photosynthetic efficiency (Chweya & Mnzava, 1997).

The conditional influence of plot as a random effect did not contribute meaningfully to the amount of variance in the peak leaf length date model (marginal $r^2 = 0.13$ and conditional $r^2 = 0.15$), suggesting additional sources of variation not explored here. However, plot as a random effect accounted for considerable proportion of the variation in the date of peak number of leaves (marginal $r^2 = 0.17$ and conditional $r^2 = 0.35$) suggesting mixed effects of both drought treatment and plot-level properties on leaf number phenology. This present study shows the importance of simultaneous measurement and consideration of morphological and phenological traits in plant responses to global change studies. Furthermore, the study underscores the need for more in-depth investigation into pulse use and resource allocation responses between vegetative and reproductive traits (below and above-ground) in dryland plants.

Flowering and Fruiting Phenology

Our hypothetical prediction that drought treatment will advance the flowering phenology of *C. gynandra* was supported with droughted plants reaching peak flowering earlier than undroughted plants. Early flowering is an important adaptive mechanism in plants to cope with drought, allowing for the limited resources to be allocated to reproduction, which is important because water scarcity may signal early senescence (Hänel & Tielbörger, 2015; Kigel et al., 2011; Seleiman et al., 2021). The drought escape strategy has been observed in other studies. Declining precipitation advanced the mean first-flowering date in 9 of 24 herbaceous species in a semi-arid grassland ecosystem (Lesica & Kittelson, 2010), while drought stress resulted in earlier onset of flowering and bolting i.e., the transition from a vegetative state to progenitive development indicated by elongation of the first reproductive stem or tiller in winter annuals from a dryland ecosystem (Aronson et al., 1992). With *C. gynandra* plants advancing their peak flowering dates in response to drought, there is a likelihood for future dry conditions to drive apart interactive ecological processes such as plant-pollinator and seed disperser and predator relationships. *Cleome gynandra* is pollinated by bees and butterflies to which it offers a nutrient-rich nectar reward, while ants and flies are known nectar thieves for this species (Raju & Rani, 2016). The survival of these pollinators may be negatively impacted under drought conditions if their activity does not overlap with the shifts in the flowering phenology of *C. gynandra*. The effects of shifting flowering phenology could not only harm pollinator survival as their food sources become limited but also the plants, due to the loss of the opportunity for sexual reproduction, which may result in reduced reproductive success and fitness (Etterson & Mazer, 2016; Wright et al., 2013).

Some plants provide a pollinator attracting service for other co-existing species in their ecosystems (Hunter & Aarssen, 1988). These beneficiary plants do not only profit from the visits of the attracted pollinators but in the maintenance of higher numbers of pollinators in their community thus increasing pollination efficiency, particularly in sequentially flowering communities where species maintain a particular order of flowering phenology (Hunter & Aarssen, 1988). Disruptions of pollinator-attraction relationships due to drought have been shown to reduce seed set in beneficiary plants that produced substantial number of flowers (Hunter & Aarssen, 1988). With its showy white flowers and the ability to form dense monospecific stands in the ecosystem (Raju & Rani, 2016), it is likely that *C. gynandra* also acts as a pollinator attractant for other plants.

Shifts in the flowering phenology of *C. gynandra* could therefore be harmful to this and other ecosystem services provided by this plant.

In this study, accelerated peak flowering did not result in changed flowering duration or an extended or contracted flowering end date under drought treatments, suggesting that drought-induced advances in peak flowering may not necessarily extend the growing season for summer annuals such as *C. gynandra*. The results are similar and contrary to the findings of Aronson et al., (1992) who showed that water stress accelerated the transition to flowering in desert populations of the winter annual species *Bromus fasciculatus* and *Brachypodium distachyon* but had no effect on *Erucaria hispanica*. In the same study, *B. fasciculatus* and *E. hispanica* further responded to drought stress by advancing their fruit maturation dates and contracting the reproductive phase while *Brachypodium distachyon* showed a longer reproductive phase (Aronson et al., 1992). In this study, drought treatment did not affect the peak fruiting date of *C. gynandra*, despite the shift in peak flowering date toward earlier phenology, suggesting that perhaps these stages of development, though related are somewhat phenologically independent of each other. Collectively, these findings suggest that dryland plants exhibit differential responses to drought and in-depth studies into more species may shed light on the likely patterns of reproductive phenology responses to global change in these poorly studied ecosystems.

Reproductive Output

Although early flowering is a commonly observed drought escape strategy in drylands (Aronson et al., 1992; Fox, 1990; Heschel et al., 2004; Seleiman et al., 2021), reproductive fitness trait responses to water deficit have been shown to be more variable and inconsistent. In some species, advanced reproductive maturity allows for a greater proportion of resources to be allocated to reproduction at the expense of vegetative growth. For example, Volis et al.(2002) showed that an early flowering response under low and unpredictable rainfall resulted in higher fecundity which equated to relatively high yield for *Hordeum spontaneum* (barley) from drylands compared to those from non-dryland sites. In some species, however, e.g. the self-compatible annual herb *Polygonum persicaria* (smartweed), the number of fruits did not vary under drought stress and moist water conditions (Heschel et al., 2004). Similarly, the number of flowers and fruits of *C. gynandra* was not different with drought treatment in this study. Collectively, the findings of this present study and those reported in the literature suggest that reproductive fitness responses to drought in dryland species is not well understood, clearly highlighting an area of research that warrants further investigation.

Conclusions

In this species-level study, I present multiple vegetative growth, reproductive output, and phenological responses of a C4 subtropical herbaceous annual, *C. gynandra* throughout the entire plant growth and developmental stages from germination to senescence across a 0% to 60% drought gradient. While the data did not support drought treatment effects on the phenotypic plasticity of stem height, leaf length and number of leaves produced by *C. gynandra*, this drought-escaping species responded by shifting its vegetative and flowering phenology. Although this rapid development response to drought treatment is an ingenious strategy to ensure completion of the life cycle and fruit set, the resulting limited temporal availability of moisture, makes it a costly option for the plant and its associated interactions including competitors, predators, pollinators and even humans that depend on the species as a food, medicinal and cash crop. Advances in peak flowering date are particularly concerning because this trend threatens reproductive fitness of these socio-cultural, economically, and ecologically important plant, particularly if shifting flowering phenology results mis-matched activity of potential pollinators, seed predators and plant competitors. At peak flowering, the plants are in maximum flower, and could be risking the next generation of progeny if this reproductive timing effort and investment does not yield fruit and seed under changing climates. This experiment offers important insights into the capacity of *C. gynandra* to track climate and the likely phenotypic and phenological responses to a drying earth in dryland ecosystems. Future studies should take into account resource allocation responses between vegetative and reproductive traits including below and above-ground parts of dryland plants as well as the interactive effects of precipitation and temperature.

CHAPTER 4

4 DROUGHT AND FLOODING EFFECTS ON GERMINATION, GROWTH AND FLOWERING PHENOLOGY OF *CLEOME GYNANDRA* L.

Abstract

Climate change is altering precipitation patterns in drylands by shifting the timing and amounts of precipitation and through increased frequency and longevity of extreme events such as droughts and floods. There is a need to increase our understanding of the responses and mechanisms that plants growing in drylands may use to survive these changes in the hydrological cycle. My study focused on germination, vegetative growth and reproductive timing responses of *Cleome gynandra*, a widely consumed leafy vegetable of high nutritional and medicinal value which forms an important part of the diet of rural populations across Africa and Asia. The plants were subjected to flood and drought conditions in a greenhouse experiment, simulating 45% increase and 45% decrease in rainfall, respectively. I found that flood conditions resulted in higher germination percentage of *C. gynandra* than in the drought and control rainfall treatments. However, the maximum leaf number and maximum stem height of plants were not different among rainfall treatments. The study also revealed that the timing of first flower and peak flower production did not differ among rainfall treatments. Instead, I found that *C. gynandra* plants reached maturity (flowering onset) at significantly shorter

stem height under flood conditions compared to the control rainfall treatment. Shorter stem height at flowering onset could compromise seed production quantity and quality, as well as limit accessibility of plants to pollinators, potentially leading to reproductive failure. I recommend that farmers and conservation scientists collect and store seeds of *C. gynandra* for future restoration as changes in the hydrological cycle resulting from climate change could affect long-term replenishment of the seed bank.

Introduction

Climate change is altering global precipitation patterns, including the amount, frequency and timing of rainfall events, and prolonging dry seasons or extending wet seasons (Collins et al., 2013; Pachauri et al., 2015). However, changes in precipitation patterns vary geographically. Generally, global precipitation over the 21st and 22nd century is projected to increase gradually, although some regions, particularly the semi-arid regions of the midlatitudes and subtropics such as the Mediterranean, the southwest USA, southwestern Australia, southern Africa, have been experiencing consecutive declines in precipitation amounts with extended dry seasons (Collins et al., 2013; Pachauri et al., 2015). These dryland regions will continue to experience large-scale drying in the face of increasing global temperatures and rising evapotranspiration rates, further increasing the risk of agricultural drought, the number of consecutive dry days (Collins et al., 2013).

Empirical evidence suggests increased dryness and occurrence of extreme precipitation events in drylands, albeit with notable variations across global, regional and local trends in precipitation. Drylands in the Southern Hemisphere, predominantly southern Africa and most of Australia showed trends of increased precipitation during the summer months (December, January, and February), based on a 40-year dataset from 1979-2018 (Daramola & Xu, 2022). However, a localized study in Namibia showed that precipitation amounts remained unchanged across four sites along a rainfall gradient. Rather, the study found a general increase in extreme precipitation events such as heavy rainfall and drought, with temporal and spatial variations corresponding to the degree of aridity (Lu et al., 2016). There was a significant decline in the frequency of storm events and a trend toward increased storm intensity in the hyper-arid central Namib Desert but there was no change in either of these parameters at the wetter site in the Windhoek area (Lu et al., 2016). Another study, conducted in the Windhoek area where the mean annual precipitation (MAP) is approximately 350 mm, showed that the frequency of dry years (defined in that study as MAP less than 200 mm), has nearly quadrupled over a period of 70 years, between 1946-2016, indicating a clear pattern of decreased rainfall (Shikangalah & Mapani, 2019). The study also showed that the peak rainfall month in the Windhoek area has shifted from January to March. These trends led to a projection for a decrease in MAP of about 125 mm for 2017–2060 in this area (Shikangalah & Mapani, 2019).

In addition to drought, floods in Namibia have become more frequent, occurring nearly every year, especially in the highly populated regions in north-central and north-eastern parts of the country (Spear et al., 2018). In north-central Namibia, recurring floods have been experienced for hundreds of years as a result of the combination of localized rainfall in the area and rainwater from the Angolan highlands (where annual rainfall exceeds 900 mm), that feed into the Cuvelai-Etosha basin causing floods, known in the local Oshiwambo language as "*efundja*" (Shaamhula et al., 2021). The Cuvelai-Etosha basin, a low lying, flat plain made up of inter-connected shallow river channels of variable widths, that stretches from the south of Angola, through northern Namibia, and drains into the Etosha pan (Mendelsohn et al., 2002; Ministry of Environment & Tourism of Namibia, 2011). The Zambezi region in Namibia, where MAP is highest in the country, the largest flood (over a since 30-y period 1969) was recorded in 2009 which was followed by subsequent floods in 2010 and 2011 (Skakun et al., 2014). Another study in the Zambezi region has shown an increase in flooding frequency between 2009 to 2013, further identifying zones with increased probability of flooding in the future (Long et al., 2014). Floods, resulting from heavy precipitation events are therefore recorded in Namibia and are expected to occur more frequently by the end of the 21st century (Spear et al., 2018).

Studies conducted in terrestrial ecosystems have shown that there is generally a positive relationship between increased MAP and aboveground versus belowground biomass, net primary and productivity and photosynthesis (Wu et al., 2011). Meanwhile, these relationships are notably negative when precipitation is decreased (Wu et al., 2011). Vegetation responses are not only affected by the amount of precipitation but also other rainfall characteristics such as the timing, frequency and intensity of extreme precipitation events (e.g., droughts and floods), resulting in altered net primary productivity (Lázaro et al., 2001; Reyer et al., 2013). This is critical in drylands where plants are well adapted to respond to precipitation pulses and ecosystem productivity may shift dramatically with such responses (Reyer et al., 2013). Some plants in drylands respond to drought by increasing proportional biomass investment belowground compared to above ground (Aronson et al., 1992). For example, conditions of moisture deficit resulted in reduced plant size and increased root and reproduction tissue for the annual forb, *Polygonum persicaria* (Heschel et al., 2004). On the other hand, flooding reduces oxygen diffusion and supply to the plant through the roots, compromising respiration and other cellular metabolism which may cause the plants to die (Reyer et al., 2013). Only a limited number of studies have focused on how plants in natural systems may respond to extreme precipitation events and most have been conducted in mesic ecosystems (Beier et al., 2012). It is therefore important to conduct studies to understand how extreme precipitation events (such as droughts and floods) which are expected to increase with global climate change could affect plant populations to better evaluate their potential to cope with the on-going changes in the earth’s climate. In drylands where precipitation occurs in pulses of high temporal and spatial variability (Noy-Meir, 1973), forecasted changes in further variability in precipitation patterns may result into novel plant responses noteworthy of scientific investigation.

Cleome gynandra L. is a widely consumed leafy vegetable, known for its high nutritional and medicinal value that forms an important part of the diet of rural populations across Africa and Asia (Chweya & Mnzava, 1997; Kwarteng et al., 2018). *Cleome gynandra* is an especially important semi-wild crop species in northern Namibia, where it is harvested for local consumption, as a cash crop and a cultural emblem of traditional celebrations (Chataika et al., 2020). As a green leafy vegetable, *C. gynandra* is a rich source of protein, vitamins A and C and minerals such as calcium, iron and magnesium (Kwarteng et al., 2018) and as a relish, offers rural communities in Namibia, as across many African and Asian countries much needed nutritional supplement; in a way, mitigating malnutrition (Chweya & Mnzava, 1997; Kwarteng et al., 2018). While this vegetable has been used by the indigenous people in Namibia and elsewhere, and sold in informal markets, for hundreds of years (Chataika et al., 2020), *Cleome gynandra* is now emerging as an important commodity in the formal markets in Namibia where it is sold as an African vegetable soup (windomarket.com). Yet, changing rainfall conditions pose a potential threat to the species. Given the predictions of an increase in the occurrence of extreme precipitation events for Namibia (Mason & Joubert, 1997; Spear et al., 2018), studies on the effects of flooding and drought on the persistence of *C. gynandra* are needed to inform the mitigation of climate change impacts on this important indigenous vegetable. The overall aim of this study was to determine the effects of simulated drought and flood conditions on the germination, vegetative development, and reproductive timing of *Cleome gynandra*. To accurately assess the long-term availability of this valuable resource under changing climates, it is important to study how extreme precipitation events such as droughts and storms, might affect the germination success, foliage production and reproductive phenology of *Cleome gynandra*. I hypothesized that both extreme drought and flooding will decrease germination success and stunt the vegetative growth of *C. gynandra*. Furthermore, I expected the stunted vegetative growth to result in advanced flowering dates of *C. gynandra*, as the plants accelerate their development under these conditions. The results from this study will help forecast the harvest yields and availability of *C. gynandra* as a crop during years of extreme precipitation events and may be useful for local farmers to plan for the harvesting of *C. gynandra* under different rainfall years. Data from this study may also be useful to potential entrepreneurs who may be interested in horticultural production of *C. gynandra*.

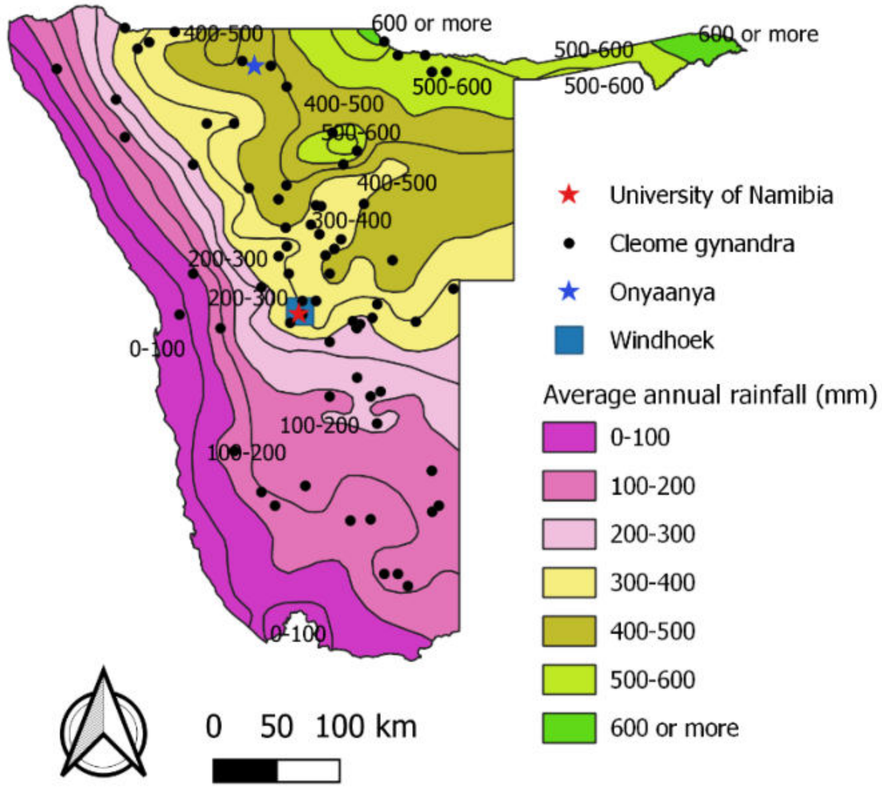


Figure 24. Map of Namibia Showing Seed Collection Site at Onyaanya Village (Blue Star) and Greenhouse Location at the University of Namibia, Windhoek Campus (Red Star).

The distribution of *Cleome gynandra*, across the country, based on herbarium collection is shown as solid black circles.

Materials and Methods

The study was conducted in a glasshouse at the University of Namibia, Windhoek Campus (22.6122° S, 17.0584° E; Figure 24). Opening slats on all three exterior sides of the glasshouse allow ventilation and gas exchange with the outside (Figure 26), but there was no additional temperature or humidity regulation. The glasshouse therefore offers a semi-controlled environment, in which the water supply can be regulated.

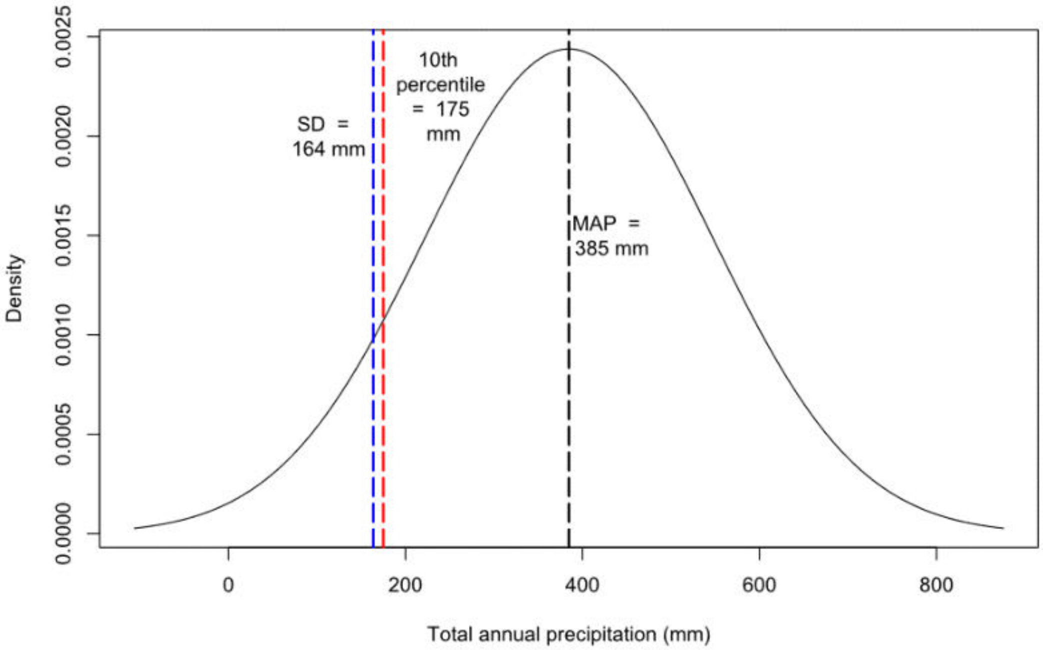


Figure 25. The Probability Density Function of the Total Annual Rainfall in Windhoek, Namibia for the Period 1960-2015.

The dashed black line represents the mean annual rainfall (385 mm) while the blue line is the standard deviation (164 mm). The red line represents 10th percentile of the distribution, hence the 1 in 10 years drought occurrence simulation.

Because annual precipitation varies substantially from year to year across ecosystems (and especially in drylands), it is recommended that experiments manipulating precipitation use historical records of the study area to account for site-specific variation (Knapp et al., 2017). Accordingly, I used a probability distribution of historical total annual precipitation data for central Namibia spanning 1960-2015, to define extreme precipitation events that I simulated in this study. Dry years are defined as those with total annual precipitation <10th percentile (Knapp et al., 2015). The mean annual precipitation in central Namibia is approximately 385 mm (standard deviation =164 mm), based on the 1960-2015 dataset from the Windhoek Meteorological Station (Namibia Meteorological Service, 2020). These data (mean: 385 mm, standard deviation:164 mm) were used to construct a probability density function (Figure 25), from which a 10% probability of a drought year occurrence was computed. The 10^{th} percentile of the total annual precipitation was determined at or below 175 mm. I divided this value by the MAP (175 mm / 385 mm) and obtained 0.45 or 45%, which represents the recommended rainfall manipulation simulating a one-in-10 years probability of drought in this savanna ecosystem. This greenhouse experiment therefore manipulated precipitation at three treatment levels, namely: drought (45% below MAP =173 mm), control (MAP: 385 mm) and flood (45% above MAP = 558 mm), in a single factor design. The drought treatment were therefore defined as 45% less, while the flood treatment was considered as 45%

more precipitation than MAP I conducted the experiment during the summer rainy season for Namibia from November 2021 - April 2022 (~26 weeks). Since the average annual number of rainy days in the Windhoek area is 57 days (https://weather-and-climate.com/), the average rainfall frequency can be estimated at approximately 2 rain days per week (57/26). Since rainfall measurements are based on the volume of water needed to moisten a known surface area and depth e.g., 1mm of rainfall refers the amount of water required to fill a 1-square meter area to a depth of 1mm (https://www.fao.org/, n.d.), I simulated the rainfall treatments to match the surface area of the plant pots. Two rainfall events per week equates to a total of 52 events over the 26-week growing season. I divided the MAP of 385 mm by 52 to obtain the rainfall amount per event (7.40 mm). Using plant pots of a mean diameter of 20 cm and height of 20 cm, MAP at pot-level was calculated as rainfall amount at each event x surface area of pot = 0.740 cm * π*10 cm^2 = 232.5 cm^3 = 232.5 ml per event. Because the 232.5 ml was not sufficiently moistening the top 1 mm of the soil in the pot, the pot-level MAP was upscaled by 17.5 mm (simulated at 250 mm), from which a 45% drought was calculated as (140 mm) and 45% flooding (360 mm).

Seeds of *Cleome gynandra* were obtained from Onyaanya village in the Onyaanya constituency, 35 km east of Ondangwa in the Oshikoto region, northern Namibia (Figure 24). The seeds were harvested over the 2021 growing season during January-April and stored at room temperature until the experiment commenced in October 2021. No viability tests were conducted on the *C. gynandra* seeds used in the experiment. The study followed a randomized block design to account for microclimate variability in the greenhouse. The greenhouse was divided into 3 blocks and plant pots with the three rainfall treatments were represented equally in each block. Each rainfall treatment was replicated with 50 plant pots, totalling 150 pots for the entire study.

I lined the bottom of the pots with small pebbles to promote aeration and filled the pots w a 1 to 1 ratio mixture of potting soil and sifted sand. Each plant pot was seeded with 60 *C. gynandra* seeds. Seeding was carried out on 27 October 2021. For the first six weeks of the experiment, the pots were watered using shower-headed garden watering cans until saturated, to allow for germination and seedling development, regardless of the rainfall treatment assignment. Rainfall treatments were applied from 17 December 2021 to 11 April 2022, covering the summer growing season in Namibia. The pots were observed every day and all germinated seedlings were tagged with their respective emergence date. Plant measurements (stem height; number of leaves, inflorescences, flowers, and fruits per plant) were taken every third day. Stem height measurements were taken using a 30 cm ruler, and all other plant variables were recorded as counts. Because the study included a flowering phenology component, it was critical to monitor the plants for the entire reproductive period. However, because the end of flowering generally coincided with plant senescence, I was unable to harvest the plants at the end of the experiment for biomass allocation assessment.

The pots were watered every third day, approximately twice a week as per rainfall frequency for the Windhoek area (https://weather-and-climate.com/), with the appropriate amounts of 250 mm for the control, 140 mm for drought and 360 mm for flood, corresponding to the simulated rainfall treatments.

Figure 26. The View of the Greenhouse at the School of Science Building, University of Namibia (A) Exterior View, (B) Interior View and (C) A *Cleome gynandra* Seedling Growing in a Plant Pot Inside the Greenhouse.

Statistical Analysis

Since rainfall treatments were applied about six weeks into the experiment, germination percentage was calculated as the percentage of post-treatment germinants relative to the total seeds that had not germinated at treatment commencement. For example, if 15 and 5 seedlings germinated in a given pot before and after the application of rainfall treatments respectively, then post treatment germination percentage was calculated as (5/45)*100 to account for pre-treatment germination. To avoid pseudo replication, mean values of all variables were analyzed for each pot, therefore the plant pots were the sampling units in this experiment.

I used a one-way analysis of variance (ANOVA) to test for differences in the germination percentage, maximum leaf number and maximum stem height of plants among the rainfall treatments. Data were normalized through log-transformation. The ANOVA results were further tested with a Tukey's Honestly Significant difference test (Tukey's HSD), a post hoc pairwise comparison, at alpha level = 0.05 to identify differences among means.

The first flowering date was defined as the date on which the first open flower was observed while peak flowering date was defined as the date that the maximum number of flowers were recorded for each individual that reached the reproductive stage. These flowering phenology metrics were expressed as the number of days since the pots were seeded. Because only one plant reached maturity in the drought treatment, reproductive variables (i.e., first flowering date, peak flowering date and stem height at first flower) were compared between the flood and control rainfall treatments using a two-sided t-test.

Results

Germination Percentage and Vegetative Growth

A total of 1067 seeds germinated (503 post treatment) over the course of the experiment, however, only 27 plants reached maturity, with one, 10 and 16 individuals in the drought, flood, and control rainfall treatments respectively, producing at least one flower. Germination percentage was generally low across rainfall treatments, averaging at 6%, 7% and 11% in the drought, control, and flood conditions respectively. The highest maximum germination percentage of 32% was recorded under flooded conditions (Table 6).

Table 6. Descriptive Statistics Summary of Germination Percentage Among Treatments. All values are based on individual plant pot means. n = number of pots.

Treatment	Mean %	Minimum %	Maximum %	Sample size (n)
Drought	6.18± 0.717	1.75	22.45	44
Control	6.84± 0.689	1.69	16.22	45
Flood	11.03± 1.10	1.69	32	48

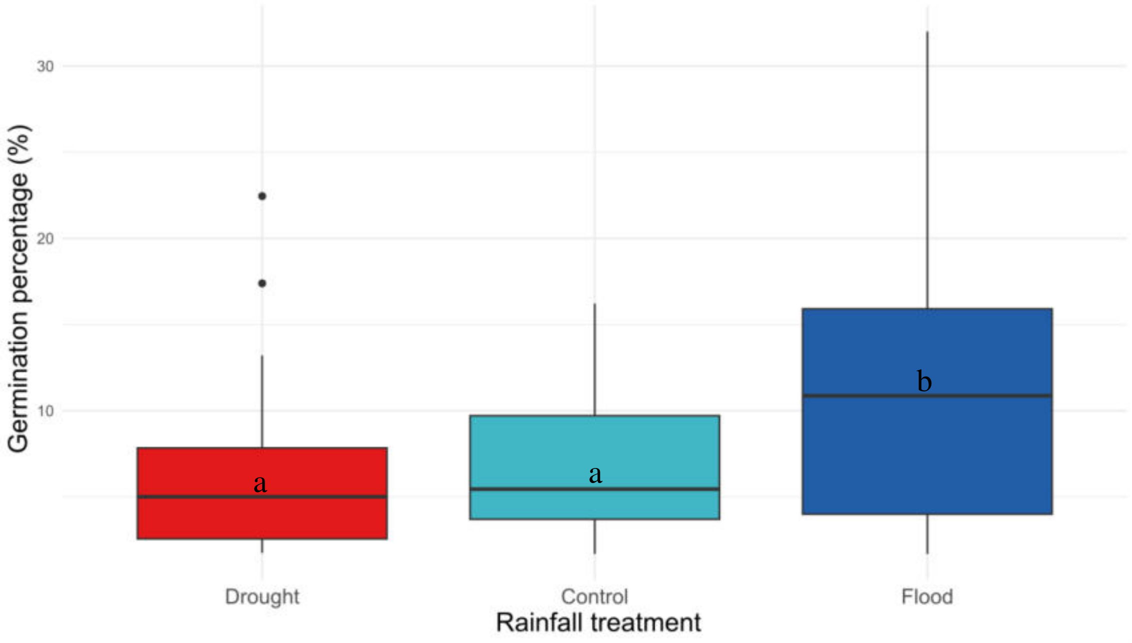


Figure 27. Boxplot of Germination Percentage of *Cleome gynandra* Seeds Among the Drought, Control and Flood Rainfall Treatments in the Greenhouse.

The letters inside boxplots represent the post-hoc (Tukey HSD) for the ANOVA test comparing rainfall treatment effects on the germination percentage of *C. gynandra*. Different letters show that the mean difference is significant at $P < 0.05$.

The analysis of variance test revealed significant fixed effects of rainfall treatment on the germination percentage of *Cleome gynandra* seeds in the greenhouse (ANOVA: $F_{2,119} = 5.694$, $P = 0.0044$). The Tukey Honestly Significant Difference (Tukey HSD) multiple comparison test revealed that the germination percentage of *C. gynandra* was higher in the flood treatment (11.03 %, SE = 1.10, n = 48) than in the drought (6.18 %, SE = 0.72, P = 0.0055, n = 44) and control (6.84 %, SE = 0.69, P = 0.037, n = 45) rainfall treatments. Germination percentage did not vary between the drought and control rainfall treatments (P= 0.78) (Table 6, Figure 27).

Drought and flooding conditions did not affect the maximum stem height (ANOVA: $F_{2,119}$ =2.801, P= 0.064) and the maximum number of leaves (ANOVA: $F_{2,100}$ = 0.119, P= 0.888) of *Cleome gynandra* under greenhouse conditions. The mean stem height of *C. gynandra* in the drought, control and flood treatments were 1.38 cm (SE = 0.20, n = 39), 2.14 cm (SE = 0.32, n = 42) and 1.43 cm (SE = 0.13, n = 41) respectively (Table 7). The mean maximum number of leaves produced by *C. gynandra* under drought, control and flood treatments were 3.27 (SE = 0.35; n = 32), 3.69 (SE = 0.46; n = 28) and 3.51 (SE = 0.49; n = 43).

Table 7. The Mean Stem Height and Mean Maximum Number of Leaves of *C. gynandra* Under the Different Rainfall Treatments.

Treatment	Stem height (cm), (Mean ±se)	Maximum number of leaves, (Mean ±se)
Drought	1.38±0.20	3.27±0.35
Control	2.14±0.32	3.69±0.46
Flood	1.43±0.13	3.51±0.49

Flowering Phenology

Since only one plant in the drought treatment reached maturity, flowering phenology comparisons were only made between the control and flood treatments, using a two-sample t-test. The first flowering date of *C. gynandra* did not vary between the flood (Julian date: 121, SE = 6.59, n = 9) and control (Julian date: 137, SE = 6.77, n =15) rainfall treatments under greenhouse conditions (t = 1.32, df =22, P = 0.19). Similarly, the peak flowering date of *C. gynandra* did not vary between the flood (Julian date: 121, SE = 6.02, n = 9) and control (Julian date: 137, SE = 5.79, n = 16) rainfall treatments (t = 1.59, df = 23, P = 0.12). However, the stem height at first flower was significantly shorter in the flooded (8.59 cm, SE = 1.27, n = 9) *C. gynandra* plants compared to those in the control (13.1 cm, SE = 1.12, n = 15) treatment (t = 2.51, df = 22, P = 0.019; Figure 28).

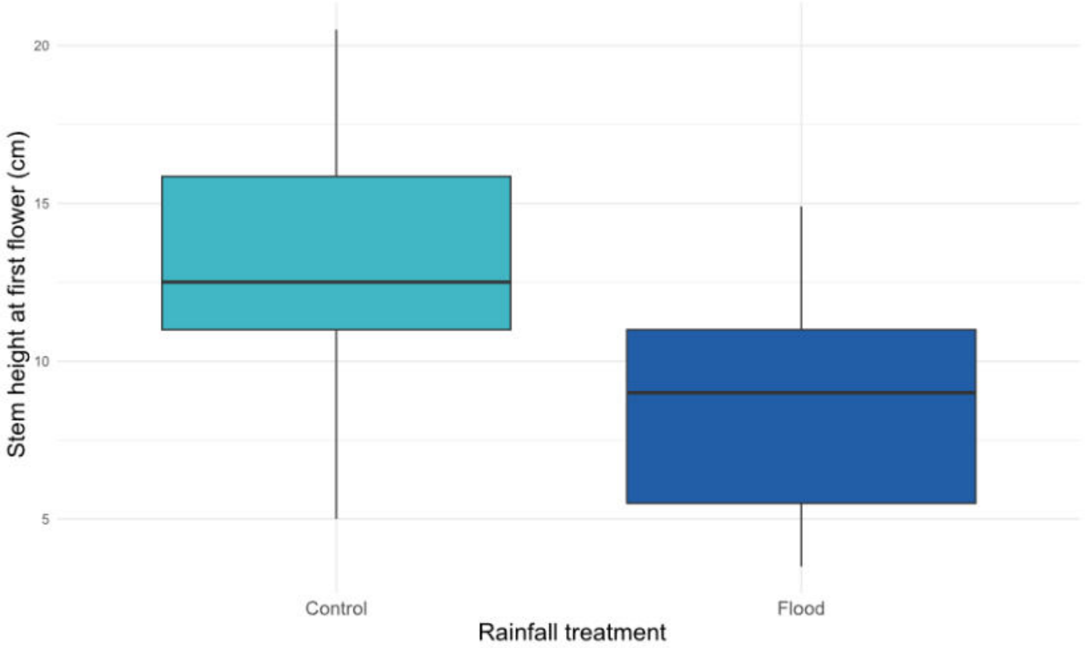


Figure 28. Boxplots Comparing the Mean Stem Height of *C. gynandra* at Flowering Onset Between Flood and Control Rainfall Treatments.

Discussion

Germination Percentage and Vegetative Growth

In this study, I generally found low germination percentage of *Cleome gynandra* seeds across treatments. A study by Kamotho et al., (2013) found that *C. gynandra* seeds stored at room temperature showed the least germination percentage while seeds stored at sub-zero temperatures, particularly -20 °C and 5 °C yielded higher viability and therefore germinability. The study also revealed that the germination percentage of freshly harvested *C. gynandra* seeds tended to be as low as 14.5% but increased to 95% following six months in storage (Kamotho et al., 2013). In this study, I used freshly collected seeds that remained stored at room temperature prior to the experiment which could explain the low germination percentage obtained. Additional factors such as soil pH and other nutrients could also have affected the low germination percentage.

The results of this study also showed that flooding increased germination percentage of *Cleome gynandra* in the greenhouse, suggesting that the additional 45% rainfall provided sufficient moisture to promote germination. However, with only 10 individuals reaching maturity, the flooded conditions did not result in increased growth and establishment of the germinated seedlings. These results also suggest that increased flooding could deplete the soil seed banks of *Cleome gynandra* because germinated seedlings may not reach maturity to replenish the soil with seeds, threatening the long-term existence of the species under climate change scenarios that predict higher occurrence of floods. Although some studies have shown that shoot responses such as petiole and stem elongation are commonly observed across species during flooding (Blom et al., 1990), I did not observe this pattern in this study. In this greenhouse study, the shoot responses (stem height and number of leaves), did not differ across rainfall treatments (Table 7). The lack of rainfall treatment effect on the vegetative growth response of *C. gynandra* under greenhouse conditions is corroborated in the field study. Experimental drought did not affect the stem height, or the number of leaves produced by *C. gynandra* when the total rainfall amount was reduced by 20%, 40% and 60% under field conditions. However, both the vegetative and flowering phenology of *C. gynandra* were advanced under drought conditions in the field.

Flowering Phenology

Plants use different strategies to cope with flooded environmental conditions, including adjustments to the timing of reproduction (Blom et al., 1990; Sultan, 2003). Some species postpone their flowering dates and survive in a vegetative state during flooding periods while others accelerate their flowering timing to produce seeds before the floods worsen or during the dry periods between two successive flood events (Blom et al., 1990; Sultan, 2003). I did not find any difference in the first and peak flowering dates of *Cleome gynandra* across rainfall treatments, although this could be due to the small sample size of plants that reached reproductive maturity. The shorter stem height at first flower under flooding conditions, however, suggests that flooded *C. gynandra* plants may invest fewer resources to above-ground vegetative growth prior to reproduction. Plants with stunted growth at reproduction may not possess adequate leaf surface area to carry out enough photosynthesis needed to support the production of flowers and seeds. In contrast to other studies, I did not find differences in leaf number of *C. gynandra* in response to rainfall treatments. For example, Blom et al., (1990) found that flooded plants had reduced number of leaves, biomass and lower seed output (Blom et al., 1990). From the perspective of *C. gynandra* as a food plant, harvested for its nutritious foliage and flowers, the onset of reproductive phase at minimized stem height suspends full vegetative development and constrain the harvestability of the plants, particularly given the monocarpic nature of most annual species (Tooke & Battey, 2010). Furthermore, stunted growth at the onset of flowering may also limit the visibility and access of plants to pollinators and negatively affect seed production during times of flood.

Conclusions

Precipitation patterns in drylands are changing dramatically with climate change and altering the hydrological cycles in these ecosystems. A notable climate change prediction for drylands is an increase in the occurrence of extreme precipitation events and prolonged dry seasons or extended wet seasons. During drought, soil moisture input may be inadequate to support plant growth while flooding can limit oxygen supply in the plant for cellular respiration through the roots. There is a need to increase our understanding of the responses and mechanisms that plants growing in drylands may retain, develop and utilize to survive these climate-change induced shifts in the hydrological patterns. In this greenhouse experiment, I focused on the germination, vegetative growth and reproductive timing responses of *C. gynandra* subjected to flood and drought conditions. The study revealed that flooding resulted in higher germination percentage of *C. gynandra* than in the drought and control rainfall treatments. However, this higher germination percentage did not translate into increased shoot responses as maximum leaf number and maximum stem height were not different among rainfall treatments. This outcome may have negative ecological consequences as increased flooding could deplete soil seed banks if plants germinate but do not reach reproductive maturity. The timing of first flower and peak flower production also did not differ among rainfall treatments. Instead, I found that *C. gynandra* plants reached maturity (onset of flowering) at significantly shorter stem height under flood conditions compared to the control rainfall treatment. Shorter stem height at flowering onset could limit accessibility of plants to pollinators, potentially leading to reproductive failure. Further studies are recommended to compare photosynthetic rates, stomatal conductance, and below and above ground allocation of resources in *C. gynandra* under the different rainfall treatments should also be considered. Nevertheless, it may become necessary for farmers and conservation scientists to collect and store seeds of *C. gynandra* for future restoration as changes in the hydrological cycle resulting from anthropogenic climate change could affect long-term replenishment of the seed bank.

CONCLUSION

The on-going changes in the earth's climate and environment at large warrant an urgent need for ecological data necessary to understand potential responses, consequences, and survival mechanisms of dryland plants to these changes. As the largest terrestrial biome, with unpredictable precipitation patterns and infertile soils, drylands are particularly vulnerable to climate change. However, empirical evidence on flowering phenology trends and responses to climate change from drylands remains scarce. In my dissertation, I focused on the responses of vegetative and flowering phenology to climate change in dryland plants. Plant phenology, particularly the timing of flowering offers a sensitive and reliable biological indicator of climate change because plants use climatic and other environmental cues to initiate production of flowers. I extracted phenological data from published studies and herbarium specimens, and conducted field and greenhouse rainfall manipulation experiments, to investigate environmental drivers and responses of vegetative and flowering phenology in drylands.

In my meta-analysis, I showed that although most species are responding to climate change through accelerated flowering, some species show delayed responses. The overall summary effects suggest that dryland plants advanced their mean flowering dates by 2.12 days decade^{-1}, 2.83 days °C^{-1} and 2.91 days mm^{-1}, respectively, responding to time series, temperature, and precipitation. Differential flowering phenology responses were evident across taxonomic and functional groups, with the grass family Poaceae and bulb forming

Amaryllidaceae showing the highest and least time series responses respectively, while Brassicaceae did not show any responsiveness. Both temperature and precipitation are important predictors of flowering time in drylands, however, the interaction effects of these variables on flowering phenology responses in drylands should be studied closely to better understand their individual roles and combined effect on flowering time. The significant phenological sensitivity further suggests that climate change could alter the composition, structure, and function of dryland ecosystems, and potentially drive apart existing ecological relationships among species. Furthermore, mismatched ecological interactions could seriously impact livelihoods and food security in drylands, where a third of the world's human population reside, surviving principally through agro-pastoralism i.e., the integration of crop and livestock production as the main source of livelihoods (UNCCD, 2016).

Taking advantage of the long-term temporal span of natural history collections, I reconstructed flowering dates from herbarium specimens and showed that the flowering phenology responses of herbaceous plants collected across Namibian drylands varied across taxa, aridity zones and seed dispersal functional types. The results showed that the flowering phenology of herbaceous plants across Namibian drylands have advanced in response to both temperature and precipitation. Herbarium-phenology data presented in chapter 2 of this dissertation also revealed that plants in arid to semi-arid regions showed high phenological sensitivity to temperature and weaker responsiveness to precipitation. In contrast, plants in the hyper-arid to arid zones showed an opposite trend; a lower phenological sensitivity to temperature and stronger responsiveness to precipitation. This suggests an interactive effect of temperature and precipitation on the flowering phenology across the aridity gradient. Meanwhile, serotinous plants showed greater sensitivity to both temperature and precipitation than non-serotinous plants.

In chapter 3, I conducted a species-level field study, in which I simulated drought using rainout shelters and monitored the vegetative and flowering phenology and reproductive output responses of a C4 subtropical herbaceous annual, *Cleome gynandra* to a 0%, 20%, 40% and 60% drought treatment gradient. The drought treatment did not affect the vegetative growth traits (stem height, leaf length and number of leaves) of *C. gynandra*; however, this drought-escaping species responded to reduced moisture, by accelerating both its vegetative and flowering phenology. Advanced vegetative and reproductive phenology responses to drought treatment could limit the temporal availability of leaves, flowers, and seeds in *C. gynandra*. Advances in peak flowering date are particularly concerning because this trend threatens fitness of this socio-cultural, economically, and ecologically important plant that is harvested as a cash crop and for local consumption. This field experiment demonstrated the importance of considering both phenotypic and phenological responses in climate change studies.

Lastly, I examined the effects of extreme precipitation events on the germination, vegetative growth, and reproductive timing responses of *Cleome gynandra* plants subjected to flood and drought conditions in a greenhouse experiment. The study revealed that flooding resulted in higher germination percentage of *C. gynandra* than in the drought and control rainfall treatments. However, this higher germination percentage did not translate into increased shoot responses as maximum leaf number and maximum stem height were not different among rainfall treatments. This outcome may have negative ecological consequences as increased flooding could deplete soil seed banks if plants germinate but do not reach reproductive maturity. First and peak flowering dates did not differ among rainfall treatments, although *C. gynandra* plants reached maturity (onset of flowering) at significantly shorter stem height under flood conditions compared to the control rainfall treatment. Shorter stem height at flowering onset could limit accessibility of plants to pollinators, potentially leading to reproductive failure.

Overall, I showed in this study that the flowering phenology of dryland plants is responsive to time series, temperature, and precipitation, with some species advancing their flowering dates and others delaying theirs. There is also variation in the magnitude of response across taxa and functional groups. Experimental evidence shows that drought treatment advanced both the vegetative and flowering phenology of *Cleome gynandra* without affecting the stem height, leaf length and number of leaves. Future studies should consider resource allocation responses between vegetative and reproductive traits including below and above-ground parts of dryland plants under the different rainfall treatments, as well as the interactive effects of precipitation and temperature on vegetative and flowering phenology. It is recommended that farmers and conservation scientists collect and store seeds of *C. gynandra* for future restoration as changes in the hydrological cycle resulting from climate change could affect long-term replenishment of the seed bank.

REFERENCES

Allen, M. (2009). Meta-Analysis: Random Effects Analysis. *Communication Monographs*, *76*(4), 398–407. https://doi.org/10.1080/03637750903310386

Angert, A. L., Horst, J. L., Huxman, T. E., & Venable, D. L. (2010). Phenotypic plasticity and precipitation response in Sonoran Desert winter annuals. *American Journal of Botany*, *97*(3), 405–411.

Aono, Y., & Kazui, K. (2008). Phenological data series of cherry tree flowering in Kyoto, Japan, and its application to reconstruction of springtime temperatures since the 9th century. *International Journal of Climatology*, *28*(7), 905–914. https://doi.org/10.1002/joc.1594

Arfin Khan, M. A., Beierkuhnlein, C., Kreyling, J., Backhaus, S., Varga, S., & Jentsch, A. (2018). Phenological sensitivity of early and late flowering species under seasonal warming and altered precipitation in a seminatural temperate grassland ecosystem. *Ecosystems*, *21*(7), 1306–1320.

Arnold, T. W. (2010). Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *The Journal of Wildlife Management*, *74*(6), 1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

Aronson, J., Kigel, J., Shmida, A., & Klein, J. (1992). Adaptive phenology of desert and Mediterranean populations of annual plants grown with and without water stress. *Oecologia*, *89*(1), 17–26. https://doi.org/10.1007/BF00319010

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *ArXiv Preprint ArXiv:1406.5823*.

Baumann, M., Ozdogan, M., Richardson, A. D., & Radeloff, V. C. (2017). Phenology from Landsat when data is scarce: Using MODIS and Dynamic Time-Warping to combine multi-year Landsat imagery to derive annual phenology curves. *International Journal of Applied Earth Observation and Geoinformation*, *54*, 72–83. https://doi.org/10.1016/j.jag.2016.09.005

Beatley, J. C. (1974). Phenological Events and Their Environmental Triggers in Mojave Desert Ecosystems. *Ecology*, *55*(4), 856–863. JSTOR. https://doi.org/10.2307/1934421

Beier, C., Beierkuhnlein, C., Wohlgemuth, T., Penuelas, J., Emmett, B., Körner, C., Boeck, H. de, Christensen, J. H., Leuzinger, S., Janssens, I. A., & Hansen, K. (2012). Precipitation manipulation experiments – challenges and recommendations for the future. *Ecology Letters*, *15*(8), 899–911. https://doi.org/10.1111/j.1461-0248.2012.01793.x

Bertin, R. I. (2008). Plant Phenology and Distribution in Relation to Recent Climate Change. *The Journal of the Torrey Botanical Society*, *135*(1), 126–146.

Blom, C. W. P. M., Bögemann, G. M., Laan, P., van der Sman, A. J. M., van de Steeg, H. M., & Voesenek, L. A. C. J. (1990). Adaptations to flooding in plants from river areas. *Aquatic Botany*, *38*(1), 29–47. https://doi.org/10.1016/0304-3770(90)90097-5

Bond, W. (1985). Canopy-stored seed reserves (serotiny) in Cape Proteaceae. *South African Journal of Botany*, *51*(3), 181–186.

Bowers, J. E., & Dimmitt, M. A. (1994). Flowering Phenology of Six Woody Plants in the Northern Sonoran Desert. *Bulletin of the Torrey Botanical Club*, *121*(3), 215–229. JSTOR. https://doi.org/10.2307/2997177

Browning, D. M., Crimmins, T. M., James, D. K., Spiegal, S., Levi, M. R., Anderson, J. P., & Peters, D. P. C. (2018). Synchronous species responses reveal phenological guilds: Implications for management. *Ecosphere*, *9*(9), e02395. https://doi.org/10.1002/ecs2.2395

Calinger, K. M., Queenborough, S., & Curtis, P. S. (2013a). Herbarium specimens reveal the footprint of climate change on flowering trends across north-central North America. *Ecology Letters*, *16*(8), 1037–1044. https://doi.org/10.1111/ele.12135

Calinger, K. M., Queenborough, S., & Curtis, P. S. (2013b). Herbarium specimens reveal the footprint of climate change on flowering trends across north-central North America. *Ecology Letters*, *16*(8), 1037–1044. https://doi.org/10.1111/ele.12135

Chambers, L. E., Altwegg, R., Barbraud, C., Barnard, P., Beaumont, L. J., Crawford, R. J. M., Durant, J. M., Hughes, L., Keatley, M. R., Low, M., Morellato, P. C., Poloczanska, E. S., Ruoppolo, V., Vanstreels, R. E. T., Woehler, E. J., & Wolfaardt, A. C. (2013). Phenological Changes in the Southern Hemisphere. *PLoS ONE*, *8*(10), 1–12. https://doi.org/10.1371/journal.pone.0075514

Chan, Y., Lacap, D. C., Lau, M. C. Y., Ha, K. Y., Warren-Rhodes, K. A., Cockell, C. S., Cowan, D. A., McKay, C. P., & Pointing, S. B. (2012). Hypolithic microbial communities: Between a rock and a hard place. *Environmental Microbiology*, *14*(9), 2272–2282. https://doi.org/10.1111/j.1462-2920.2012.02821.x

Chataika, B. Y., Akundabweni, L. S.-M., Achigan-Dako, E. G., Sibiya, J., & Kwapata, K. (2020). Utilization of Spider Plants (*Gynandropsis gynandra*, L. Briq) amongst Farming Households and Consumers of Northern Namibia. *Sustainability*, *12*(16), Article 16. https://doi.org/10.3390/su12166604

Chen, J., Zhang, Y., Pan, J., Chen, F., Liu, T., & Zhou, Z. (2016). Peak flowering responses to the global warming of woody species in Heilongjiang Province, northeastern China. *Journal of Beijing Forestry University*, *38*(11), 50–56.

Chmura, H. E., Kharouba, H. M., Ashander, J., Ehlman, S. M., Rivest, E. B., & Yang, L. H. (2019). The mechanisms of phenology: The patterns and processes of phenological shifts. *Ecological Monographs*, *89*(1), e01337. https://doi.org/10.1002/ecm.1337

Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1555), 3149–3160. https://doi.org/10.1098/rstb.2010.0142

Chweya, J. A., & Mnzava, N. A. (1997). *Cat's Whiskers, Cleome Gynandra L.* (Vol. 11). Bioversity International.

Cleland, E. E., Allen, J. M., Crimmins, T. M., Dunne, J. A., Pau, S., Travers, S. E., Zavaleta, E. S., & Wolkovich, E. M. (2012). Phenological tracking enables positive species responses to climate change. *Ecology*, *93*(8), 1765–1771.

Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A., & Schwartz, M. D. (2007). Shifting plant phenology in response to global change. *Trends in Ecology & Evolution*, *22*(7), 357–365. https://doi.org/10.1016/j.tree.2007.04.003

Coburn, K. M., Vevea, J. L., & Coburn, M. K. M. (2019). Package 'weightr.' *Retrvied from Https://Cran. Rproject. Org/Web/Packages/Weightr/Weightr. Pdf.*

Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichefet, T., Friedlingstein, P., Gao, X., Gutowski, W.J., Johns, T., Krinner, G., Shongwe, M., Tebaldi, C., Weaver, A.J., & Wehner, M. (2013). *Long-term Climate Change: Projections, Commitments and Irreversibility*. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., & Midgley, P.M. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Cowling, R. M., Esler, K. J., Midgley, G. F., & Honig, M. A. (1994). Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. *Journal of Arid Environments*, *27*(2), 141–158. https://doi.org/10.1006/jare.1994.1054

Crimmins, T. M., Crimmins, M. A., & Bertelsen, C. D. (2011). Onset of summer flowering in a 'Sky Island' is driven by monsoon moisture. *New Phytologist*, *191*(2), 468–479. https://doi.org/10.1111/j.1469-8137.2011.03705.x

Crimmins, T. M., Crimmins, M. A., & David Bertelsen, C. (2010). Complex responses to climate drivers in onset of spring flowering across a semi-arid elevation gradient. *Journal of Ecology*, *98*(5), 1042–1051. https://doi.org/10.1111/j.1365-2745.2010.01696.x

Currier, C. M., & Sala, O. E. (2022). Precipitation versus temperature as phenology controls in drylands. *Ecology*, *103*(11), e3793. https://doi.org/10.1002/ecy.3793

Damalas, C. A. (2008). Distribution, biology, and agricultural importance of *Galinsoga parviflora* (Asteraceae). *Weed Biology and Management*, *8*(3), 147–153. https://doi.org/10.1111/j.1445-6664.2008.00290.x

Daramola, M. T., & Xu, M. (2022). Recent changes in global dryland temperature and precipitation. *International Journal of Climatology*, *42*(2), 1267–1282. https://doi.org/10.1002/joc.7301

Daru, B. H., Kling, M. M., Meineke, E. K., & van Wyk, A. E. (2019). Temperature controls phenology in continuously flowering *Protea* species of subtropical Africa. *Applications in Plant Sciences*, 11.

Davis, C. C., Willis, C. G., Primack, R. B., & Miller-Rushing, A. J. (2010). The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1555), 3201–3213. https://doi.org/10.1098/rstb.2010.0130

de Beurs, K. M., Cook, R. B., Mazer, S., Haggerty, B., Hove, A., Henebry, G. M., Barnett, L., Thomas, C. L., & Pohlad, B. R. (2013). Phenology in higher education: Ground-based and spatial analysis tools. In *Phenology: An Integrative Environmental Science* (pp. 585–602). Springer.

Demarée, G. R., & Rutishauser, T. (2011). From "Periodical Observations" to "Anthochronology" and "Phenology" – the scientific debate between Adolphe Quetelet and Charles Morren on the origin of the word "Phenology." *International Journal of Biometeorology*, *55*(6), 753–761. https://doi.org/10.1007/s00484-011-0442-5

Dirkx, E., Hager, C., Tadross, M., Bethune, S., & Curtis, B. (2008). Climate change vulnerability and adaptation Assessment. *Desert Research Foundation of Namibia and Climate Systems Analysis Group. Prepared for the Ministry of Environment and Tourism.*

Dose, V., & Menzel, A. (2004). Bayesian analysis of climate change impacts in phenology. *Global Change Biology*, *10*(2), 259–272. https://doi.org/10.1111/j.1529-8817.2003.00731.x

Elzinga, J. A., Atlan, A., Biere, A., Gigord, L., Weis, A. E., & Bernasconi, G. (2007). Time after time: Flowering phenology and biotic interactions. *Trends in Ecology & Evolution*, *22*(8), 432–439. https://doi.org/10.1016/j.tree.2007.05.006

Etterson, J. R., & Mazer, S. J. (2016). How climate change affects plants' sex lives. *Science*, *353*(6294), 32–33. https://doi.org/10.1126/science.aag1624

Fava, W. S., da Cunha, N. L., & Lorenz, A. P. (2019). Reproductive phenology of *Leptolobium dasycarpum* and *L. elegans* across the Brazilian savanna based on herbarium records. *Flora*, *255*, 34–41. https://doi.org/10.1016/j.flora.2019.03.020

Fay, P. A., Carlisle, J. D., Knapp, A. K., Blair, J. M., & Collins, S. L. (2000). Altering rainfall timing and quantity in a mesic grassland ecosystem: Design and performance of rainfall manipulation shelters. *Ecosystems*, *3*(3), 308–319.

Fazlioglu, F. (2019). Shifts in the timing of the early flowering in plants from a semi-arid ecoregion under climate change. *Biologia*, *74*(5), 437–446.

Feng, S., & Fu, Q. (2013). Expansion of global drylands under a warming climate. *Atmospheric Chemistry and Physics Discussions*, *13*(6), 14637–14665. https://doi.org/10.5194/acpd-13-14637-2013

Feulner, G., Rahmstorf, S., Levermann, A., & Volkwardt, S. (2013). *Why is the Northern Hemisphere warmer than the Southern Hemisphere?* EGU2013-8172.

Fitter, A., & Fitter, R. (2002). Rapid changes in flowering time in British plants. *Science*, *296*(5573), 1689–1691.

Fox, G. A. (1990). Drought and the Evolution of Flowering Time in Desert Annuals. *American Journal of Botany*, *77*(11), 1508–1518. https://doi.org/10.2307/2444763

Franks, S. J., Sim, S., & Weis, A. E. (2007). Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences*, *104*(4), 1278–1282. https://doi.org/10.1073/pnas.0608379104

Ge, Q., Wang, H., Rutishauser, T., & Dai, J. (2015). Phenological response to climate change in China: A meta-analysis. *Global Change Biology*, *21*(1), 265–274. https://doi.org/10.1111/gcb.12648

Gherardi, L. A., & Sala, O. E. (2013). Automated rainfall manipulation system: A reliable and inexpensive tool for ecologists. *Ecosphere*, *4*(2), 1–10. https://doi.org/10.1890/ES12-00371.1

Godoy, O., Richardson, D. M., Valladares, F., & Castro-Díez, P. (2009). Flowering phenology of invasive alien plant species compared with native species in three Mediterranean-type ecosystems. *Annals of Botany*, *103*(3), 485–494. https://doi.org/10.1093/aob/mcn232

Greve, P., Roderick, M. L., Ukkola, A. M., & Wada, Y. (2019). The aridity Index under global warming. *Environmental Research Letters*, *14*(12), 124006. https://doi.org/10.1088/1748-9326/ab5046

Günster, A. (1994a). Seed bank dynamics, longevity, viability and predation of seeds of serotinous plants in the central Namib Desert. 11. *Journal of Arid Environments, 28*,195-205.

Günster, A. (1994b). Variability in life history parameters of four serotinous plants in the Namib Desert. *Vegetatio*, *114*(2), 149–160. https://doi.org/10.1007/BF00048394

Hänel, S., & Tielbörger, K. (2015). Phenotypic response of plants to simulated climate change in a long-term rain-manipulation experiment: A multi-species study. *Oecologia*, *177*(4), 1015–1024.

Harris, I., Osborn, T. J., Jones, P., & Lister, D. (2020). Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific Data*, *7*(1), Article 1. https://doi.org/10.1038/s41597-020-0453-3

Hegazy, A. K., Kabiel, H. F., Al-Rowaily, S. L., Lovett-Doust, L., & Borki, A. E.-N. S. A. (2017). Plant communities and reproductive phenology in mountainous regions of northern Libya. *Journal of Forestry Research*, *28*(4), 741–761. https://doi.org/10.1007/s11676-016-0345-8

Heschel, M. S., Sultan, S. E., Glover, S., & Sloan, D. (2004). Population Differentiation and Plastic Responses to Drought Stress in the Generalist Annual *Polygonum persicaria*. *International Journal of Plant Sciences*, *165*(5), 817–824. https://doi.org/10.1086/421477

Higgins, J. P., Thomas, J., Chandler, J., Cumpston, M., Li, T., Page, M. J., & Welch, V. A. (2019). *Cochrane handbook for systematic reviews of interventions*. John Wiley & Sons.

Howell, A., Winkler, D. E., Phillips, M. L., McNellis, B., & Reed, S. C. (2020). Experimental Warming Changes Phenology and Shortens Growing Season of the Dominant Invasive Plant *Bromus tectorum* (Cheatgrass). *Frontiers in Plant Science*, *11*. https://www.frontiersin.org/articles/10.3389/fpls.2020.570001

https://www.fao.org/. (n.d.). *Rainfall and evaporation*. Retrieved March 31, 2023, from https://www.fao.org/3/r4082e/r4082e05.htm

Huang, Dai, J., Wang, W., Li, J., Feng, C., & Du, J. (2020). Phenological changes in herbaceous plants in China's grasslands and their responses to climate change: A meta-analysis. *International Journal of Biometeorology*, *64*(11), 1865–1876. https://doi.org/10.1007/s00484-020-01974-1

Huang, Li, Y., Fu, C., Chen, F., Fu, Q., Dai, A., Shinoda, M., Ma, Z., Guo, W., Li, Z., Zhang, L., Liu, Y., Yu, H., He, Y., Xie, Y., Guan, X., Ji, M., Lin, L., Wang, S., Yan, H., & Wang, G. (2017). Dryland climate change: Recent progress and challenges. *Reviews of Geophysics*, *55*(3), 719–778. https://doi.org/10.1002/2016RG000550

Huang, Yu, Guan, Wang, & Guo. (2016). Accelerated dryland expansion under climate change. *Nature Climate Change*, *6*(2), 166–171. https://doi.org/10.1038/nclimate2837

Hulme, M. (1996). Recent Climatic Change in the World's Drylands. *Geophysical Research Letters*, *23*(1), 61–64. https://doi.org/10.1029/95GL03586

Hunter, A. F., & Aarssen, L. W. (1988). Plants Helping Plants. *BioScience*, *38*(1), 34–40. https://doi.org/10.2307/1310644

Ibáñez, I., Primack, R. B., Miller-Rushing, A. J., Ellwood, E., Higuchi, H., Lee, S. D., Kobori, H., & Silander, J. A. (2010). Forecasting phenology under global warming. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1555), 3247–3260.

Jiang. (2021). Trends in Flowering Phenology of Herbaceous Plants and Its Response to Precipitation and Snow Cover on the Qinghai—Tibetan Plateau from 1983 to 2017. *Sustainability*, *13*(14), 7640. https://doi.org/10.3390/su13147640

Jiang, Y., Li, B., Yuan, Y., Sun, Q., Zhang, T., Liu, Y., Li, Y., & Li, R. (2021). Divergent shifts in flowering phenology of herbaceous plants on the warming Qinghai–Tibetan plateau. *Agricultural and Forest Meteorology*, *307*, 108502. https://doi.org/10.1016/j.agrformet.2021.108502

Jones, C. A., & Daehler, C. C. (2018). Herbarium specimens can reveal impacts of climate change on plant phenology; a review of methods and applications. *PeerJ*, *6*, e4576.

Joubert, D. F., Rothauge, A., & Smit, G. N. (2008). A conceptual model of vegetation dynamics in the semiarid Highland savanna of Namibia, with particular reference to bush thickening by *Acacia mellifera*. *Journal of Arid Environments*, *72*(12), 2201–2210. https://doi.org/10.1016/j.jaridenv.2008.07.004

Kamenetsky, R., Peterson, R. L., Melville, L. H., Machado, C. F., & Bewley, J. D. (2005). Seasonal adaptations of the tuberous roots of *Ranunculus asiaticus* to desiccation and resurrection by changes in cell structure and protein content. *New Phytologist*, *166*(1), 193–204. https://doi.org/10.1111/j.1469-8137.2004.01306.x

Kamotho, G. N., Mathenge, P. W., Muasya, R. M., & Dulloo, M. E. (2013). Effects of Packaging and Storage Conditions on Quality of Spider Plant (*Cleome gynandra* L.) Seed. *African Journal of Food, Agriculture, Nutrition and Development*, *13*(5), Article 5. https://doi.org/10.4314/ajfand.v13i5

Kang, S. M., Seager, R., Frierson, D. M. W., & Liu, X. (2015). Croll revisited: Why is the northern hemisphere warmer than the southern hemisphere? *Climate Dynamics*, *44*(5), 1457–1472. https://doi.org/10.1007/s00382-014-2147-z

Kangombe, F., Indongo, Mbango, & Kwembeya, E. (2016). Ethnobotanical study of medicinal plants in Omusati region, Namibia. *Proceedings of the National Research Symposium, Windhoek 23-25 September 2015.*

Kehrberger, S., & Holzschuh, A. (2019a). How does timing of flowering affect competition for pollinators, flower visitation and seed set in an early spring grassland plant? *Scientific Reports*, *9*(1), Article 1. https://doi.org/10.1038/s41598-019-51916-0

Kehrberger, S., & Holzschuh, A. (2019b). Warmer temperatures advance flowering in a spring plant more strongly than emergence of two solitary spring bee species. *PLOS ONE*, *14*(6), e0218824. https://doi.org/10.1371/journal.pone.0218824

Kettler, T., Doran, J. W., & Gilbert, T. (2001). Simplified method for soil particle-size determination to accompany soil-quality analyses. *Soil Science Society of America Journal*, *65*(3), 849–852.

Kigel, J., Konsens, I., Rosen, N., Rotem, G., Kon, A., & Fragman-Sapir, O. (2011). Relationships Between Flowering Time and Rainfall Gradients Across Mediterranean-Desert Transects. *Israel Journal of Ecology and Evolution*, *57*(1–2), 91–109. https://doi.org/10.1560/IJEE.57.1-2.91

Klaassen, E., & Kwembeya, E. (2013). *A checklist of Namibian indigenous and naturalised plants*. 597.

Knapp, A. K., Avolio, M. L., Beier, C., Carroll, C. J. W., Collins, S. L., Dukes, J. S., Fraser, L. H., Griffin-Nolan, R. J., Hoover, D. L., Jentsch, A., Loik, M. E., Phillips, R. P., Post, A. K., Sala, O. E., Slette, I. J., Yahdjian, L., & Smith, M. D. (2017). Pushing precipitation to the extremes in distributed experiments: Recommendations for simulating wet and dry years. *Global Change Biology*, *23*(5), 1774–1782. https://doi.org/10.1111/gcb.13504

Knapp, A. K., Hoover, D. L., Wilcox, K. R., Avolio, M. L., Koerner, S. E., La Pierre, K. J., Loik, M. E., Luo, Y., Sala, O. E., & Smith, M. D. (2015). Characterizing differences in precipitation regimes of extreme wet and dry years: Implications for climate change experiments. *Global Change Biology*, *21*(7), 2624–2633. https://doi.org/10.1111/gcb.12888

Körner, C., & Basler, D. (2010). Phenology under global warming. *Science*, *327*(5972), 1461–1462.

Kwarteng, A. O., Abogoom, J., Adu Amoah, R., Nyadanu, D., Ghunney, T., Nyam, K. C., Ziyaaba, J. Z., Danso, E. O., Asiedu, D. D., & Whyte, T. (2018). Current knowledge and breeding perspectives for the spider plant (*Cleome gynandra* L.): A potential for enhanced breeding of the plant in Africa. *Genetic Resources and Crop Evolution*, *65*(5), 1529–1550. https://doi.org/10.1007/s10722-018-0626-5

Kwembeya, E. G. (2021). Tracking biological footprints of climate change using flowering phenology of the geophytes: *Pancratium tenuifolium* and *Scadoxus multiflorus*. *International Journal of Biometeorology*. https://doi.org/10.1007/s00484-020-02052-2

Kwembeya, E. G., & Pazvakawambwa, L. (2019). The changing flowering phenology of *Crinum* lilies in arid and semi-arid regions: Implications for phenological responses to climate change. *Biologia*, 1–10.

Laity, J. J. (2009). *Deserts and desert environments* (Vol. 3). John Wiley & Sons.

Lang, P. L. M., Willems, F. M., Scheepens, J. F., Burbano, H. A., & Bossdorf, O. (2019). Using herbaria to study global environmental change. *New Phytologist*, *221*(1), 110–122. https://doi.org/10.1111/nph.15401

Lavoie, C. (2013). Biological collections in an ever changing world: Herbaria as tools for biogeographical and environmental studies. *Perspectives in Plant Ecology, Evolution and Systematics*, *15*(1), 68–76. https://doi.org/10.1016/j.ppees.2012.10.002

Lavoie, C., & Lachance, D. (2006). A new herbarium-based method for reconstructing the phenology of plant species across large areas. *American Journal of Botany*, *93*(4), 512–516. https://doi.org/10.3732/ajb.93.4.512

Lázaro, R., Rodrigo, F. S., Gutiérrez, L., Domingo, F., & Puigdefábregas, J. (2001). Analysis of a 30-year rainfall record (1967–1997) in semi–arid SE Spain for implications on vegetation. *Journal of Arid Environments*, *48*(3), 373–395. https://doi.org/10.1006/jare.2000.0755

Lesica, P., & Kittelson, P. (2010). Precipitation and temperature are associated with advanced flowering phenology in a semi-arid grassland. *Journal of Arid Environments*, *74*(9), 1013–1017.

Li, Han, G., Wang, Z., Zhao, M., Wang, Z., & Zhao, H. (2014). Influences of warming and nitrogen addition on plant reproductive phenology in Inner Mongolia desert steppe. *Chinese Journal of Ecology*, *33*, 849–856.

Liu, H., Lu, C., Wang, S., Ren, F., & Wang, H. (2021). Climate warming extends growing season but not reproductive phase of terrestrial plants. *Global Ecology and Biogeography*, *30*(5), 950–960. https://doi.org/10.1111/geb.13269

Lizaso, J. I., Ruiz-Ramos, M., Rodríguez, L., Gabaldon-Leal, C., Oliveira, J. A., Lorite, I. J., Sánchez, D., García, E., & Rodríguez, A. (2018). Impact of high temperatures in maize: Phenology and yield components. *Field Crops Research*, *216*, 129–140. https://doi.org/10.1016/j.fcr.2017.11.013

Llorens, L., & Peñuelas, J. (2005). Experimental Evidence of Future Drier and Warmer Conditions Affecting Flowering of Two Co-occurring Mediterranean Shrubs. *International Journal of Plant Sciences*, *166*(2), 235–245. https://doi.org/10.1086/427480

Long, S., Fatoyinbo, T. E., & Policelli, F. (2014). Flood extent mapping for Namibia using change detection and thresholding with SAR. *Environmental Research Letters*, *9*(3), 035002. https://doi.org/10.1088/1748-9326/9/3/035002

Louw, E.-L., Hoffman, E. W., Theron, K. I., & Midgley, S. J. E. (2015). Physiological and phenological responses of *Protea* 'Pink Ice' to elevated temperatures. *South African Journal of Botany*, *99*, 93–102. https://doi.org/10.1016/j.sajb.2015.04.002

Love, N. L. R., & Mazer, S. J. (2021). Region-specific phenological sensitivities and rates of climate warming generate divergent temporal shifts in flowering date across a species' range. *American Journal of Botany*, *108*(10), 1873–1888. https://doi.org/10.1002/ajb2.1748

Lu, X., Wang, L., Pan, M., Kaseke, K. F., & Li, B. (2016). A multi-scale analysis of Namibian rainfall over the recent decade – comparing TMPA satellite estimates and ground observations. *Journal of Hydrology: Regional Studies*, *8*, 59–68. https://doi.org/10.1016/j.ejrh.2016.07.003

Lüdecke, M. D. (2021). *Package 'sjPlot.'*

Ma, T., & Zhou, C. (2012). Climate-associated changes in spring plant phenology in China. *International Journal of Biometeorology*, *56*(2), 269–275. https://doi.org/10.1007/s00484-011-0428-3

MacGillivray, F., Hudson, I. L., & Lowe, A. J. (2010). Herbarium collections and photographic images: Alternative data sources for phenological research. In *Phenological research* (pp. 425–461). Springer.

Maestre, F. T., Benito, B. M., Berdugo, M., Concostrina-Zubiri, L., Delgado-Baquerizo, M., Eldridge, D. J., Guirado, E., Gross, N., Kéfi, S., Le Bagousse-Pinguet, Y., Ochoa-Hueso, R., & Soliveres, S. (2021). Biogeography of global drylands. *New Phytologist*, *231*(2), 540–558. https://doi.org/10.1111/nph.17395

Maestre, F. T., Eldridge, D. J., Soliveres, S., Kéfi, S., Delgado-Baquerizo, M., Bowker, M. A., García-Palacios, P., Gaitán, J., Gallardo, A., Lázaro, R., & Berdugo, M. (2016). Structure and functioning of dryland ecosystems in a changing world. *Annual Review of Ecology, Evolution, and Systematics*, *47*, 215–237. https://doi.org/10.1146/annurev-ecolsys-121415-032311

Maestre, F. T., Salguero-Gómez, R., & Quero, J. L. (2012). It is getting hotter in here: Determining and projecting the impacts of global environmental change on drylands. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1606), 3062–3075. https://doi.org/10.1098/rstb.2011.0323

Majeran, W., & van Wijk, K. J. (2009). Cell-type-specific differentiation of chloroplasts in C4 plants. *Trends in Plant Science*, *14*(2), 100–109. https://doi.org/10.1016/j.tplants.2008.11.006

Mamtimin, B., Et-Tantawi, A. M. M., Schaefer, D., Meixner, F. X., & Domroes, M. (2011). Recent trends of temperature change under hot and cold desert climates: Comparing the Sahara (Libya) and Central Asia (Xinjiang, China). *Journal of Arid Environments*, *75*(11), 1105–1113. https://doi.org/10.1016/j.jaridenv.2011.06.007

Mason, S. J., & Joubert, A. M. (1997). Simulated Changes in Extreme Rainfall Over Southern Africa. *International Journal of Climatology*, *17*(3), 291–301. https://doi.org/10.1002/(SICI)1097-0088(19970315)17:3<291::AID-JOC120>3.0.CO;2-1

Matthews, E. R., & Mazer, S. J. (2016). Historical changes in flowering phenology are governed by temperature x precipitation interactions in a widespread perennial herb in western North America. *New Phytologist*, *210*(1), 157–167. https://doi.org/10.1111/nph.13751

Mazer, S. J., Gerst, K. L., Matthews, E. R., & Evenden, A. (2015). Species-specific phenological responses to winter temperature and precipitation in a water-limited ecosystem. *Ecosphere*, *6*(6), 27. https://doi.org/10.1890/es14-00433.1

Mazer, S. J., Travers, S. E., Cook, B. I., Davies, T. J., Bolmgren, K., Kraft, N. J. B., Salamin, N., & Inouye, D. W. (2013). Flowering date of taxonomic families predicts phenological sensitivity to temperature: Implications for forecasting the effects of climate change on unstudied taxa. *American Journal of Botany*, *100*(7), 1381–1397. https://doi.org/10.3732/ajb.1200455

McGinnies, W. (1979). General description of desert. *Arid Land Ecosystems: Volume 1: Structure, Functioning and Management*, *1*, 5.

Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the disruption of plant–pollinator interactions. *Ecology Letters*, *10*(8), 710–717. https://doi.org/10.1111/j.1461-0248.2007.01061.x

Mendelsohn, J., Jarvis, A, Roberts, C, & Robertson, T. (2002). *Atlas of Namibia: A portrait of the land and its people*. New Africa Books (Pty) Ltd.

Menzel, A., & Fabian, P. (1999). Growing season extended in Europe. *Nature*, *397*(6721), 659. https://doi.org/10.1038/17709

Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F. M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A., Wielgolaski, F., Zach, S., & Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, *12*(10), 1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Miles, L., Newton, A. C., DeFries, R. S., Ravilious, C., May, I., Blyth, S., Kapos, V., & Gordon, J. E. (2006). A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, *33*(3), 491–505.

Miller, W., & Miller, D. (1987). A micro-pipette method for soil mechanical analysis. *Communications in Soil Science and Plant Analysis*, *18*(1), 1–15.

Miller-Rushing, A. J., & Primack, R. B. (2008). Global Warming and Flowering Times in Thoreau's Concord: A Community Perspective. *Ecology*, *89*(2), 332–341. https://doi.org/10.1890/07-0068.1

Ministry of Environment & Tourism of Namibia. (2011). National Policy on Climate Change for Namibia. *Grantham Research Institute on Climate Change and the Environment*. http://www.lse.ac.uk/GranthamInstitute/law/national-policy-on-climate-change-for-namibia/

Mishra, S., Moharana, S., & Dash, M. (2011). Review on Cleome gynandra. *International Journal of Research in Pharmacy and Chemistry*, *1*(3), 681–689.

Mo, F., Zhang, J., Wang, J., Cheng, Z.-G., Sun, G.-J., Ren, H.-X., Zhao, X.-Z., Cheruiyot, W. K., Kavagi, L., Wang, J.-Y., & Xiong, Y.-C. (2017). Phenological evidence from China to address rapid shifts in global flowering times with recent climate change. *Agricultural and Forest Meteorology*, *246*, 22–30. https://doi.org/10.1016/j.agrformet.2017.06.004

Mohan, J. E., Wadgymar, S. M., Winkler, D. E., Anderson, J. T., Frankson, P. T., Hannifin, R., Benavides, K., Kueppers, L. M., & Melillo, J. M. (2019). Chapter 3 - Plant reproductive fitness and phenology responses to climate warming: Results from native populations, communities, and ecosystems. In J. E. Mohan (Ed.), *Ecosystem Consequences of Soil Warming* (pp. 61–102). Academic Press. https://doi.org/10.1016/B978-0-12-813493-1.00004-1

Moore, L. M., & Lauenroth, W. K. (2017). Differential effects of temperature and precipitation on early- vs. Late-flowering species. *Ecosphere*, *8*(5), e01819. https://doi.org/10.1002/ecs2.1819

Munguía-Rosas, M. A., Ollerton, J., Parra-Tabla, V., & De-Nova, J. A. (2011). Meta-analysis of phenotypic selection on flowering phenology suggests that early flowering plants are favoured. *Ecology Letters*, *14*(5), 511–521.

Munson, S. M., & Long, A. L. (2017). Climate drives shifts in grass reproductive phenology across the western USA. *New Phytologist*, *213*(4), 1945–1955.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Namibia Meteorological Service. (2020). *Namibia Meteorological Service*. http://www.meteona.com/

National Herbarium of Namibia. (1994). *Guide for collecting plants*. http://www.nbri.org.na/sections/herbarium

Nord, E. A., & Lynch, J. P. (2009). Plant phenology: A critical controller of soil resource acquisition. *Journal of Experimental Botany*, *60*(7), 1927–1937. https://doi.org/10.1093/jxb/erp018

Noy-Meir, I. (1973). Desert Ecosystems: Environment and Producers. *Annual Review of Ecology and Systematics*, *4*(1), 25–51. https://doi.org/10.1146/annurev.es.04.110173.000325

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*(3), 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Oshingi, S., Fekadu, F. D., Emmanuel, O. O., Traud, W., & Mary, O. A.-O. (2019). Cleome gynandra L. origin, taxonomy and morphology: A review. *African Journal of Agricultural Research*, *14*(32), 1568–1583.

Pachauri, Mayer, L., & Intergovernmental Panel on Climate Change (Eds.). (2015). *Climate change 2014: Synthesis report*. Intergovernmental Panel on Climate Change.

Park, D. S., Breckheimer, I., Williams, A. C., Law, E., Ellison, A. M., & Davis, C. C. (2018). Herbarium specimens reveal substantial and unexpected variation in phenological sensitivity across the eastern United States. *Philosophical Transactions of the Royal Society B*, *374*(1763), 20170394.

Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, *13*(9), 1860–1872. https://doi.org/10.1111/j.1365-2486.2007.01404.x

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

Pearson, K. D. (2019a). A new method and insights for estimating phenological events from herbarium specimens. *Applications in Plant Sciences*, *7*(3), e01224. https://doi.org/10.1002/aps3.1224

Pearson, K. D. (2019b). Spring- and fall-flowering species show diverging phenological responses to climate in the Southeast USA. *International Journal of Biometeorology*. https://doi.org/10.1007/s00484-019-01679-0

Peguero-Pina, J. J., Vilagrosa, A., Alonso-Forn, D., Ferrio, J. P., Sancho-Knapik, D., & Gil-Pelegrín, E. (2020). Living in Drylands: Functional Adaptations of Trees and Shrubs to Cope with High Temperatures and Water Scarcity. *Forests*, *11*(10), Article 10. https://doi.org/10.3390/f11101028

Peñuelas, J., Filella, I., & Comas, P. (2002). Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology*, *8*(6), 531–544. https://doi.org/10.1046/j.1365-2486.2002.00489.x

Peñuelas, J., Filella, I., Zhang, X., Llorens, L., Ogaya, R., Lloret, F., Comas, P., Estiarte, M., & Terradas, J. (2004). Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytologist*, *161*(3), 837–846. https://doi.org/10.1111/j.1469-8137.2004.01003.x

Polgar, C. A., & Primack, R. B. (2011). Leaf-out phenology of temperate woody plants: From trees to ecosystems. *New Phytologist*, *191*(4), 926–941. https://doi.org/10.1111/j.1469-8137.2011.03803.x

Poulter, B., Frank, D., Ciais, P., Myneni, R. B., Andela, N., Bi, J., Broquet, G., Canadell, J. G., Chevallier, F., Liu, Y. Y., Running, S. W., Sitch, S., & van der Werf, G. R. (2014). Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature*, *509*(7502), 600–603. https://doi.org/10.1038/nature13376

Prăvălie, R. (2016). Drylands extent and environmental issues. A global approach. *Earth-Science Reviews*, *161*, 259–278. https://doi.org/10.1016/j.earscirev.2016.08.003

Primack, D., Imbres, C., Primack, R. B., Miller-Rushing, A. J., & Tredici, P. D. (2004). Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany*, *91*(8), 1260–1264. https://doi.org/10.3732/ajb.91.8.1260

Quintana, D. S. (2015). From pre-registration to publication: A non-technical primer for conducting a meta-analysis to synthesize correlational data. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.01549

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. *https://www.R-project.org/*

Rafferty, N. E., Bertelsen, C. D., & Bronstein, J. L. (2016). Later flowering is associated with a compressed flowering season and reduced reproductive output in an early season floral resource. *Oikos*, *125*(6), 821–828. https://doi.org/10.1111/oik.02573

Rafferty, N. E., & Nabity, P. D. (2017). A global test for phylogenetic signal in shifts in flowering time under climate change. *Journal of Ecology*, *105*(3), 627–633. https://doi.org/10.1111/1365-2745.12701

Raju, A. J. S., & Rani, D. S. (2016). *Reproductive ecology of Cleome gynandra and Cleome viscosa (Capparaceae)*. 14.

Reyer, C. P. O., Leuzinger, S., Rammig, A., Wolf, A., Bartholomeus, R. P., Bonfante, A., de Lorenzi, F., Dury, M., Gloning, P., Abou Jaoudé, R., Klein, T., Kuster, T. M., Martins, M., Niedrist, G., Riccardi, M., Wohlfahrt, G., de Angelis, P., de Dato, G., François, L., Menzel, A., & Pereira, M. (2013). A plant's perspective of extremes: Terrestrial plant responses to changing climatic variability. *Global Change Biology*, 19(1), 75–89. https://doi.org/10.1111/gcb.12023

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, *421*(6918), 57–60. https://doi.org/10.1038/nature01333

Rowell, M. (2000). Changing a laboratory method: An example concerning particle size analysis. *Agricola*, *11*, 61–65.

Sandmeier, M., & Dajoz, I. (2000). Flowering Phenology and Gender Variation in *Pennisetum typhoides*. *International Journal of Plant Sciences*, *161*(1), 81–87. https://doi.org/10.1086/314239

Santos Neves, S. P., Pedreira de Miranda, L. d'Afonseca, Rossatto, D. R., & Funch, L. S. (2017). The roles of rainfall, soil properties, and species traits in flowering phenology along a savanna-seasonally dry tropical forest gradient. *Brazilian Journal of Botany*, *40*(3), 665–679. https://doi.org/10.1007/s40415-017-0368-1

Schuchardt, M. A., Berauer, B. J., von Heßberg, A., Wilfahrt, P., & Jentsch, A. (2021). Drought effects on montane grasslands nullify benefits of advanced flowering phenology due to warming. *Ecosphere*, *12*(7), e03661. https://doi.org/10.1002/ecs2.3661

Schwartz, M. D., & Reiter, B. E. (2000). Changes in North American spring. *International Journal of Climatology*, *20*(8), 929–932. https://doi.org/10.1002/1097-0088(20000630)20:8<929::AID-JOC557>3.0.CO;2-5

Schwinning, S., & Sala, O. E. (2004). Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia*, *141*(2), 211–220. https://doi.org/10.1007/s00442-004-1520-8

Seghieri, J., Carreau, J., Boulain, N., De Rosnay, P., Arjounin, M., & Timouk, F. (2012). Is water availability really the main environmental factor controlling the phenology of woody vegetation in the central Sahel? *Plant Ecology*, *213*(5), 861–870. https://doi.org/10.1007/s11258-012-0048-y

Segrestin, J., Bernard-Verdier, M., Violle, C., Richarte, J., Navas, M.-L., & Garnier, E. (2018). When is the best time to flower and disperse? A comparative analysis of plant reproductive phenology in the Mediterranean. *Functional Ecology*, *32*(7), 1770–1783. https://doi.org/10.1111/1365-2435.13098

Sekhwela, M. B. M., & Yates, D. J. (2007). A phenological study of dominant acacia tree species in areas with different rainfall regimes in the Kalahari of Botswana. *Journal of Arid Environments*, *70*(1), 1–17. https://doi.org/10.1016/j.jaridenv.2006.12.006

Seleiman, M. F., Al-Suhaibani, N., Ali, N., Akmal, M., Alotaibi, M., Refay, Y., Dindaroglu, T., Abdul-Wajid, H. H., & Battaglia, M. L. (2021). Drought Stress Impacts on Plants and Different Approaches to Alleviate Its Adverse Effects. *Plants*, *10*(2), 259. https://doi.org/10.3390/plants10020259

Shaamhula, L. V., Smit, H. A. P., & van der Merwe, J. (2021). Community responses to the annual flooding (efundja) in the Cuvelai-Etosha basin, Northern Namibia. *International Journal of Disaster Risk Reduction*, *61*, 102372. https://doi.org/10.1016/j.ijdrr.2021.102372

Sherry, R. A., Zhou, X., Gu, S., Arnone, J. A., Schimel, D. S., Verburg, P. S., Wallace, L. L., & Luo, Y. (2007). Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences*, *104*(1), 198–202. https://doi.org/10.1073/pnas.0605642104

Shikangalah, R. N., & Mapani, B. (2019). Precipitation variations and shifts over time: Implication on Windhoek city water supply. *Physics and Chemistry of the Earth, Parts A/B/C*, *112*, 103–112. https://doi.org/10.1016/j.pce.2019.03.005

Skakun, S., Kussul, N., Shelestov, A., & Kussul, O. (2014). Flood Hazard and Flood Risk Assessment Using a Time Series of Satellite Images: A Case Study in Namibia. *Risk Analysis*, *34*(8), 1521–1537. https://doi.org/10.1111/risa.12156

Song, Z., Du, Y., Primack, R. B., Miller-Rushing, A. J., Ye, W., & Huang, Z. (2021). Surprising roles of climate in regulating flowering phenology in a subtropical ecosystem. *Ecography*, *44*(9), 1379–1390. https://doi.org/10.1111/ecog.05629

Sorensen, L. (2007). A Spatial Analysis Approach to the Global Delineation of Dryland Areas of Relevance to the CBD Programme of Work on Dry and Sub-Humid Lands. *UNEP-WCMC: Cambridge, UK.*

Sparks, T. H., & Carey, P. D. (1995). The Responses of Species to Climate Over Two Centuries: An Analysis of the Marsham Phenological Record, 1736-1947. *Journal of Ecology*, *83*(2), 321–329. JSTOR. https://doi.org/10.2307/2261570

Spear, Zaroug, M. A. H., Daron, J. D., Ziervogel, G., Angula, M. N., Haimbili, E. N., Hegga, S. S., Baudoin, M.-A., New, M., Kunamwene, I., Togarepi, C., & Davies, J. E. (2018). *Vulnerability and responses to climate change in drylands: The case of Namibia*. 41.

Stuble, K. L., Bennion, L. D., & Kuebbing, S. E. (2021). Plant phenological responses to experimental warming—A synthesis. *Global Change Biology*, *27*(17), 4110–4124. https://doi.org/10.1111/gcb.15685

Sultan, S. E. (2003). Phenotypic plasticity in plants: A case study in ecological development. *Evolution and Development*, *5*(1), 25–33. https://doi.org/10.1046/j.1525-142X.2003.03005.x

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, *65*(1), 13–21. https://doi.org/10.1007/s00265-010-1037-6

Takkis, K., Tscheulin, T., & Petanidou, T. (2018). Differential Effects of Climate Warming on the Nectar Secretion of Early- and Late-Flowering Mediterranean Plants. *Frontiers in Plant Science*, *9*. https://www.frontiersin.org/articles/10.3389/fpls.2018.00874

Thanos, C. A. (2004). *Bradychory—The coining of a new term*. Proceedings 10th medecos conference, Millpress, Rotterdam.

Thomson, J. D. (1978). Effects of Stand Composition on Insect Visitation in Two-Species Mixtures of *Hieracium*. *The American Midland Naturalist*, *100*(2), 431–440. https://doi.org/10.2307/2424843

Thuiller, W., Midgley, G. F., Hughes, G. O., Bomhard, B., Drew, G., Rutherford, M. C., & Woodward, F. I. (2006). Endemic species and ecosystem sensitivity to climate change in Namibia. *Global Change Biology*, *12*(5), 759–776. https://doi.org/10.1111/j.1365-2486.2006.01140.x

Tooke, F., & Battey, N. H. (2010). Temperate flowering phenology. *Journal of Experimental Botany*, *61*(11), 2853–2862. https://doi.org/10.1093/jxb/erq165

Uyi, O. O., & Igbinosa, I. B. (2010). *The status of Chromolaena odorata and its biocontrol in West Africa*. 1–2.

Valencia, E., Méndez, M., Saavedra, N., & Maestre, F. T. (2016). Plant size and leaf area influence phenological and reproductive responses to warming in semiarid Mediterranean species. *Perspectives in Plant Ecology, Evolution and Systematics*, *21*, 31–40. https://doi.org/10.1016/j.ppees.2016.05.003

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*(3), 1–48. https://doi.org/10.18637/jss.v036.i03

Viechtbauer, W., & Viechtbauer, M. W. (2015). Package 'metafor.' *The Comprehensive R Archive Network. Package 'Metafor'. Http://Cran. r-Project. Org/Web/Packages/Metafor/Metafor. Pdf.*

Vitasse, Y., & Basler, D. (2013). What role for photoperiod in the bud burst phenology of European beech. *European Journal of Forest Research*, *132*(1), 1–8. https://doi.org/10.1007/s10342-012-0661-2

Volis, S. (2009). Plasticity, its cost, and phenotypic selection under water and nutrient stress in two annual grasses. *Biological Journal of the Linnean Society*, *97*(3), 581–593. https://doi.org/10.1111/j.1095-8312.2009.01239.x

Volis, S., Mendlinger, S., & Ward, D. (2002). Differentiation in populations of *Hordeum spontaneum* along a gradient of environmental productivity and predictability: Life history and local adaptation. *Biological Journal of the Linnean Society*, *77*(4), 479–490. https://doi.org/10.1046/j.1095-8312.2002.00120.x

Voznesenskaya, E. V., Koteyeva, N. K., Cousins, A., & Edwards, G. E. (2018). Diversity in structure and forms of carbon assimilation in photosynthetic organs in *Cleome* (Cleomaceae). *Functional Plant Biology*, *45*(10), 983–999. https://doi.org/10.1071/FP17323

White, & Nackoney. (2003). Drylands, people, and ecosystem goods and services: A web-based geospatial analysis (PDF version). *World Resources Institute ([Available at: Http://Pdf. Wri. Org/Drylands. Pdf Accessed on 30/01/2012]).*

Willis, C. G., Ruhfel, B., Primack, R. B., Miller-Rushing, A. J., & Davis, C. C. (2008a). Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences*, *105*(44), 17029–17033. https://doi.org/10.1073/pnas.0806446105

Willis, Ellwood, Primack, Davis, Pearson, Gallinat, A. S., Yost, J. M., Nelson, G., Mazer, S. J., Rossington, N. L., Sparks, T. H., & Soltis, P. S. (2017). Old Plants, New Tricks: Phenological Research Using Herbarium Specimens. *Trends in Ecology & Evolution*, *32*(7), 531–546. https://doi.org/10.1016/j.tree.2017.03.015

Willis, Ruhfel, Primack, Miller-Rushing, & Davis. (2008b). Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences*, *105*(44), 17029–17033. https://doi.org/10.1073/pnas.0806446105

Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers, S. E., Pau, S., Regetz, J., Davies, T. J., Kraft, N. J. B., Ault, T. R., Bolmgren, K., Mazer, S. J., McCabe, G. J., McGill, B. J., Parmesan, C., Salamin, N., Schwartz, M. D., & Cleland, E. E. (2012). Warming experiments underpredict plant phenological responses to climate change. *Nature*, *485*(7399), 494–497. https://doi.org/10.1038/nature11014

Wright, S. I., Kalisz, S., & Slotte, T. (2013). Evolutionary consequences of self-fertilization in plants. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1760), 20130133. https://doi.org/10.1098/rspb.2013.0133

Wu, Z., Dijkstra, P., Koch, G. W., Peñuelas, J., & Hungate, B. A. (2011). Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. *Global Change Biology*, *17*(2), 927–942. https://doi.org/10.1111/j.1365-2486.2010.02302.x

Yahdjian, L., & Sala, O. E. (2002). A rainout shelter design for intercepting different amounts of rainfall. *Oecologia*, *133*(2), 95–101. https://doi.org/10.1007/s00442-002-1024-3

Zhang, X., Tarpley, D., & Sullivan, J. T. (2007). Diverse responses of vegetation phenology to a warming climate. *Geophysical Research Letters*, *34*(19). https://doi.org/10.1029/2007GL031447

Zhou, Z., Li, Y., Song, J., Ru, J., Lei, L., Zhong, M., Zheng, M., Zhang, A., Hui, D., & Wan, S. (2019). Growth controls over flowering phenology response to climate change in three temperate steppes along a precipitation gradient. *Agricultural and Forest Meteorology*, *274*, 51–60. https://doi.org/10.1016/j.agrformet.2019.04.011

APPENDIX A

SUPPLEMENTARY INFORMATION FOR CHAPTER 1

Table A1. Full univariate random effects meta-analysis models of flowering date responses to time series, temperature and precipitation assessed according to study type (herbarium phenology or field observation phenology), family and functional group.

The effect size, sample size (number of species-specific flowering phenology responses, n), p-value, citations (sample size, n) and the number of studies included in each model.

Model	Effect size	Sample size (n)	P-value	Citations (sample size, n)	Number of studies
Flowering date ~time series					
All data	-2.12	277	< 0.0001	Peñuelas et al., 2002 (23); Keatley et al., 2004 (4); Lesica & Kittleson, 2010 (32); Rafferty et al., 2015 (1); Moore & Lauenroth, 2017 (21); Munson & Long, 2017 (15); Fazlioglu,2019 (172); Kwembeya & Pazvakawambwa, 2019 (6); Kwembeya, 2020 (2); Love & Mazer, 2021 (1)	10
Herbarium phenology	-2.63	196	< 0.0001	Munson & Long, 2017 (15); Fazlioglu,2019 (172); Kwembeya & Pazvakawambwa, 2019 (6); Kwembeya, 2020 (2); Love & Mazer, 2021(1)	5
Field observation phenology	-0.88	81	< 0.0001	Peñuelas et al., 2002 (23); Keatley et al., 2004 (4); Lesica & Kittleson, 2010 (32); Rafferty et al., 2015 (1); Moore & Lauenroth, 2017 (21)	5
Plant family					
Asteraceae	-2.17	58	< 0.0001	Peñuelas et al., 2002 (1); Lesica & Kittleson, 2010 (4); Moore & Lauenroth, 2017 (5); Fazlioglu,2019 (48)	4
Poaceae	-3.91	35	< 0.0001	Moore & Lauenroth, 2017 (6); Munson & Long, 2017 (15); Fazlioglu,2019 (14)	3
Fabaceae	-1.66	17	< 0.0001	Peñuelas et al., 2002 (7); Keatley et al., 2004 (1);	4

Model	Effect size	Sample size (n)	P-value	Citations (sample size, n)	Number of studies
				Lesica & Kittleson, 2010 (2); Fazlioglu,2019 (7)	
Euphorbiaceae	-2.81	12	< 0.0001	Fazlioglu,2019 (12)	1
Boraginaceae	-2.07	10	0.0016	Lesica & Kittleson, 2010 (4); Fazlioglu,2019 (6)	2
Rosaceae	-2.23	8	< 0.0001	Peñuelas et al., 2002 (8)	1
Brassicaceae	-1.12	8	0.21	Lesica & Kittleson, 2010 (5); Moore & Lauenroth, 2017 (1); Fazlioglu,2019 (1); Love & Mazer, 2021 (1)	4
Scrophulariaceae	-2.08	8	< 0.0001	Lesica & Kittleson, 2010 (1); Fazlioglu,2019 (7)	2
Amaryllidaceae	-0.82	8	0.047	Kwembeya & Pazvakawambwa, 2019 (6); Kwembeya, 2020 (2)	2
Nyctaginaceae	-2.58	7	< 0.0001	Fazlioglu,2019 (7)	1
Polygonaceae	-2.59	7	< 0.0001	Moore & Lauenroth, 2017 (1); Fazlioglu,2019 (7)	2
Functional group					
Forb	-1.88	166	< 0.0001	Peñuelas et al., 2002 (4); Keatley et al., 2004 (4); Lesica & Kittleson, 2010 (32); Moore & Lauenroth, 2017 (7); Fazlioglu,2019 (110); Kwembeya & Pazvakawambwa, 2019 (6); Kwembeya, 2020 (2); Love & Mazer, 2021 (1)	8
Grass	-3.91	35	< 0.0001	Moore & Lauenroth, 2017 (6); Munson & Long, 2017 (15); Fazlioglu,2019 (14)	3
Shrub	-2.02	47	< 0.0001	Peñuelas et al., 2002 (5); Moore & Lauenroth, 2017 (4); Fazlioglu,2019 (38)	3
Tree	-1.86	20	< 0.0001	Peñuelas et al., 2002 (14); Rafferty et al., 2015 (1); Fazlioglu,2019 (5)	3

Model	Effect size	Sample size (n)	P-value	Citations (sample size, n)	Number of studies
Flowering date ~temperature					
All data	-2.83	71	< 0.0001	Peñuelas et al., 2002 (1); Crimmins et al., 2011 (26); Mazer et al., 2015 (3); Munson & Long, 2017 (15); Daru et al., 2019 (25); Love & Mazer, 2021 (1)	6
Herbarium phenology	-4.22	41	< 0.0001	Munson & Long, 2017 (15); Daru et al., 2019 (25); Love & Mazer, 2021 (1)	3
Field observation phenology	-0.95	30	< 0.0001	Peñuelas et al., 2002 (1); Crimmins et al., 2011 (26); Mazer et al., 2015 (3)	3
Plant family					
Proteaceae	-2.98	25	< 0.0001	Daru et al., 2019 (25)	1
Poaceae	-4.11	24	< 0.0001	Crimmins et al., 2011 (9); Munson & Long, 2017 (15)	2
Asteraceae	-0.85	7	0.00023	Crimmins et al., 2011 (6); Mazer et al., 2015 (1)	2
Functional group					
Forb	-1.24	14	< 0.0001	Crimmins et al., 2011 (12); Mazer et al., 2015 (1); Love & Mazer, 2021 (1)	3
Grass	-4.11	24	< 0.0001	Crimmins et al., 2011 (9); Munson & Long, 2017 (15)	2
Shrub	-2.51	29	< 0.0001	Peñuelas et al., 2002 (1); Crimmins et al., 2011 (5); Mazer et al., 2015 (1); Daru et al., 2019 (22)	4
Temperature variable					
Mean annual temperature	-5.91	16	< 0.0001	Munson & Long, 2017 (15); Love & Mazer, 2021 (1)	2
Mean monthly temperature	-2.78	54	< 0.0001	Crimmins et al., 2011 (26); Mazer et al., 2015 (3); Daru et al., 2019 (25)	3
Flowering date ~ precipitation					

Model	Effect size	Sample size (n)	P-value	Citations (sample size, n)	Number of studies
All data	-2.91	148	< 0.0001	Crimmins et al., 2011 (112); Mazer et al., 2015 (3); Daru et al., 2019 (25); Kwembeya & Pazvakawambwa, 2019 (6); Kwembeya 2020 (2)	5
Herbarium phenology	-2.61	33	< 0.0001	Daru et al., 2019 (25); Kwembeya & Pazvakawambwa, 2019 (6); Kwembeya 2020 (2)	3
Field observation phenology	-2.97	115	< 0.0001	Crimmins et al., 2011 (112); Mazer et al., 2015 (3)	2
Plant family					
Poaceae	-2.74	27	< 0.0001	Crimmins et al., 2011 (27)	1
Asteraceae	-3.05	25	< 0.0001	Crimmins et al., 2011 (24); Mazer et al., 2015 (3)	2
Proteaceae	-2.91	25	< 0.0001	Daru et al., 2019 (25)	1
Fabaceae	-3.04	9	< 0.0001	Crimmins et al., 2011 (9)	1
Amaryllidaceae	-1.21	8	< 0.0001	Kwembeya & Pazvakawambwa, 2019 (6); Kwembeya 2020 (2)	3
Functional group					
Forb	-2.98	66	< 0.0001	Crimmins et al., 2011 (54); Mazer et al., 2015 (3); Kwembeya & Pazvakawambwa, 2019 (6); Kwembeya, 2020 (2)	4
Grass	-2.74	27	< 0.0001	Crimmins et al., 2011 (27)	1
Shrub	-3.03	49	< 0.0001	Crimmins et al., 2011 (26); Mazer et al., 2015 (1); Daru et al., 2019 (22)	3
Precipitation variable					
total monthly precipitation	-2.97	115	< 0.0001	Crimmins et al., 2011 (112); Mazer et al., 2015 (3)	2

Model	Effect size	Sample size (n)	P-value	Citations (sample size, n)	Number of studies
mean seasonal precipitation	-1.21	8	< 0.0001	Kwembeya & Pazvakawambwa, 2019 (6); Kwembeya 2020 (2)	2
mean monthly precipitation	-2.91	25	< 0.0001	Daru et al., 2019 (25)	1

APPENDIX B

SUPPLEMENTARY INFORMATION FOR CHAPTER 2

Table B1. The taxa, number of specimens (sample) and different categorical traits of the herbaceous plants examined for flowering phenology trends and responsiveness to climate change.

Species	Sample size (n)	Life form	Serotiny	Family
Acrotome fleckii (Gürke) Launert	65	Annual	Non-serotinous	Lamiaceae
Acrotome inflata Benth.	48	Annual	Non-serotinous	Lamiaceae
Aptosimum lineare Marloth & Engl.	101	Perennial	Serotinous	Scrophulariaceae
Blepharis grossa (Nees) T.Anderson	43	Annual	Non-serotinous	Acanthaceae
Cleome angustifolia Forssk.	103	Annual	Non-serotinous	Cleomaceae
Cleome elegantissima Briq.	60	Annual	Non-serotinous	Cleomaceae
Cleome foliosa Hook.f.	107	Annual	Non-serotinous	Cleomaceae
Cleome gynandra L.	75	Annual	Non-serotinous	Cleomaceae
Cleome hirta (Klotzsch) Oliv.	40	Annual	Non-serotinous	Cleomaceae
Cleome monophyla L.	33	Annual	Non-serotinous	Cleomaceae
Cleome oxyphylla Burch. var. *oxyphylla*	45	Annual	Non-serotinous	Cleomaceae
Cleome paxii (Schinz) Gilg & Gilg-Ben.	22	Annual	Non-serotinous	Cleomaceae
Cleome rubella Burch.	56	Annual	Non-serotinous	Cleomaceae
Cleome semitetrandra Sond.	19	Annual	Non-serotinous	Cleomaceae
Cleome suffruticosa Schinz	93	Annual	Non-serotinous	Cleomaceae
Geigeria alata (Hochst. & Steud.) Benth & Hook.f. ex Oliv. *& Hiern*	48	Facultative perennial	Serotinous	Asteracereae
Geigeria ornativa O.Hoffm.	164	Facultative perennial	Serotinous	Asteracereae
Nidorella resedifolia DC. subsp. *resedifolia*	93	Annual	Non-serotinous	Asteracereae

Species	Sample size (n)	Life form	Serotiny	Family
Ocimum americanum L.	117	Annual	Non-serotinous	Lamiaceae
Ocimum filamentosum Forssk.	56	Annual	Non-serotinous	Lamiaceae
Petalidium setosum C.B.Clarke ex Schinz	52	Perennial	Serotinous	Acanthaceae
Petalidium variabile (Engl.) C.B.Clarke	87	Perennial	Serotinous	Acanthaceae
Tribulus zeyheri Sond. subsp. *zeyheri*	73	Annual	Non-serotinous	Zygophyllaceae
Tribulus cristatus C.Presl	31	Annual	Non-serotinous	Zygophyllaceae
Tribulus pterophorus C.Presl	17	Annual	Non-serotinous	Zygophyllaceae
Tribulus terrestris L.	36	Annual	Non-serotinous	Zygophyllaceae

Table B2. Predictors in the best fit model of flowering dates of species as predicted by time series (years), temperature and precipitation across phenophases as determined by lowest AIC values.

Species	Sample size (n)	Terms in best fit model	Phenophase
Blepharis grossa (Nees) T.Anderson	24	Temperature	Early flowering
Cleome angustifolia Forssk.	42	Year, Temperature	Early flowering
Cleome foliosa Hook.f.	10	Year, Temperature	Early flowering
Geigeria alata (Hochst. & Steud.) Benth & Hook.f. ex Oliv. & Hiern	43	Temperature	Early flowering
Geigeria ornativa O.Hoffm.	73	Year, Temperature	Early flowering
Ocimum americanum L.	27	Temperature	Early flowering
Ocimum filamentosum Forssk.	10	Temperature	Early flowering
Petalidium setosum C.B.Clarke ex Schinz	12	Precipitation, Temperature	Early flowering
Petalidium variabile (Engl.) C.B.Clarke	22	Temperature	Early flowering
Acrotome fleckii (Gürke) Launert	27	Temperature	Peak flowering
Acrotome inflata Benth.	29	Temperature	Peak flowering
Aptosimum lineare Marloth & Engl.	88	Temperature	Peak flowering
Blepharis grossa (Nees) T.Anderson	15	Temperature	Peak flowering
Cleome angustifolia Forssk.	30	Temperature	Peak flowering

Species	Sample size (n)	Terms in best fit model	Phenophase
Cleome elegantissima Briq.	37	Temperature	Peak flowering
Cleome foliosa Hook.f.	42	Temperature	Peak flowering
Cleome gynandra L.	40	Year, Temperature	Peak flowering
Cleome hirta (Klotzsch) Oliv.	20	Temperature	Peak flowering
Cleome monophyla L.	15	Temperature	Peak flowering
Cleome oxyphylla Burch. var. *oxyphylla*	32	Temperature	Peak flowering
Cleome rubella Burch.	15	Temperature	Peak flowering
Cleome semitetrandra Sond.	10	Precipitation, Temperature	Peak flowering
Cleome suffruticosa Schinz	42	Temperature	Peak flowering
Geigeria ornativa O.Hoffm.	87	Temperature	Peak flowering
Nidorella resedifolia DC. subsp. *resedifolia*	67	Temperature	Peak flowering
Ocimum americanum L.	18	Temperature	Peak flowering
Petalidium setosum C.B.Clarke ex Schinz	27	Temperature	Peak flowering
Petalidium variabile (Engl.) C.B.Clarke	41	Temperature	Peak flowering
Tribulus zeyheri Sond. subsp. *zeyheri*	37	Temperature	Peak flowering
Tribulus pterophorus C.Presl	12	Temperature	Peak flowering
Acrotome fleckii (Gürke) Launert	35	Temperature	Late flowering
Acrotome inflata Benth.	13	Precipitation, Temperature	Late flowering
Cleome angustifolia Forssk.	31	Temperature	Late flowering
Cleome elegantissima Briq.	23	Temperature	Late flowering
Cleome foliosa Hook.f.	55	Temperature	Late flowering
Cleome gynandra L.	32	Precipitation, Temperature	Late flowering
Cleome hirta (Klotzsch) Oliv.	19	Temperature	Late flowering
Cleome monophyla L.	18	Precipitation, Temperature	Late flowering
Cleome oxyphylla Burch. var. *oxyphylla*	13	Temperature	Late flowering
Cleome paxii (Schinz) Gilg & Gilg-Ben.	17	Temperature	Late flowering
Cleome rubella Burch.	39	Temperature	Late flowering
Cleome suffruticosa Schinz	46	Year, Temperature	Late flowering
Nidorella resedifolia DC. subsp. *resedifolia*	25	Temperature	Late flowering
Ocimum americanum L.	72	Temperature	Late flowering
Ocimum filamentosum Forssk.	38	Temperature	Late flowering

Species	Sample size (n)	Terms in best fit model	Phenophase
Petalidium setosum C.B.Clarke ex Schinz	13	Precipitation, Temperature	Late flowering
Petalidium variabile (Engl.) C.B.Clarke	24	Temperature	Late flowering
Tribulus zeyheri Sond. subsp. *zeyheri*	32	Year, Temperature	Late flowering
Tribulus cristatus C.Presl	20	Temperature	Late flowering
Tribulus terrestris L.	26	Temperature	Late flowering

Table B3. Predictors in the best fit model of flowering dates of various families as predicted by time series (years), temperature and precipitation across phenophases as determined by lowest AIC values.

Family	Terms in best fit model	Phenophase
Lamiaceae	Temperature	Early flowering
Acanthaceae	Temperature	Early flowering
Cleomeceae	Temperature	Early flowering
Asteraceae	Year, Temperature	Early flowering
Zygophyllaceae	Precipitation, Temperature	Early flowering
Lamiaceae	Temperature	Peak flowering
Scrophulariaceae	Temperature	Peak flowering
Acanthaceae	Year, Temperature	Peak flowering
Cleomeceae	Temperature	Peak flowering
Asteraceae	Year, Temperature	Peak flowering
Zygophyllaceae	Temperature	Peak flowering
Lamiaceae	Year, Temperature	Late flowering
Acanthaceae	Precipitation, Temperature	Late flowering
Cleomeceae	Year, Temperature	Late flowering
Asteraceae	Temperature	Late flowering
Zygophyllaceae	Temperature	Late flowering

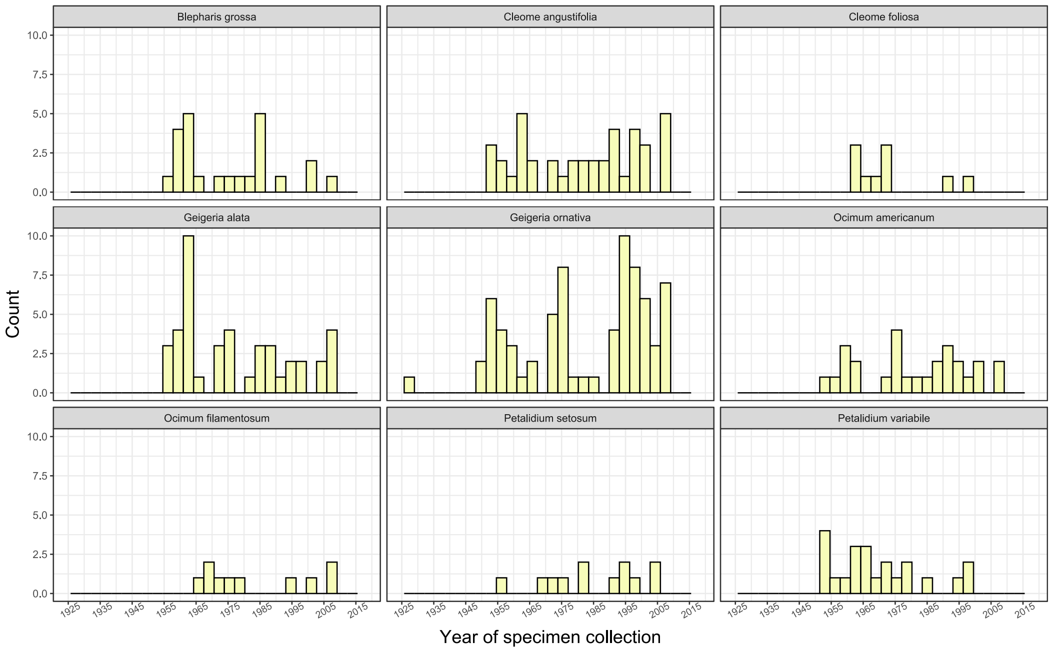


Figure B1. Histograms of early flowering time series expressed as year of specimen collection across species.

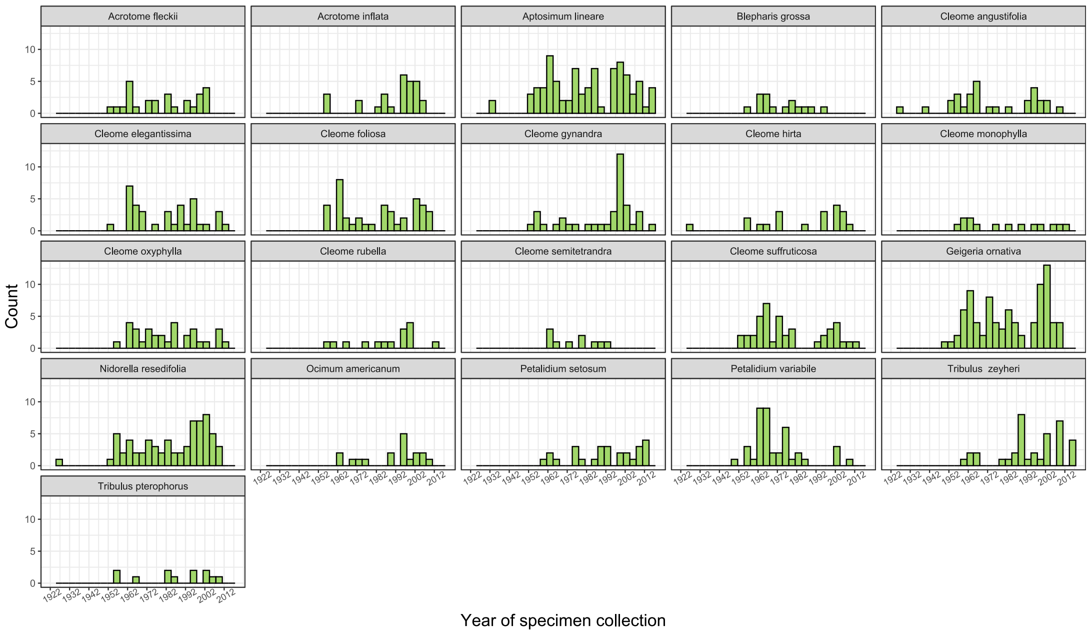


Figure B2. Histograms of peak flowering time series expressed as year of specimen collection across species.

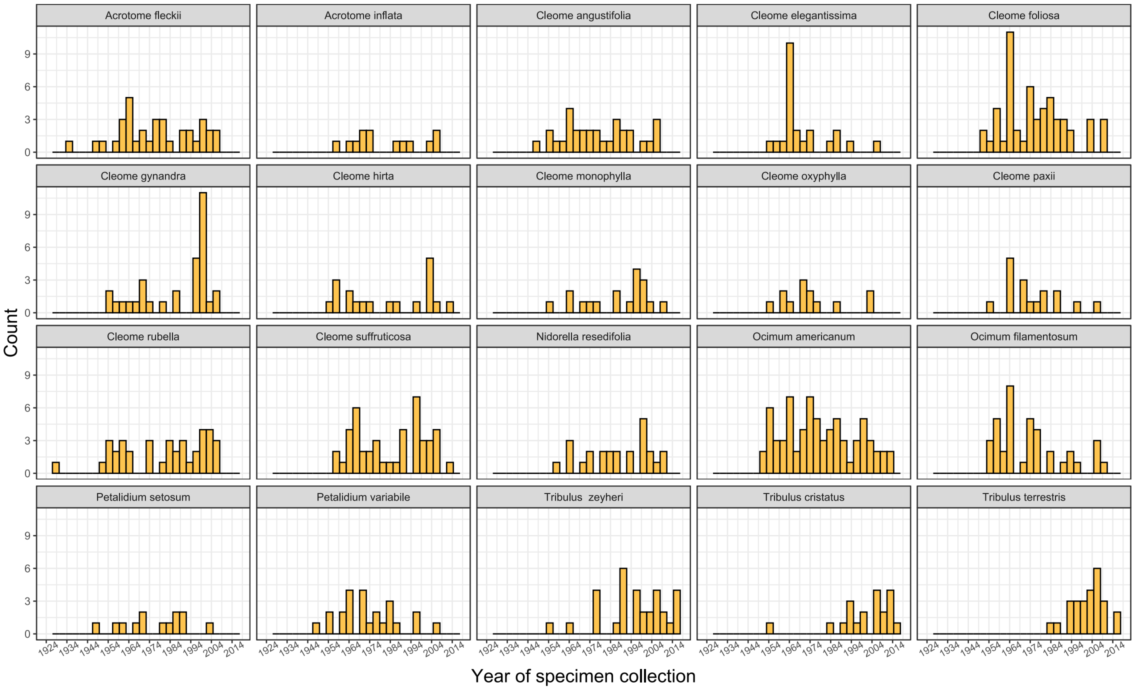


Figure B3. Histograms of late flowering time series expressed as year of specimen collection across species.

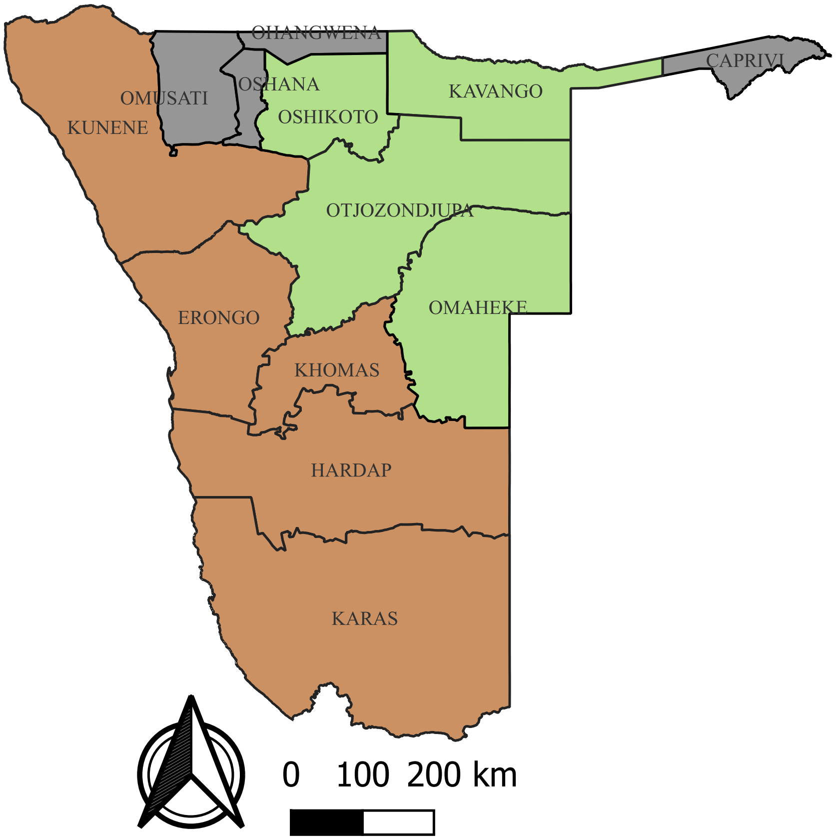


Figure B4. Map of Namibia showing the location of regions from which herbarium specimens were collected and demarcation of aridity zones. The brown color represents regions included in the hyper-arid to arid zone (MAP ≤ 400 mm) and the green color represents the arid to semi-arid zone (MAP ≥ 400). Grey represents regions that were excluded due to limited number of specimens.

APPENDIX C

SUPPLEMENTARY INFORMATION FOR CHAPTER 3

Figure C1. The rainout shelters used in the experiment showing the different treatments. (A) The 0% exclusion plots (representing the control treatment) had no plastic covers. B) The 20% exclusion plots are covered with 4 plastic covers, (C) The 40 % exclusion plots are covered with 8 plastic covers and (D) The 60 % exclusion plots are covered with 12 plastic covers.

Table C1. Linear mixed effects models testing the effect of drought treatment as a "fixed effect" applied across on 19 randomly selected plots (plot number is therefore given in the model structure as a random effect) on vegetative growth, reproductive timing and output response variables of the green leafy vegetable species *Cleome gynandra*. An (*) represents a significant effect while ns symbolizes non-significant drought effect. The P-value was extracted from the model using the Anova = type 3 function in R.

Response variable (Sample size, n)	Model description	P-value
Maximum stem height (121)	model_Stem_height1B <- lmer(log(Stem_height) ~ (Drought_Treatment) + (1|Plot_No), data = MaxStemheight_2022)	0.4456 ns
Average leaf length (121)	model_Ave_leaflength1 <- lmer(log(Ave_leaflength1) ~	0.4585 ns

Response variable (Sample size, n)	Model description	P-value
	(Drought_Treatment) + (1|Plot_No), data = Ave_leaflength_2022)	
Maximum number of leaves (120)	model_MaxLeaves2A <- glmer(No_of_leaves ~ Drought_Treatment + (1 |Plot_No), data = MaxLeaves_2022, family = poisson())	0.1083 ns
Maximum stem height date (121)	model_Stem_height1B <- lmer(log(Peak stem height date) ~ (Drought_Treatment) + (1|Plot_No), data = MaxStemheight_2022)	0.06461 ns
Average leaf length date (121)	model_Ave_leaflength1 <- lmer(log(Peak leaf length date) ~ (Drought_Treatment) + (1|Plot_No), data = Ave_leaflength_2022)	0.003596 **
Maximum number of leaves date (120)	model_MaxLeaves2A <- glmer(Peak number of leaves date ~ Drought_Treatment + (1 |Plot_No), data = MaxLeaves_2022, family = poisson())	0.0218 *
Maximum number of flowers (118)	model_Max_Flowers1 <- glmer(No_of_flowers ~ Drought_Treatment + (1 |Plot_No), data = Max_Flowers_2022, family = poisson())	0.06749 ns
Maximum number of fruits (112) #	model_Max_Fruits3A <- glmer(No_of_fruits ~ Drought_Treatment + (1 |Plot_No), data = Max_Fruits_2022, family = poisson())	0.08001 ns
First flowering date (119) @	model_FFD1A <- lmer(log(First_Flowering_Date) ~ Drought_Treatment + (1 |Plot_No), data = FFD_2022)	0.4698 ns
Peak flowering date (118)	model_PFD3 <- glmer(Peak_Flowering_Date ~ Drought_Treatment + (1 |Plot_No), data = PFD_2022, family = poisson())	0.02632 *

Response variable (Sample size, n)	Model description	P-value
Peak fruiting date (112)	model_peak_fruit1 <- glmer(Peak_fruiting_date ~ Drought_Treatment + (1 |Plot_No), data = Max_Fruits_2022, family = poisson())	0.2691 ns
Flowering end date	model_FED2 <- glmer(Flowering_end_date ~ Drought_Treatment + (1 |Plot_No), data = Flowering_End_Date_Revised, family = poisson())	0.5029 ns
Flowering duration	model_FD2 <- glmer(Flowering_duration ~ Drought_Treatment + (1 |Plot_No), data = Flowering_End_Date_Revised, family = poisson())	0.9531 ns