

PHENOTYPIC PLASTICITY AND SPECIES DENSITY OF *EUPHORBIA*  
*HETEROPHYLLA* L. AND *SIDA ACUTA* BURM. F. IN RELATION TO  
ENVIRONMENTAL FACTORS IN NORTHERN GUINEA SAVANNAH, NIGERIA

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NIGERIA

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BY

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NIGERIA

OCTOBER 2015

## DECLARATION

I declare that the work in this Thesis entitled Phenotypic Plasticity and Species Density of *Euphorbia heterophylla* L. and *Sida acuta* Burm. F. in Relation to Environmental Factors in Northern Guinea Savannah, Nigeria has been carried out by me in the Department of Biological Sciences. The information derived from the literature has been duly acknowledged in the text and a list of references provided. No part of this thesis was previously presented for another degree or diploma at this or any other institution.

Usman Yuguda Abubakar

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Signature

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date

## CERTIFICATION

This thesis entitled PHENOTYPIC PLASTICITY AND SPECIES DENSITY OF *EUPHORBIA HETEROPHYLLA* L. AND *SIDA ACUTA* BURM. F. IN RELATION TO ENVIRONMENTAL FACTORS IN NORTHERN GUINEA SAVANNAH, NIGERIA by Usman Yuguda ABUBAKAR meets the regulations governing the award of the degree of Master of Science in Botany of the Ahmadu Bello University, and is approved for its contribution to knowledge and literary presentation.

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## Abstract

Phenotypic plasticity is a key mechanism associated with the spread of invasive plants and previous studies have found that weeds are generally more plastic than co-occurring species. Although there are a large body of evidence for superiority in particular traits among weeds species when compared to non-weeds species, it is less clear if weeds have similar pattern of phenotypic plasticity, and whether this plasticity confers a fitness advantage. An experiment was conducted in (2014) to assess the phenotypic variations and plasticity pattern of *Euphorbia heterophylla* and *Sida acuta* to varying environmental factors in glasshouse with full factorial combination of soil nutrients, water availability, and plant density. The plants were subjected to different level of stress. Significant differences were observed between the species, and morphological trait indicated that *S. acuta* with its opportunistic response recorded its highest mean values in soil rich in nutrients and low density (stem height  $11.01\text{cm}\pm 2.74^c$  and  $8.52\pm 1.43^{bc}$  numbers of leaves) ( $p<0.01$ ), while *E. heterophylla* had generalist strategy with higher performance and greater plasticity in all treatments combination (stem height  $46.30\text{cm}\pm 7.56^a$ ,  $42.29\text{cm}\pm 6.73^a$  and numbers of leaves  $11.94\pm 1.67^a$ ,  $17.61\pm 2.68^a$ ) ( $p<0.01$ ), hence, higher plasticity. Reproductive biomass increased with increasing soil nutrient from 0.07 to 0.12 for *E. heterophylla*, while no significant difference in reproductive biomass for *S. acuta* was observed. Density had significant effect on relative reproductive biomass (5.42) ( $p<0.01$ ), relative leaf biomass (21.53) ( $p<0.01$ ), relative root biomass (16.39) ( $p<0.01$ ), and relative stem biomass (35.97) ( $p<0.01$ ) while water had no significant effect, except relative stem biomass (11.76) ( $p<0.01$ ). The soil nutrient significantly affected the biomass allocation to leaves, stem and reproductive organs, except root biomass ( $p<0.01$ ). *S. acuta* exhibited a Master-of-some pattern of phenotypic plasticity, and *E. heterophylla* had a complex pattern exhibiting Jack-

and-Master strategy. Overall *E. heterophylla* had higher plasticity than *S. acuta*. This result suggests that the high magnitude of plasticity to nutrient variation of these two species might give them an advantage to outcompete others and could be responsible for their abundance in the study area.

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## **Abbreviations, Definitions, Glossary and Symbols**

W1: low water level, amount of water at 500ml was applied once a week.

W2: medium water level, 500ml of water was applied twice a week.

W3: high water level, 500ml of water was applied every other day.

D1: low density level, 3 plants in each pot.

D2: medium density level, 5 plants in each pot.

D3: high density level, 10 plants in each pot.

S1: soil from the top, low nutrient level.

S2: soil from the slope, medium nutrient,

S3: soil from the base, highest nutrient,

H: absolute height

BRO: biomass of roots

BS: biomass of stems

BL: biomass of leaves

BRE: reproductive biomass

BV: vegetative biomass

BT: total biomass

RSR: root-shoot ratio

RS: relative biomass of stem

RL: relative biomass of leaves

RRE: relative reproductive biomass



## CHAPTER ONE

### 1.0

### INTRODUCTION

#### 1.1. Background of the Study

Environments are highly heterogeneous both in space and time, and organisms must either acclimate to, or escape from, adverse conditions. Phenotypic plasticity, or the capacity of a given genotype to render different phenotypes under different environmental conditions, is a means to cope with environmental heterogeneity that is particularly adequate for sessile organisms (Bradshaw, 1965; Sultan, 2000).

Plants have a remarkable ability to alter their development in response to myriad environmental signals or stress. This phenotypic plasticity allows them to continually adapt to their local environment, a necessity for plants as sessile organisms. This plasticity enables growth optimization for the local environment, allows range expansion into heterogeneous habitats, and may provide an advantage as the changing climate affects growth conditions around the globe.

Many studies have shown that plants are plastic for numerous ecologically important traits, ranging from morphology, physiology and anatomy, to developmental and reproductive timing, breeding system and offspring developmental patterns (Sultan, 2000).

Phenotypic variation can be solely because of due to differences in growth rates under environments with contrasting resource availability, i.e., “passive plasticity” (Coleman *et al.*, 1994; Wright and McConnaughay, 2002) or as a result of “active plasticity”, in which changes in growth trajectories are induced by changes in the environment that lead to ontogenetic or true plasticity (Wright and McConnaughay, 2002). It is suggested that studies should try to distinguish between these two types of plasticity (Japhet *et al.*, 2009).

For any given plant species or population, determining responses to environmental changes will require an understanding of the environmentally induced variation in the phenotype of individual plants. Once regarded as noise, phenotypic plasticity is now understood to be genetically controlled, heritable and of potential importance to species' evolution (Bradshaw, 2006; Lande, 2009). With mounting evidence from molecular and developmental biology, we are now at the threshold of gaining a sophisticated understanding of the mechanisms of plasticity, which will be crucial for predicting changes in species distributions, community composition and crop productivity under climate change (van Kleunen and Fischer, 2001; van Kleunen *et al.*, 2007).

Scientists agree that phenotypic plasticity concerns environmentally induced changes to phenotypes. However, environments can influence phenotypes in diverse and complicated ways, and it is among these varied effects that opinions about plasticity begin to diverge. For this reason, it has become a major focus of empirical and theoretical studies of organisms living in spatially and temporally varying habitats (van Kleunen *et al.*, 2000; Sultan, 2001; Callahan and Pigliucci, 2002).

Variation, the fuel that feeds evolutionary change, originates at the levels of both the genotype and the phenotype. Genetically identical organisms reared under different conditions may display quite distinct characteristics. Until recently, the types and sources of such phenotypic variation have been given little consideration in evolutionary theory, and the ecological ramifications are less well understood. But knowledge of the mechanisms and developmental patterns underlying phenotypic variation is crucial to the understanding of important evolutionary phenomena.

Variation in trait expression induced by environmental factors might affect interactions among plants. Individuals within a species may vary by orders of magnitude in size, growth rates, allocation to different organs, reproduction, and chemical constituency. Plastic responses may be permanent once induced, relatively fixed for a given growing season, or may be dynamic on a scale

of hours, as in the case of light effects on photosynthetic chemistry or herbivore effects on defence chemistry (Baldwin, 1999). Although the cues that trigger phenotypic differences are environmental, the ability to respond to cues is genetically based and can evolve under natural selection (Bradshaw, 1973; Via, 1994). Because individual genotypes have the potential for adaptive divergence, plasticity in plants probably broadens ecological ranges and reduces the impact of selection (Mazer and Schick, 1991; Sultan, 1995). Although phenotypic plasticity may not always be adaptive, the adaptive benefits of plastic traits as “buffers against spatial or temporal variability in habitat conditions” and “means of optimizing the acquisition and use of resources” (Grime *et al.*, 1985; Robinson and Rorison, 1988) have been widely documented and reviewed (Bradshaw, 1965; Schlichting, 1986; Sultan, 1987, 1995; Debat and David, 2001). Phenotypic plasticity can be visualized by the use of reaction norms, which plot values for a specific phenotypic trait across two or more environments or treatments (Schlichting and Pigliucci, 1998).

#### 1.1.1. *Sida acuta* Burm. f.

*S. acuta* is native to Central America, but has spread throughout the tropics and sub-tropics in the Pacific, Asia and Africa (Holm *et al.*, 1977). The small perennial shrub, *S. acuta* has successfully invaded the tropics worldwide, largely as a contaminant in pasture seed. Its tolerance of a wide range of growing conditions has enabled *S. acuta* to become established in these diverse habitats. A long-lived ([perennial](#)) [herbaceous](#) plant or small [shrub](#) ([sub-shrub](#)) usually growing 30-100 cm tall, but occasionally reaching up to 1.5 m in height. However, it often behaves as a short-lived ([annual](#)) plant in the wet-dry savannahs of northern Australia. It infests various crops and habitats, but has been most problematic in pastures and rangelands, particularly in savannah-type biomes with pronounced wet and dry seasons. It can form dense monospecific stands in these regions because of its lack of palatability (Nuwanyakpaet *al.*, 1983), and has had a pronounced economic impact in northern Australia, Papua New Guinea and many Pacific Islands” (Holm *et al.*,

1977). However, much of the history and introduction and spread of this fairly inconspicuous plant has not been documented. In many areas, such as the Galapagos Islands, the species has been naturalized long enough to become well integrated into the local ecosystems (Porter, 1983). In the West Indies, *S. acuta* is well integrated into the local floras to the point that is considered by many as native in the region. With the broad distribution over which *S. acuta* is already established, it is likely to colonize many of the geographic areas in the subtropics and tropics where it has not already become naturalized. *S. acuta* is found on most soil types, except seasonally flooded clays or soils derived from limestone (Agriculture Protection Board, 1993). It competes vigorously with other plant species, but does best in disturbed habitats in tropical or sub-tropical regions with a distinct wet and dry season. It is a weed of degraded pastures, tree plantations, cereals, root crops, vegetable fields, planted forests, lawns, roadsides, and waste places (Pitt, 1992; Flanagan *et al.*, 2000). It has been reported at up to 1500 m altitude in Indonesia, at medium and higher elevations in Kenya and in the foothills of the Andes in Peru (Holm *et al.*, 1977; Waterhouse and Norris, 1987; Parsons and Cuthbertson, 1992). The stems are unpalatable to stock (Nuwanyakpaet *et al.*, 1983). Foliage of *S. acuta* has been observed to cause poisoning in cattle, with consumption of even a relatively small amount of foliage over an extended period of time leading to lysosomal storage disease (Furlanet *et al.*, 2008), which selectively graze other plants, allowing *S. acuta* to dominate. Overgrazing accelerates this process. It survives mowing, slashing and cultivation. Propagation is entirely by seeds which are produced in profusion and germinate readily following a post-harvest ripening period of 1-3 months at high temperatures (Mott, 1980). However, most seeds have a hard seed-coat which requires scarification, mechanically or by bacterial action, before the seeds will germinate (Parsons and Cuthberston, 1992).

### 1.1.2. *Euphorbia heterophylla* L.

*E. heterophylla* originated in the tropical and subtropical regions of America but is now distributed throughout tropical Africa, Asia and the Pacific in a total of at least 65 countries. *E. heterophylla* grows in moist tropical and subtropical regions on a wide range of soils, principally in shaded waste places and in cultivated areas (Parsons and Cuthbertson, 1992). Seeds are produced in great quantities with high viability. Light and alternate temperatures (25/3°C) stimulate germination (Kissmann and Groth, 1993). Each fruit bears three seeds which are expelled when the fruit is ripe. In Brazil, seeds germinate and seedlings emerge throughout most of the year. Seed longevity is high, and seeds may remain viable with a low dormancy level after being eaten by birds (Kissmann and Groth, 1993). *E. heterophylla* seeds germinate over a wide range of conditions, which explains why the plant is becoming an increasingly serious problem; germination was at least 95% when exposed to a solution of pH 2.5-10 or a solution with osmotic potential of up to -0.8 MPa. Seed germination occurred at temperatures ranging from 20-40°C with maximum germination (97%) at 35°C (Brecke, 1995). Etejere and Okoko (1989) reported 95% seed viability. Seeds had no dormancy period and germinated in response to sufficient water. *E. heterophylla* is a C<sub>4</sub> plant and its growth habit is highly dependent on light intensity. Paliwal and Ilangovan (1988) performed autoecological studies on several species, including *E. heterophylla*. They showed that photosynthetic processes and the rate of photosynthesis decreased with increasing leaf age. For *E. heterophylla* a good correlation was evident between the photosynthetic rate, stomatal resistance, protein content, transpiration rate, biomass, photosynthetic pigments and nitrate reductase activity.

## 1.2. Statement of the Research Problem

Phenotypic plasticity as a phenomenon is well understood and has been well documented. However, knowledge of phenotypic plasticity at a level of community and community interactions

is limited (Gardiner, 2013), and most studies of phenotypic plasticity have not related it with species abundance.

Although the theoretic framework for the role of phenotypic plasticity in biological invasion has been well established, the number of studies to-date is still small and these have revealed mixed results (Richards *et al.*, 2006). There are conflicting reports that invasive species should have high phenotypic plasticity (Sultan, 2001). In general, high phenotypic plasticity has been thought to confer superior invasive and competitive abilities (Bloom *et al.*, 1985; Aerts *et al.*, 1991; Aerts, 1999; Sultan 2000, 2001), but direct empirical tests of this theory are less common (Hulme, 2008) and previous reviews have not achieved quantitative conclusions (Daehler, 2003; Richards *et al.*, 2006).

Empirical studies comparing plasticity in invasive and non-invasive plants are now so numerous that they have been subjected to meta-analysis twice—but the meta-analyses came to different conclusions (Palacio-López and Gianoli, 2011), with one concluding that invaders showed higher plasticity and the other finding no evidence for such a trend. Likewise, plasticity may be adaptive if it increases fitness (or permits smaller declines in fitness in response to harsher conditions) (van Kleunen and Fischer, 2005; Richards *et al.*, 2006), but whether higher plasticity has resulted in higher fitness or invasion success in invasive species has not been made entirely clear by literature reviews or by models (Daehler, 2003).

Inconsistency may be due to the fact that no work has tried to relate species plasticity with its abundance in natural plant community. In relation to the above, most work have measured phenotypic plasticity under manipulated experimental conditions in the laboratory which may not adequately predict the real response of the plant in nature. It will be more valuable if a multi-

species approach is used to predict how plasticity of a given species relates to its abundance in nature.

Most restoration projects have not considered the ability of plants to respond to novel environmental changes (plasticity) in selecting plants for restoration projects. At present, more and more attention is drawn to restoration and conservation of high quality habitats. To assess speed of recovery after habitat restoration, it is important to identify species that respond rapidly and when environmental conditions improve (Lindborg *et al.*, 2005).

### **1.3. Justification**

Studies on phenotypic plasticity offer a unique opportunity to investigate biological and ecological traits across different environments, which are largely unknown for many weeds/invasive species (Luo, 2009). This information could be very important because the mechanism behind invasion success might not only lie in the performance in optimum environments, as observed in a greenhouse or in a heavily-invaded field habitat, but also in the responses to stressful conditions. If phenotypic plasticity could be shown to be consistently associated with species abundance, this trait could serve as a reliable predictor for invasive potential.

The understanding of phenotypic plasticity will be crucial for predicting changes in species distribution, community composition, and crop productivity under what seems global climate change (van Kleunen and Fischer, 2007; Lande, 2009). Results from this study will provide information which will be valuable for developing models that will help to predict spread of those species, thereby developing effective management phase.

Today, the practice of ecological restoration is receiving immense attention because it offers the hope of recovery from much of the environmental damage inflicted by misuse or mismanagement of the Earth's natural resources (Restoration drama, 2002). The use of plant for environmental restoration/reclamation of degraded soils especially in the tropics is an area of study with a lot of potentials, hence, results from this study will help in selecting species for restoration programme since it is assumed that species with high phenotypic plasticity should be good candidates for restoration of degraded lands (Ewel and Putz, 2004).

Studies of phenotypic plasticity have special significance for understanding the response of known invaders to global change. The possible shrinkage or expansion of invaders' range as a consequence of nitrogen deposition, climate warming, increased atmospheric CO<sub>2</sub>, or other aspects of environmental change is an issue of serious consequence to land and resource managers. If phenotypic plasticity could be shown to be consistently associated with invasiveness, this could serve as a reliable predictor for invasive potential of such species.

#### **1.4. Aim of the Research**

To evaluate phenotypic plasticity in two weed species and relate it to their abundance in a natural nutrient gradient.

#### **1.5. Objectives**

- I. To determine phenotypic plasticity in relation to different soil (nutrient) gradient.
- II. To determine if traits difference is related to phenotypic plasticity
- III. To determine phenotypic plasticity is related to species abundance

#### **1.6. Hypotheses**



- I. There is no difference in phenotypic plasticity in relation to different soil (nutrient) gradient.
- II. Traits differences are not related to phenotypic plasticity.
- III. There is no relationship between phenotypic plasticity and abundance of species.

## **CHAPTER 2**

### **2.0 LITERATURE REVIEW**

#### **2.1. The Concept of Phenotypic Plasticity**

With all the conceptual and empirical progress of the last decades, it is still common to encounter basic misconceptions about plasticity whenever the topic comes up for discussion. One such misconception is to view plasticity as an “alternative” to genetic variation (Pigliucci, 2001). Plasticity is a trait – a property of a genotype – which can be visualized graphically as a pattern of expression in different environments called a reaction norm. Like other traits, plasticity is subject to evolution by natural selection. Phenotypic plasticity refers to the potential of specific traits of a genotype to respond to different environments. This property can affect the performance and reproductive success of individual organisms, which in turn will impact the make-up of the next generation and thus contribute to evolution by natural selection. A given genotype may be plastic for a certain trait in a certain set of environments, but not plastic for other traits in the same set of environments, or for the same trait in a different set of environments (Bradshaw, 1965; Sultan, 1995; Pigliucci, 2001).

#### **2.2. Weeds and Invasive Plants**

Weeds and invasive plants are recognized as one of the major threats to ecosystem function and biological diversity through competition, suppression and displacement of native species

(Wilcoveet *al.*, 1998; Salaet *al.*, 2000). Because there are few ecosystems in the world, terrestrial or aquatic, that has not been affected by invasions, the negative effects of weed and invasive species are still a global concern (Heywood, 1989).

Both invasive plants and weeds are noxious plant species or genotypes that cause economic and environmental damage (Luo, 2009). The definition of invasive plants is “the proliferation and persistence of a species in a new range such that it has detrimental consequences to both biotic and abiotic components. This persistence is not dependent on deliberate human intervention.” (Mack, 1996). The definition of a weed, on the other hand, is a plant that grows “entirely or predominantly in situations markedly disturbed by man (without, of course, being deliberately cultivated)” (Baker, 1974).

Weeds are similar to invasive plants in terms of their potential to dominate a community. But they are also different (Luo, 2009). First, weeds can be native as well as non-native species (Luo, 2009), whereas, invasive plants are “alien species that show a tendency to spread out of control. Although not synonymous with "exotic plants," the "invasive" label is now typically reserved for plants that have been introduced from other regions and spread like wildfire in their new habitats. Indigenous plants that spread rapidly and overpower the competition tend to be referred to now as simply "aggressive," "thuggish" or "ill-behaved," in common parlance” (Beaulieu, 2014). Secondly, only plants that cause economic or environmental harm in “markedly disturbed” areas are called weeds, while invasive plants are not necessarily associated with intensive human activities (Luo, 2009).

Although invasive plants and weeds can be very different, these two terms are often used interchangeably and sometimes indiscriminately. Invasive plants are sometimes said to be weedy, while weeds are sometimes called invaders. So the borderline between invasive plants and weeds

is vague. However, they share common characteristics such as rapid growth and massive seed production (Goodwin *et al.*, 1999).

### **2.3. Phenotypic Plasticity and Invasive species**

Biological invasions have long been considered a widespread component of human-caused global change (Vitousek, 1992). The number of plant species accidentally or purposely transported by humans across continents has significantly increased in the last centuries (Mack *et al.*, 2000). Some of these species become abundant in their introduced range and spread rapidly across diverse habitats, outcompeting native species, changing the structure and functioning of native plant communities, and causing both environmental and economic problems (Wilcove *et al.*, 1998). Despite the enormous effort over the last two decades dedicated to the study of invasive plant species, the evolutionary mechanisms that lead to invasiveness in introduced species remain unclear in many cases (Lavergne and Molofsky, 2007). It is commonly thought that if a species is able to maintain fitness across a broad variety of environmental conditions it is more likely to become invasive (Hulme, 2008). A major way that plants achieve this kind of niche breadth is by means of adaptive phenotypic plasticity (Sultan, 1998).

Two main nonexclusive hypotheses have been posed to explain the role of phenotypic plasticity in plant invasions (Zouet *et al.*, 2009). First, invasive species may be more plastic than native or alien non-invasive species, and second, invasive populations may be more plastic compared to populations in the native range. The last hypothesis is especially interesting as it allows for tests of the evolution of phenotypic plasticity in the introduced range. It has also been hypothesized that invasive species are able to undergo rapid evolutionary change (Mooney and Cleland, 2001; Lee, 2002). Invasions of novel environments usually involve changes in selection forces that may lead to evolutionary change (Mooney and Cleland, 2001). In this context, rapid evolution of plasticity may play an important role in the success of introduced species in introduced habitats if plasticity

in functional traits is accompanied by a fitness advantage in the novel environment (Richards *et al.*, 2006). Alternatively, phenotypic plasticity may grant initial survival in novel habitats, and then natural selection could operate at the local scale, driving evolution of ecotypes (Sexton *et al.*, 2002).

#### **2.4. Phenotypic Plasticity in Natural Plant Community**

Plants in natural populations exhibit phenotypic plasticity as a means of coping with environmental heterogeneity. Phenotypic plasticity has been widely cited as facilitating the successful establishment of species in novel environments (Dybdahl and Kane 2005; Richards *et al.*, 2006; Funk, 2008; Hulme, 2008). Phenotypic plasticity is a general and common feature, probably shared by most organisms (Coquillard, 2012). Plasticity is an inherent attribute of a trait for a genotype and can be subject to natural selection and, thus, can evolve (Bradshaw, 1965). Phenotypic plasticity may be neutral, maladaptive or adaptive with regard to an individual's fitness (Ghalamboret *et al.*, 2007). Plasticity provides a mechanism for adaptation in spatially and temporally variable environments (DeWitt and Scheiner, 2004). Plants display plastic responses to a wide variety of ecological conditions including variation in the abiotic environment, disturbance, herbivory, parasitism, mutualistic relationships, and the presence, absence, or identity of neighbours (Callaway *et al.*, 2003). Plastic responses may be permanent once induced, relatively fixed for a given growing season, or may be dynamic on a scale of hours, as in the case of light effects on photosynthetic chemistry or herbivore effects on defence chemistry (Baldwin, 1999; Pearcy, 1999).

Theoretically, high plasticity is likely to influence the potential invasiveness of species because it may enable them to express advantageous phenotypes over a broad range of environments (Matesanz *et al.*, 2010), potentially enhancing their ecological success and their impact across ecosystems (Daehler, 2003; Hulme, 2008). For instance, it has been postulated that plasticity

would reduce the risk of stochastic local extinction after the arrival of a few genotypes and augment the likelihood of species to become invasive under environmental conditions to which they were not pre-adapted (Sultan, 2001; Bossdorf *et al.*, 2005; Ghalambore *et al.*, 2007).

It is now clear that phenotypic plasticity alters a variety of interactions between individuals and their environment through life-traits and/or behaviour : indirect interactions in multi-species assemblages, direct interactions between species such as inducible defences/offenses (Ramos-Jiliberto, 2003; Miner *et al.*, 2005; Ramos-Jiliberto *et al.*, 2008) and niche construction (Donohue, 2005). Because phenotypic plasticity is able to modify such interactions, it ultimately affects ecological processes, such as population stability, trophic relationships, population dynamics, species coexistence within communities and biodiversity (Mouritsen and Poulin, 2005).

A popular hypothesis about phenotypic plasticity of invasive species is that: invasive species are more plastic than native/non-invasive species, which facilitates their adaptation to a wide range of environments. This idea that high phenotypic plasticity has contributed to the success of invasive plants was proposed half a century ago (Baker, 1965). But direct empirical tests of this theory are less common (Hulme, 2008) and research in recent times in general has not supported this theory (Daehler, 2003; Richards *et al.*, 2006). Recent studies have suggested that invasive species might not always have a greater competitive advantage over their non-invasive native counterparts (Hawkes, 2007). Abrahamson and Gadgil (1973) demonstrated that invasive species did not have higher reproductive effort compared to non-invasive native species. In addition, Sans *et al.*, (2004) compared three congeners including two exotic invasive and one native species and found that the reproductive effort of the native species was the highest in all treatments. High reproductive effort is usually associated with stressed environments (Li *et al.*, 2001). Thus, plants in stressed

environments should invest more resources into reproductive and not vegetative structures. However, studies have provided evidence that reproductive effort did not hold constant with changes in the different environments (Sultan and Bazzaz, 1993b, c). Hence, there are still inconsistencies in studies of reproductive effort.

Morphological traits are important to resource partitioning in many plants (Coleman and McConnaughay, 1995; Wang *et al.*, 2006). Reproductive effort, which shows the proportion of the plant's resources allocated to reproductive activities, is an important component of plant fitness (Bazzaz *et al.*, 1987; Weiner, 1988). Reproductive effort of plants varies across different several environments by the adjusting partitioning of resources and morphological traits (in relation to reproductive fitness).

Richards *et al.*, (2006) drew on Baker (1965) to pose three testable scenarios regarding the importance of phenotypic plasticity in plant invasions and the role of plasticity in maintaining fitness across different environments. These are relative to a non-invasive species. The scenarios are; an invasive species might be a:

1. "Master-of-some" if phenotypic plasticity in response to more favourable conditions enables a larger increase in fitness.
2. "Jack-of-all-trades" if phenotypic plasticity in response to stressful conditions enables greater fitness homeostasis (i.e. a smaller decline in fitness).
3. "Jack-and-master", when characteristics of (1) and (2) are combined such that phenotypic plasticity in response to more favourable environments enables greater fitness, and plasticity in response to more stressful conditions permits a smaller decline in fitness (i.e. greater fitness homeostasis).

Similarly, the novel environmental conditions that are experienced upon invasion of a new habitat, increasing temperatures, higher CO<sub>2</sub> levels and associated climate changes over recent decades have introduced novel environmental conditions. This might favour more phenotypically plastic species (Chown *et al.*, 2007) and result in an increased competitive ability of invasive plants over co-occurring native, non-invasive species (Dukes, 2007).

One alternative hypothesis is that closely related species show more similar patterns of plasticity than distantly related species, regardless of non-native or invasive status (i.e. plasticity is evolutionarily conserved) (Cook-Patton and Agrawal, 2011). Some evidence for this idea comes from Hoffmann and Franco (2003), who measured leaf trait plasticity in tropical forest and savannah species pairs, and found that genus explained up to 69% of the variation in plasticity among species. In another study, Kembel and Cahill (2005) combined data across 102 species from multiple families and found a strong signal of phylogenetic conservatism in how the species responded with root proliferation to soil nutrients patches, although not in other traits.

Although these examples highlight the fact that plasticity can be adaptive under some environmental conditions, research linking successful establishment of novel environments due to plasticity is limited (Herrera, 2013). Several approaches have been implemented to test the hypothesis that high levels of plasticity have enabled species to colonize and establish in novel environments. Experiments have compared the plasticities of introduced invasive species to native species when plants were grown in greenhouses or common gardens (Funk 2008; Godoy *et al.*, 2011). Generally, these studies found evidence that the introduced invasive species had greater plasticity or that both groups displayed similar levels of plasticity.

Experiments have also compared the plasticities of introduced invasive species from Europe or Asia to introduced non-invasive North American congeners when these were grown in

greenhouses or common gardens. Burns (2004) found evidence that introduced invasive species had greater plasticity, whereas Muth and Pigliucci (2006) found no evidence of a relationship between invasiveness and plasticity. Lambrecht-McDowell and Radosevich (2005) and Flory *et al.*, (2011), compared the plasticity of introduced invasive populations from Europe and China to native populations from North America and China when these were grown in common gardens, respectively. In both experiments, there was no evidence that introduced populations expressed greater plasticity than native populations. These differences might be because of genetic differences in resource acquisition, allocation and phenotypic plasticity (Gratani, 2014). Collectively, these studies provide ambiguous information on the role of plasticity in facilitating the establishment of invasive species in novel environments.

Phenotypic plasticity is not a whole-plant response, but a property of individual meristems, leaves, branches and roots, triggered by local environmental conditions (De Kroon *et al.*, 2005). Communication and behavioural integration of interconnected modules can change the local responses in different ways: it may enhance or diminish local plastic effects, thereby increasing or decreasing the differences between integrated modules exposed to different conditions (De Kroon *et al.*, 2005).

## **2.5. Reaction Norm**

Phenotypic plasticity is often depicted as a norm of reaction. Reaction norms for continuously distributed traits, such as many physiological, morphological and life-history traits are typically visualized as a line or curve on a plot of the environmental value versus the phenotypic value (Ghalamboret *et al.*, 2007). Alternatively, the reaction norm may be visualized as discrete character states (Falconer, 1990), such as in the case of developmental polymorphisms or polyphenisms.

Variation among genotypes in how they respond across environments is referred to as a genotype  $\times$  environment (G  $\times$  E) interaction (Fry, 1992) and this can be visualized by plotting the



reaction norms of multiple genotypes. G×E interactions are thus the property of populations or groups of genotypes (Falconer, 1990; Via *et al.*, 1995). Evidence suggests that plasticity has evolved and can be visualized as a change in the slope of the reaction norm between the ancestral and derived population or species (Doughty, 1995), and has been empirically shown to occur in nature between ecotypes and species subject to different selection pressures (Pigliucci, 1996; Ghalambor and Martin, 2002).

The evolution of plasticity may therefore occur independently of, or jointly with, changes in the mean trait value. While this point has been the subject of past debate, from an evolutionary genetics perspective it is most convenient to think of the mean trait value and its reaction norm as separate traits (Scheiner, 1993, Via *et al.*, 1995; de Jong, 2005). For example, selection can change the y-intercept of the reaction norm without changing the slope and vice versa (de Jong, 2005).

## **2.6. Species and their Abundance**

Biological invasions are species specific, the distribution and spread of major plant invaders can be explained by a combination of environmental factors, life-history traits and human uses (Thuiller *et al.*, 2006).

## **2.7. Environmental Variations**

Environmental variability on a small spatial scale favours phenotypic plasticity (Bradshaw, 1965; Schlichting, 1986; Sultan, 1987), and nutrient levels that fluctuate within a plants lifetime may lead to general-purpose genotypes (Schmid, 1992). Phenotypic plasticity is therefore expected of plants at the natural and disturbed or waste land habitat in order to adapt to the heterogeneous nutrient levels of their environment (Leiss and Muller-Scharer, 2001).

Currently, it is advocated by several authors that the most plastic phenotypes are harboured by organisms competing in heterogeneous environments relatively to those living in homogenous environments (van Kleunen and Fisher, 2005). Comparative studies of the responses

of plants of contrasted ecology are informative about the way that the expression of plasticity changes with habitat productivity. This can be used to assess how plasticity is related to the dominance in plant communities (Grime and Mackey, 2002). Studies demonstrated that plasticity can promote stability and health of ecological systems experiencing environment fluctuations (Miner *et al.*, 2005).

### **2.8. Global change and phenotypic plasticity in plants**

Natural systems have been profoundly transformed by human activities since the nineteenth century, but over the last three decades these changes are occurring at an unprecedented rate. Fundamental questions for evolutionary ecologists in a global change context are how plant species will respond to these new and complex environmental scenarios and what mechanisms will be involved in the process (Parmesan, 2006). Phenotypic plasticity is a proposed mechanism by which plant species may persist when faced with these rapid environmental changes (Valladares *et al.*, 2007).

Global change components, or drivers, can be grouped in five categories according to Assessment (2005); climate change, land use change, overexploitation, pollution, and invasive species. These drivers of change impact plant species and communities in various and interacting ways and exert new selective pressures to which plants respond and possibly adapt.

The study of climate change–driven effects on plants has so far gained the bulk of attention. Changes in atmospheric CO<sub>2</sub> concentration, air and water temperatures, rainfall patterns, and even the amount of solar radiation reaching the Earth's surface have been altered owing to human activities (Stanhill and Cohen, 2001), and the associated impacts on plants have been extensively documented across biomes (Parmesan, 2006; Parmesan, 2007). Overall, climate change has been shown to affect the phenology, abundance and distribution of plant species, and the composition of plant communities (Menzelet *et al.*, 2006).

Alongside climate change and land use changes, the introduction of alien species is considered among the greatest threats to biodiversity (Vitousek, 1992). In Europe alone, more than 6,000 plant species have been classified as aliens (Roy and Hulme, 2008). Invasive species alter plant–plant interactions, reduce the abundance of or displace the native flora, and affect ecosystem functioning (Mack *et al.*, 2000). Pollution, that is, contaminants introduced into the environment as well as naturally occurring substances, such as greenhouse gases or nitrogen, whose concentrations have increased because of human activities, can cause local extinction, affect physiology and biomass allocation and alter the composition of plant communities due to different sensitivities of species to the presence of pollutants (Bobbink, 1998).

Importantly, most plant species in natural conditions face multiple global change drivers simultaneously (Sala *et al.*, 2000; Reusch and Wood, 2007). For example, plants in fragmented landscapes may also face increases in temperature or reductions in rainfall. Although the responses of plant species to interacting global change drivers remain largely unknown, there are some studies showing evidence of synergistic interactions that modify the response of plant species to multiple stresses (Honnay *et al.*, 2002; Matesanz *et al.*, 2009). For instance, Matesanz *et al.*, (2009) found that the interaction between fragmentation and habitat quality led to lower survival and lower relative growth in plants of the Mediterranean species *Centaurea hyssopifolia*.

#### 2.8.1. Phenotypic plasticity and range shifts

One of the most documented responses of plant species to climate change are range shifts, that is, the dispersal or migration of plant species toward higher latitudes and altitudes, where environmental conditions are more similar to environments in the species' historic range, (Kullman, 2002; Parmesan and Yohe, 2003; Peñuelas and Boada, 2003) and great effort has been devoted to the simulation and prediction of future species distributions and local extinctions (Thuiller, 2003; Guisan and Thuiller, 2005). Although such simulations are very helpful in a global

change context, an important limitation is that they often fail to account for the role that phenotypic plasticity may play in the persistence and later adaptation of plants to novel environments (Thuiller, 2003; Guisan and Thuiller, 2005).

Phenotypic plasticity may play an important role in the establishment of plant populations in novel environments, either after colonization of a new habitat or as a response to change in the *in situ* environmental conditions (Donohue *et al.*, 2001; Pigliucci, 2001; Richards *et al.*, 2006). If plasticity has evolved as a response to environmental heterogeneity in a specific habitat, and this within-habitat variation resembles the differences between two different habitats, plasticity may allow the establishment and persistence of the population in the altered environment (Donohue *et al.*, 2001).

In this context, it is noteworthy mentioning that plasticity may also be relevant as an indirect response to global change. For example, if a plant species shifts its distribution to track changes in climate, it might be exposed to other new environmental conditions to which it may also respond plastically. For example, a plant species may migrate northward to keep the climatic conditions constant. However, soil features and the composition of the plant community in the new environment may be different, as species differ in the ability to track changes in climate (Pigliucci and Marlow, 2001; Thuiller, 2003). Thus, species interactions and soil nutrient availability can be rather different in the new environment, despite similarities in climate.

Alongside the role of plasticity in colonization and adaptation to novel environments, the evolution of phenotypic plasticity may be critical for the persistence of plant populations in complex scenarios where different global change drivers interact. In cases where opportunities for dispersal and distribution shifts are limited by natural barriers or habitat fragmentation, rapid adaptation may be necessary to prevent extinction of plant species subject to global change

(Pamesan, 2006; Lande, 2009). For example, in fragmented or alpine habitats where dispersal and migration to other favourable sites are limited or even prohibited, evolutionary processes, including the evolution of plasticity, play a more important role in adaptation to changing environmental conditions (Jump and Peñuelas, 2005; Franks *et al.*, 2007).

Another relatively unknown form of plasticity that may be beneficial in these situations is transgenerational plasticity, that is, the effects of the maternal environment on the development of the offspring. Some studies have reported adaptive transgenerational plasticity when the maternal and the offspring environments are correlated (Mousseau and Fox, 1998). For example, in a recent study, Sultan *et al.*, (2009) found that drought-stressed plants of *Polygonum persicaria*, a plant that occurs in a wide variety of moisture conditions, produced offspring that grew longer roots and greater biomass when grown in dry conditions (Sultan *et al.*, 2009).

The role of phenotypic plasticity in colonization and adaptation has important consequences for simulations of changes in species distributions and predictions of local extinctions due to global change. Phenotypic plasticity not only allows colonization and adaptation to novel environments but also may be very beneficial in critical situations where dispersal is limited. Altogether, this suggests that the projections of shrinkage of species ranges or local extinctions may be overestimated or misleading.

### **2.9. Phenotypic Plasticity and Ecological Restoration**

A major challenge facing today's ecologists is to determine the links and relative importance of abiotic and biotic factors as drivers of ecosystem functioning (Loreau *et al.*, 2001). Such knowledge is relevant for restoration ecologists and practitioners (Mendez *et al.*, 2008). Many theories predicting how ecosystem composition, structure, and functioning are linked along degradation/restoration trajectories have been developed during recent decades (Bradshaw, 1984; Aronson *et al.*, 1993; Hobbs and Norton, 1996; Suding and Gross, 2006). Many of the

conceptual models developed often imply that the lack of certain ecosystem components and/or functions may limit restoration efforts (Whisenant, 1999). Some of them, such as the highly influential model proposed by Bradshaw (1984) for the reclamation of derelict land, assume that increases in structure (any description of community composition, and the way organisms are organized; Bradshaw, 1984) parallel the recovery of ecosystem functioning in a linear way. Although a growing number of studies are showing that this action does not always recover either ecosystem structure or functioning, particularly under semiarid climates (Andres and Ojeda 2002; Maestre and Cortina, 2004a; Chirino *et al.*, 2006; Goberna *et al.*, 2007), afforestations are still being recommended and executed in the same way as has been carried out during the past decades (Rojo *et al.*, 2002).

In the past few decades, phenotypic plasticity has become a central issue of ecological and evolutionary research (Valladares and Gianoli, 2007). It is now clear that phenotypic plasticity may be adaptive, that it can be genetically based, and that individual plastic responses may affect not only population parameters but also community-level interactions and ecological breadth (Schlichting and Pigliucci, 1998; Pigliucci, 1996; 2001; Gonzalez and Gianoli 2004; Miner *et al.*, 2005; Saldaña *et al.*, 2005; Richards *et al.*, 2006). The occurrence of phenotypic plasticity might be essential for natural populations to cope with environmental heterogeneity (Bradshaw and Hardwick 1989). Consequently, the reintroduction of individuals into degraded ecosystems should include previous evaluations of plasticity to the prevailing and/or more stressful ecological factors. Surprisingly, the concept of phenotypic plasticity has not been incorporated into the realm of restoration ecology.

The adoption of plasticity estimates may be useful in the development of restoration initiatives (Valladares and Gianoli, 2007). This leads to approach to phenotypic plasticity, whose

maximization is not necessarily adaptive for all plants dwelling in a habitat (Valladares *et al.*, 2005), and to consider the complexity of the phenotypic responses of organisms to multiple ecological factors.

Despite the wide, and renewed, interest on the topic created by the rise of the biodiversity–ecosystem functioning perspective (Naeem, 2006), the relationships between ecosystem structure, functioning, and restorability i.e. the difficulty to bring a degraded ecosystem to a desired target state, or the effort needed to do so (Cortina *et al.* 2006) have been seldom assessed (Mendez *et al.*, 2008). In one of such studies, Baeza *et al.*, (2007) evaluated the relationships between ecosystem structure and functioning in shrub lands and forests along a 30-year fire chrono-sequence in eastern Spain. They found metastable states, hysteresis, and thresholds in the successional trajectory of vegetation, as well as a negative relationship between species richness and productivity.

In other study, Maestre *et al.*, (2006) explored the relationship between ecosystem functioning and restorability in *Stipatenacissima* steppes from southeast Spain. They found that the survival of seedlings of the late-successional shrub *Pistacia lentiscus*—their measure of restorability—was mainly controlled by abiotic conditions and showed a negative relationship with surrogates of ecosystem functioning such as the infiltration capacity of the soil.

Results such as these indicate that relationships between ecosystem structure and functioning in Mediterranean environments are complex and that the functional status of the ecosystem may not necessarily determine the outcome of restoration processes (Mendez *et al.*, 2008). They also highlight some of the limitations of the predominant conceptual paradigms and set the case for an invigorated research effort in the field.

Mendez *et al.*, (2008), suggest the development of a research agenda aiming to explore the relationships between ecosystem composition/structure and its functioning along landscape or degradation gradients comprising ecosystems targeted for conservation or management. Such information would be an invaluable tool to improve current restoration protocols and procedures and would also serve as a test of theories and models currently employed by restoration ecologists (Falk *et al.*, 2006).

For instance, the utility of this approach is provided by recent studies carried out along degradation gradients in semiarid *S. tenacissima* steppes from southeast Spain (Maestre, 2004; Maestre and Cortina, 2004b; Maestre and Cortina, 2005). They have found that basic attributes of patches (landscape units that collect water, sediments, and nutrients coming from run-off), such as their density and the distance between them, and the cover of late-successional sprouting shrubs were major drivers of species diversity and richness and of soil stability, infiltration, and nutrient cycling in these steppes.

Given the inherent difficulties associated to assessing whether a particular landscape is in need of restoration (Hobbs, 2002), and what components/functions should be restored first, an in-depth consideration of the functional status of ecosystems, its drivers, and dynamics should prominently figure among the research agendas of restoration ecologists. Although challenging, any advance in the field will undoubtedly represent a step forward to develop a specific technology to establish ecologically sound restoration practices in Mediterranean ecosystems (Valladares and Gianoli, 2007).



## **CHAPTER THREE**

### **3.0 MATERIALS AND METHODS**

The research work consisted of two phases. The first experiment was a pilot survey of the study area (abandoned dumpsite behind IQSA-Ramat Hall, Ahmadu Bello University (ABU), Samaru, Zaria) as a preliminary investigation to determine the most abundant species.

The second phase was a screen house experiment at the Department of Biological Sciences garden using soil fertility, irrigation interval and plant density as treatment factors.

### **3.1. Study Area**

The study area is located within the main campus of Ahmadu Bello University, Samaru, Zaria in Kaduna State, Nigeria. The campus is located at Latitude 11° 11' N and Longitude 7° 38' E, 686 m above sea level. Zaria is located on the high plains of Northern Nigeria Guinea Savannah, some 950km away from the coast. Zaria possesses a tropical continental climate with a pronounced dry season, lasting up to seven months (October - May). During the dry season, a cool period is usually experienced between November and February. Zaria experiences a brief period of hot but dry weather in March and April, the mean daily maximum temperatures are fairly stable, and they range from 38°C to 42°C during this period. The rainy season lasts from May to September/October with long-term annual rainfall of 1040mm in about 90 rain days (Ahmadu Bello University, n.d.). The study area is an abandoned dumpsite located behind IQSA/Ramat hall with an uneven topography consisting of valleys and slopes. The site was chosen because of its extensiveness and to investigate how plant species will respond to these scenarios.

#### **3.1.1. Soil analysis**

Soil samples were collected from each of the three sites (base, slope, and top) of the study area. The samples were taken at a depth of 6 inches. The soils were air dried and sieved through 2.0mm sieve and analysed for their physicochemical properties. Soil texture class was determined using Bouyoucos (1951) hydrometer method. The textural class was determined using textural triangle (USDA, 1960). Soil pH was measured with the aid of pH meter (Black, 1965) and the organic carbon was determined using the procedure described by Wolf (1982). Total nitrogen and available phosphorus were determined using Micro-Kjeldhal (Bremner, 1965) and Trough (1950) procedures, respectively. Exchangeable cations were determined using Reith (1967) method. Atomic absorption spectro-photometry was employed to estimate calcium, potassium and magnesium concentrations using PG Instrument model AA500.

### **3.2. Study Species**

A preliminary vegetation survey of the study area was carried out to ascertain the type of species and the most abundant species. It was discovered that *Sida acuta* and *Euphorbia heterophylla* were the most common and most abundant; and they were found coexisting in all the areas sampled.

#### **3.2.1. *Sida acuta* Burm.F.**

*S. acuta* is a small, erect, perennial shrub, branching profusely from the base. It is commonly called Broom weed (Hausa: Miyantsanya) and mainly a weed of the tropics and subtropics. Although it grows widely throughout the tropics, it can be found at higher elevations. The weed is frequently found in pastures, wastelands, cultivated lands, roadsides, lawns, and in planted forests. Once the plant becomes established, it is very competitive, holding and denying sites to other plants. It does appear to do best in disturbed habitats such as dumpsites and roadsides. The plant grows well in many soils, including some heavy clay, and can tolerate dry as well as high rainfall conditions. It has a deep taproot which can withstand drought, mowing, or shallow infrequent tillage. Tough woody stems also aid in its persistence (Holm *et al.*, 1977).

#### **3.2.2. *Euphorbia heterophylla* L.**

*E. heterophylla* is herbaceous, erect and 20-200 cm in height (depending on growing conditions). It is commonly called Fireplant (Hausa: Nononkurchiya) it grows in most tropical and subtropical regions on a wide range of soils, principally in shaded waste places and in cultivated areas (Parsons and Cuthbertson, 1992). It spread by seeds that are released explosively from ripe pods. It causes serious loss of yield and quality in a wide range of crops as it competes successfully by growing rapidly and forming a dense canopy over the crop (Kissman and Groth, 1993). According to Holm *et al.* (1979), *E. heterophylla* is a major weed problem in Fiji, Ghana, Mexico, and Thailand, and a principal weed in Brazil, India, Italy, Uganda and USA. Crops in which it is reported as a major weed

include cocoa, coffee, cotton, cowpeas, maize, papaya, groundnut, sorghum, soyabean, sugarcane, tea and upland rice (Parsons and Cuthbertson, 1992).

### **3.3. Experimental Design**

A glass house experiment to study the phenotypic plasticity of the twoweed species was carried out between the month of May and August, 2014. Seeds used in this experiment were collected from the study site during the month of December, 2013. Seeds of both species were sown in plastic bags containing topsoil (5cm depth) that was obtained from the Botanical garden, ABU, Zaria, to have a uniform germination. Two weeks after emergence, the seedlings were transferred to 27.6cm diameter and 26.5cm deep plastic pots containing soil (2.4kg) from the study site.

The three factors (soil fertility, water availability, and plant density) were chosen to reflect the stressful and unstressful growing habitats for both species. The soil and plant density treatments were imposed immediately after seedlings were transferred to pots (Huang *et al.*, 2009). The water treatment (irrigation interval) was imposed four weeks after emergence (Huang *et al.*, 2009).

Each factor had three levels; High, Medium and Low;

W1: low water level, amount of water at 500ml was applied once a week (7 days).

W2: medium water level, 500ml of water was applied twice a week (3 days).

W3: high water level, 500ml of water was applied every other day (2 days).

D3: high density level, 10 plants in each pot.

D2: medium density level, 5 plants in each pot.

D1: low density level, 3 plants in each pot.

S3: soil from the base(highest nutrient).

S2: soil from the slope (medium nutrient).

S1: soil from the top(low nutrient).

A full-factorial design of the possible combinations of high, medium and low levels of soil, water and plant density was constructed (Table 3.1). Each species had 486 plants, 27 possible treatment combinations, 3 replications for each treatment combination. In order to avoid edge effects, the pots for each treatment were placed together and the position of each treatment changed every 2 weeks (Huang *et al.*, 2009).

Table 3.1:3×3×3 treatment combination of soil fertility level, plant density and irrigation interval (water)

		<b>Factor S</b>		
<b>Factor W</b>	<b>Factor D</b>	<b>1</b>	<b>2</b>	<b>3</b>
1	1	S1W1D1	S2W1D1	S3W1D1
1	2	S1W1D2	S2W1D2	S3W1D2
1	3	S1W1D3	S2W1D3	S3W1D3
2	1	S1W2D1	S2W2D1	S3W2D1
2	2	S1W2D2	S2W2D2	S3W2D2

2	3	S1W2D3	S2W2D3	S3W2D3
<hr/>				
3	1	S1W3D1	S2W3D1	S3W3D1
3	2	S1W3D2	S2W3D2	S3W3D2
3	3	S1W3D3	S2W3D3	S3W3D3

### 3.4. Measurements

The plants were harvested after 12 weeks and a total of 9-10 intact plants from each treatment was randomly selected for measurement of morphological and biomass traits (Huang *et al.*, 2009). Each plant was separated into leaves, stems, roots and reproductive organs. Dry mass were determined after oven-drying at 65°C for 48hrs. The following traits were recorded for each individual plant: absolute height (H), number of leaves, stem girth, biomass of roots (BRO), biomass of stems (BS), biomass of leaves (BL), reproductive biomass (BRE), vegetative biomass (BV), total biomass (BT), root-shoot ratio (RSR), relative biomass of stem (RS), relative biomass of leaves (RL) and relative reproductive biomass (RRE) (Huang *et al.*, 2009a).

$$BV = BRO + BS + BL$$

$$RSR = BRO / (BS + BL + BRE)$$

$$RS = BS / BT$$

$$RL = BL / BT$$

$$\text{RRE} = \text{BRE}/\text{BT}$$

### **3.5. Data Analysis**

Data were analysed with SAS software (2005 version) (SAS Institute Inc., Cary, NC, USA). Only mean values of each trait from individual plants were used in the analysis (Hurlbert, 1984). A four-way analysis of variance (ANOVA) was used to test the effects of species (S), nutrients (N), water (W), and density (D) on morphological traits. To account for the influence of plant size on biomass allocation, total biomass was used as a covariate when we tested the following traits: RL, RS, and RRE (Maestreet *al.*, 2006). The phenotypic plasticity was quantitatively estimated by the slope of norm of reaction. Correlation of BRE ( $\Upsilon$ ) on BV ( $X$ ) was conducted to characterise the allometry of reproduction in different environmental conditions.

## CHAPTER FOUR

### 4.0

### RESULTS

#### 4.1. Phenotypic Plasticity of *Euphorbia heterophylla* and *Sida acuta* Morphological Traits

Mean values for all traits were significantly different between the two species (Table 4.1). *E. heterophylla* had a longer stem, higher number of leaves, biomass and stem width.

Table 4.1 shows some of the measured morphological traits of the two weed species as influenced by soil fertility status. Stem height for both plant species varied with varying soil fertility status. Growing *E. heterophylla* in soil of high fertility resulted in the longest stem. This was followed by stem of same species grown in either low or medium soil fertility soil. Stem length of *S. acuta* was the shortest regardless of the soil fertility status. *E. heterophylla* had recorded significantly higher values for stem girth and number of leaves than *S. acuta* even though leaves produced by latter under high fertility status did not differ significantly from that of *E. heterophylla*. Varying the fertility status of the soil had no significant effect on stem girth and number of leaves of each of the plant species.

Morphological traits for the weed species as influenced by irrigation intervals is presented on Table 4.2. For each of the weed species delaying irrigation from 2 to 3 and further to 7 days interval had



no significant effect on the morphological traits measured. However, *E. heterophylla* significantly recorded higher values for each of the character measured than *S. acuta*.

Table 4.1: Morphological traits of *E. heterophylla* and *S. acuta* in response to soil fertility status

Soil status	Fertility	Weed species	Stem height (cm)	Stem girth (cm)	Number of leaves
Low fertility		<i>E. heterophylla</i>	29.99±4.39 <sup>b</sup>	1.09±0.07 <sup>a</sup>	9.12±0.82 <sup>a</sup>
Medium fertility		<i>E. heterophylla</i>	31.04±5.09 <sup>b</sup>	1.14±0.12 <sup>a</sup>	11.87±2.68 <sup>a</sup>
High fertility		<i>E. heterophylla</i>	39.02±6.62 <sup>a</sup>	1.72±1.90 <sup>a</sup>	12.43±2.11 <sup>a</sup>
Low fertility		<i>S. acuta</i>	4.67±1.38 <sup>c</sup>	0.32±0.05 <sup>b</sup>	5.44±1.13 <sup>b</sup>
Medium fertility		<i>S. acuta</i>	6.29±1.62 <sup>c</sup>	0.31±0.04 <sup>b</sup>	7.19±1.35 <sup>b</sup>
High fertility		<i>S. acuta</i>	8.82±2.31 <sup>c</sup>	0.34±0.05 <sup>b</sup>	8.61±1.62 <sup>ab</sup>

P<0.01, Mean values with same superscripts along column are not significantly different.

Table 4.2: Morphological traits of *E. heterophylla* and *S. acuta* in response to irrigation intervals

Species	Irrigation intervals (days)	Stem height (cm)	Stem girth (cm)	Number of leaves
<i>E. heterophylla</i>	7	29.99±5.29 <sup>b</sup>	1.13±0.11 <sup>a</sup>	10.22±1.61 <sup>a</sup>
<i>E. heterophylla</i>	3	33.28±5.71 <sup>ab</sup>	1.71±0.32 <sup>a</sup>	12.57±2.62 <sup>a</sup>
<i>E. heterophylla</i>	2	37.69±6.15 <sup>a</sup>	1.15±0.09 <sup>a</sup>	11.57±2.03 <sup>a</sup>
<i>S. acuta</i>	7	6.17±1.78 <sup>c</sup>	0.33±0.05 <sup>b</sup>	7.38±1.58 <sup>b</sup>
<i>S. acuta</i>	3	6.69±1.99 <sup>c</sup>	0.32±0.04 <sup>b</sup>	7.37±1.52 <sup>b</sup>
<i>S. acuta</i>	2	6.91±1.91 <sup>c</sup>	0.33±0.04 <sup>b</sup>	6.49±1.19 <sup>b</sup>

P<0.01, Mean values with same superscripts along column are not significantly different.

Stem length and girth and number of leaves for two weed species as affected by plant density is shown on Table 4.3. Plant density significantly influenced only the stem girth and number of leaves of *E. heterophylla*, while stem height for same species was significantly not influenced by the variation in plant density. Stem girth of *E. heterophylla* grown at low population density of 3 was more for when grown at 5 or 10 plants per pot. Likewise leaves produced by *E. heterophylla* when sown at 3 or 5 plants per pot were statistically similar more than for 10 plants per pot. The stem length and girth as well as number of leaves for *S. acuta* were significantly not influenced by varying plant density even though lower than for *E. heterophylla*.

Table 4.3: Morphological traits of *E. heterophylla* and *S. acuta* in response to plant density

Species level	Plant density	Stem height (cm)	Stem girth (cm)	Number of leaves
<i>E. heterophylla</i>	3	35.98±6.89 <sup>a</sup>	1.83±0.31 <sup>a</sup>	14.38±2.89 <sup>a</sup>
<i>E. heterophylla</i>	5	33.01±5.51 <sup>a</sup>	1.12±0.10 <sup>b</sup>	11.01±1.70 <sup>a</sup>
<i>E. heterophylla</i>	10	31.97±4.79 <sup>a</sup>	1.04±0.08 <sup>b</sup>	8.57±0.86 <sup>b</sup>
<i>S. acuta</i>	3	8.57±2.32 <sup>b</sup>	0.38±0.06 <sup>c</sup>	8.28±1.59 <sup>b</sup>
<i>S. acuta</i>	5	6.29±1.91 <sup>b</sup>	0.30±0.04 <sup>c</sup>	7.01±1.58 <sup>b</sup>
<i>S. acuta</i>	10	4.91±0.99 <sup>b</sup>	0.28±0.03 <sup>c</sup>	5.94±0.97 <sup>b</sup>

P<0.01, Mean values with same superscripts along column are not significantly different.

The interactions of weed species, soil fertility status and plant density on stem length, stem girth and number of leaves is presented on table Table 4.4. The response varied across morphological traits. Plant species height and number of leaves of *E. heterophylla* decreases only when population density was increased from 5 to 10 plants in low and medium fertile soil, while in high fertile soil only stem height decreased at plant density of 10 plants per pot. In the case of *S. acuta* increasing plant density from 3 to 5 plants in low fertility soil and from 5 to 10 plants per pot in high fertility soil significantly reduced stem height and number of leaves. While stem girth of *S. acuta* was significantly not influenced by varying plant density regardless of soil fertility status. It was however generally observed that values for these parameters for *E. heterophylla* were higher than for *S. acuta*. For example, *E. heterophylla* recorded higher mean values 46.30cm and 17.61 for stem height and number of leaves respectively in highly fertile soil and low plant density level compared to low soil fertility and low plant density with 26.35cm and 9.44 values respectively, which was 64% and 65% increase in stem height and number of leaves. Similarly, *S. acuta* recorded higher mean values 11.01cm and 8.52 in high soil fertility condition and low plant densities than low soil fertility and low plant density for both stem height and number of leaves respectively.

Table 4.4: Morphological traits of *E. heterophylla* and *S. acuta* in response to soil fertility and plant density treatment interactions.

Soil Fertility status	Species level	Plant density	Stem height (cm)	Stem girth (cm)	Number of leaves
Low	<i>E. heterophylla</i>	3	29.35±3.85 <sup>cd</sup>	1.10±0.07 <sup>a</sup>	9.44±0.78 <sup>b</sup>
Low	<i>E. heterophylla</i>	5	34.52±5.28 <sup>c</sup>	1.12±0.07 <sup>a</sup>	10.07±0.80 <sup>b</sup>
Low	<i>E. heterophylla</i>	10	26.06±3.55 <sup>d</sup>	1.03±0.06 <sup>a</sup>	7.85±0.71 <sup>c</sup>
Medium	<i>E. heterophylla</i>	3	32.78±6.58 <sup>c</sup>	1.21±0.14 <sup>a</sup>	14.86±3.53 <sup>a</sup>
Medium	<i>E. heterophylla</i>	5	31.71±5.66 <sup>c</sup>	1.17±0.13 <sup>a</sup>	12.69±2.46 <sup>ab</sup>
Medium	<i>E. heterophylla</i>	10	28.63±4.39 <sup>d</sup>	1.01±0.08 <sup>a</sup>	8.05±0.83 <sup>c</sup>
High	<i>E. heterophylla</i>	3	46.30±7.56 <sup>a</sup>	1.00±0.28 <sup>a</sup>	17.61±2.68 <sup>a</sup>
High	<i>E. heterophylla</i>	5	33.17±5.65 <sup>c</sup>	1.06±0.09 <sup>a</sup>	10.02±1.03 <sup>b</sup>
High	<i>E. heterophylla</i>	10	37.49±5.50 <sup>b</sup>	1.08±0.08 <sup>a</sup>	9.63±0.69 <sup>b</sup>
Low	<i>S. acuta</i>	3	7.27±2.00 <sup>ef</sup>	0.41±0.07 <sup>b</sup>	7.86±1.51 <sup>c</sup>
Low	<i>S. acuta</i>	5	3.07±0.51 <sup>g</sup>	0.25±0.03 <sup>b</sup>	4.16±0.65 <sup>d</sup>
Low	<i>S. acuta</i>	10	3.66±0.58 <sup>g</sup>	0.28±0.03 <sup>b</sup>	4.30±0.46 <sup>d</sup>
Medium	<i>S. acuta</i>	3	7.43±1.97 <sup>ef</sup>	0.32±0.04 <sup>b</sup>	8.47±1.83 <sup>c</sup>
Medium	<i>S. acuta</i>	5	6.35±1.67 <sup>f</sup>	0.31±0.04 <sup>b</sup>	7.00±1.11 <sup>c</sup>
Medium	<i>S. acuta</i>	10	5.09±0.98 <sup>f</sup>	0.28±0.03 <sup>b</sup>	6.11±0.81 <sup>c</sup>
High	<i>S. acuta</i>	3	11.01±2.74 <sup>e</sup>	0.40±0.06 <sup>b</sup>	8.52±1.43 <sup>bc</sup>
High	<i>S. acuta</i>	5	9.45±2.41 <sup>e</sup>	0.34±0.05 <sup>b</sup>	9.88±2.03 <sup>b</sup>
High	<i>S. acuta</i>	10	5.99±1.18 <sup>f</sup>	0.29±0.03 <sup>b</sup>	7.41±1.20 <sup>c</sup>

P<0.01, Mean values with same superscripts along column are not significantly different.

Morphological traits for the two weed species as influenced by varying soil fertility and irrigation interval interaction is presented on Table 4.5. Both species stem height varied with varying soil fertility status, and recorded significantly higher stem height in high soil fertility and 2-day

irrigation interval. For instance, in the interaction of high fertility soil and 2-day irrigation interval *E. heterophylla* recorded 42.29cm stem height and 11.94 number of leaves as compared to its performance in the interaction of low soil fertility and 7-day irrigation interval which was 25.24cm and 8.88 for stem height and number of leaves respectively, however, the interactions had no significant influence. Also, *S. acuta* had greater performance in the interaction of high soil fertility and 2-day irrigation interval than low soil fertility and 7-day irrigation interval, with an increase of 96% in stem height and 56% for number of leaves (Table 4.5) and was significantly influenced by varying soil fertility and irrigation interval interactions.

Both species mean morphological values increased with decreased irrigation interval, and also, decreased as density per pot increased. The increased ratio of *E. heterophylla* stem height in low density and 2-day irrigation interval compared to high density and 2-day irrigation interval interactions was 13%, while that of *S. acuta* was 37% (Table 4.6).

All morphological traits were significantly affected by four-way interaction of treatment factors. And, it increased with soil fertility increased and irrigation interval decreased, while, it decreased with density increased.

Table 4.5: Morphological traits of *E. heterophylla* and *S. acuta* in response to soil fertility and irrigation interval interaction

Soil fertility status	Species level	Irrigation	Stem height	Stem girth	Number of
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		interval	(cm)	(cm)	leaves
Low fertility	<i>E. heterophylla</i>	Low	25.24±3.34 <sup>b</sup>	1.06±0.06 <sup>a</sup>	8.88±0.85 <sup>b</sup>
Low fertility	<i>E. heterophylla</i>	Medium	28.83±4.15 <sup>b</sup>	1.08±0.08 <sup>a</sup>	9.00±0.86 <sup>b</sup>
Low fertility	<i>E. heterophylla</i>	High	35.88±4.92 <sup>a</sup>	1.11±0.06 <sup>a</sup>	9.48±0.91 <sup>b</sup>
Medium fertility	<i>E. heterophylla</i>	Low	27.37±4.55 <sup>b</sup>	1.12±0.13 <sup>a</sup>	9.50±1.57 <sup>b</sup>
Medium fertility	<i>E. heterophylla</i>	Medium	31.30±5.78 <sup>ab</sup>	1.13±0.11 <sup>a</sup>	14.44±3.21 <sup>a</sup>
Medium fertility	<i>E. heterophylla</i>	High	34.44±6.22 <sup>a</sup>	1.15±0.11 <sup>a</sup>	11.66±2.79 <sup>a</sup>
High fertility	<i>E. heterophylla</i>	Low	36.16±6.52 <sup>a</sup>	1.19±0.13 <sup>a</sup>	11.94±1.97 <sup>a</sup>
High fertility	<i>E. heterophylla</i>	Medium	38.09±6.31 <sup>a</sup>	1.16±0.29 <sup>a</sup>	13.38±2.61 <sup>a</sup>
High fertility	<i>E. heterophylla</i>	High	42.29±6.73 <sup>a</sup>	1.19±0.10 <sup>a</sup>	11.94±1.67 <sup>a</sup>
Low fertility	<i>S. acuta</i>	Low	4.83±1.66 <sup>d</sup>	0.33±0.06 <sup>b</sup>	5.09±1.26 <sup>c</sup>
Low fertility	<i>S. acuta</i>	Medium	4.60±1.45 <sup>d</sup>	0.31±0.05 <sup>b</sup>	5.41±1.29 <sup>c</sup>
Low fertility	<i>S. acuta</i>	High	4.56±0.97 <sup>d</sup>	0.30±0.04 <sup>b</sup>	5.22±0.80 <sup>c</sup>
Medium fertility	<i>S. acuta</i>	Low	5.66±1.37 <sup>d</sup>	0.30±0.03 <sup>b</sup>	7.58±1.53 <sup>bc</sup>
Medium fertility	<i>S. acuta</i>	Medium	6.51±1.73 <sup>d</sup>	0.30±0.03 <sup>b</sup>	7.69±1.47 <sup>bc</sup>
Medium fertility	<i>S. acuta</i>	High	6.69±1.75 <sup>d</sup>	0.31±0.04 <sup>b</sup>	6.30±0.95 <sup>c</sup>
High fertility	<i>S. acuta</i>	Low	8.02±2.10 <sup>c</sup>	0.35±0.05 <sup>b</sup>	8.88±1.76 <sup>b</sup>
High fertility	<i>S. acuta</i>	Medium	8.96±2.44 <sup>c</sup>	0.33±0.04 <sup>b</sup>	9.00±1.56 <sup>b</sup>
High fertility	<i>S. acuta</i>	High	9.47±2.40 <sup>c</sup>	0.35±0.05 <sup>b</sup>	7.94±1.54 <sup>bc</sup>

P<0.01, Mean values with same superscripts along column are not significantly different.

Table 4.6: Morphological traits of *E. heterophylla* and *S. acutain* response to plant density and irrigation interval interaction



Species level	Plant density	Irrigation interval	Stem height (cm)	Stem girth (cm)	Number of leaves
<i>E. heterophylla</i>	3	7	31.95±6.84 <sup>b</sup>	1.29±0.14 <sup>a</sup>	12.75±2.25 <sup>ab</sup>
<i>E. heterophylla</i>	3	3	35.81±6.77 <sup>ab</sup>	1.19±0.10 <sup>a</sup>	16.09±3.40 <sup>a</sup>
<i>E. heterophylla</i>	3	2	40.17±7.00 <sup>a</sup>	1.24±0.11 <sup>a</sup>	14.30±2.89 <sup>a</sup>
<i>E. heterophylla</i>	5	7	28.04±4.48 <sup>b</sup>	1.07±0.11 <sup>a</sup>	9.60±1.08 <sup>b</sup>
<i>E. heterophylla</i>	5	3	33.76±5.61 <sup>b</sup>	1.13±0.10 <sup>a</sup>	12.91±2.32 <sup>ab</sup>
<i>E. heterophylla</i>	5	2	37.22±6.05 <sup>a</sup>	1.16±0.09 <sup>a</sup>	10.51±1.28 <sup>b</sup>
<i>E. heterophylla</i>	10	7	29.97±4.27 <sup>b</sup>	1.04±0.08 <sup>a</sup>	8.30±0.73 <sup>b</sup>
<i>E. heterophylla</i>	10	3	30.26±4.58 <sup>b</sup>	1.03±0.07 <sup>a</sup>	8.72±0.99 <sup>b</sup>
<i>E. heterophylla</i>	10	2	35.68±5.38 <sup>ab</sup>	1.07±0.08 <sup>a</sup>	8.69±0.85 <sup>b</sup>
<i>S. acuta</i>	3	7	8.95±2.25 <sup>c</sup>	0.42±0.07 <sup>b</sup>	8.83±1.64 <sup>b</sup>
<i>S. acuta</i>	3	3	8.95±2.49 <sup>c</sup>	0.37±0.06 <sup>b</sup>	8.86±1.76 <sup>b</sup>
<i>S. acuta</i>	3	2	7.81±2.25 <sup>c</sup>	0.36±0.05 <sup>b</sup>	7.16±1.31 <sup>bc</sup>
<i>S. acuta</i>	5	7	5.32±1.58 <sup>cd</sup>	0.29±0.04 <sup>b</sup>	7.47±1.83 <sup>bc</sup>
<i>S. acuta</i>	5	3	6.33±1.94 <sup>c</sup>	0.29±0.04 <sup>b</sup>	6.94±1.50 <sup>c</sup>
<i>S. acuta</i>	5	2	7.21±2.18 <sup>c</sup>	0.32±0.05 <sup>b</sup>	6.64±1.40 <sup>c</sup>
<i>S. acuta</i>	10	7	4.25±0.85 <sup>d</sup>	0.27±0.03 <sup>b</sup>	5.86±1.03 <sup>c</sup>
<i>S. acuta</i>	10	3	4.80±1.07 <sup>d</sup>	0.28±0.03 <sup>b</sup>	6.31±1.13 <sup>c</sup>
<i>S. acuta</i>	10	2	5.69±1.01 <sup>cd</sup>	0.30±0.03 <sup>b</sup>	5.66±0.72 <sup>c</sup>

P<0.01, Mean values with same superscripts along column are not significantly different.

#### 4.2. Plasticity of Biomass Traits and Allocation

The allocation of biomass among traits varied significantly between the two species. The soil fertility level significantly affected total biomass (BT), the vegetative biomass and root biomass of

both species (Figure 1, 2, 3). The result showed that *E. heterophylla* had highest biomass in medium fertile soil (107g) which was 19% and 48% higher than the high and low fertile soil (Figure 1). The total biomass of *S. acuta* increases 37% (61.1g) in high fertile soil compared to the soil with low fertility (18.21) (Figure 1). Similarly the vegetative biomass (BV) and root biomass (BRO) showed an increase in biomass allocation as soil fertility increases (Figure 2 and 3). Conversely relative root biomass (RRO) decreases with increase in soil fertility (Figure 4). *E. heterophylla* showed 44% decline in RRO from low soil to high soil fertility, while *S. acuta* recorded 56% decline in relative root biomass allocation.

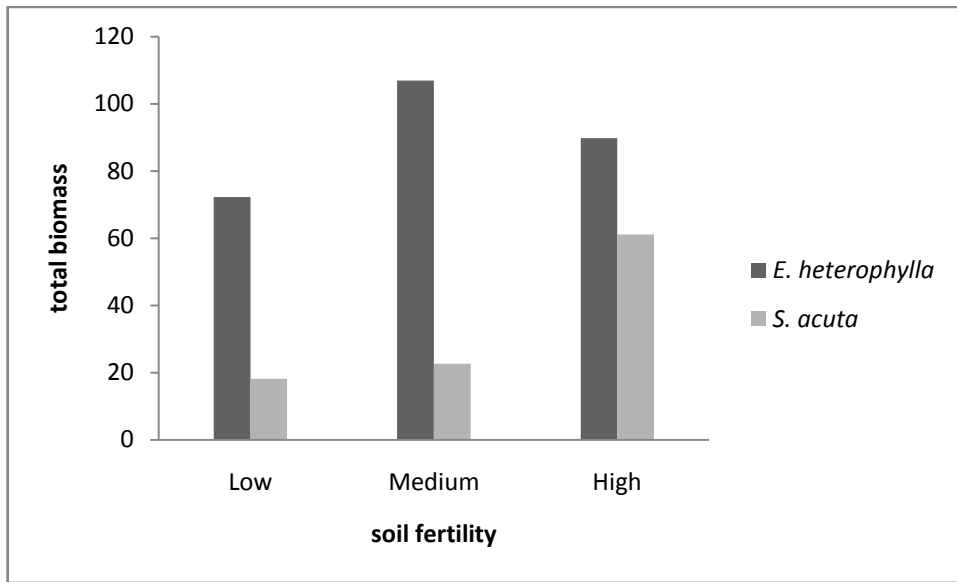


Figure 1. Total biomass production of *E. heterophylla* and *S. acuta* in response to different soil fertility status

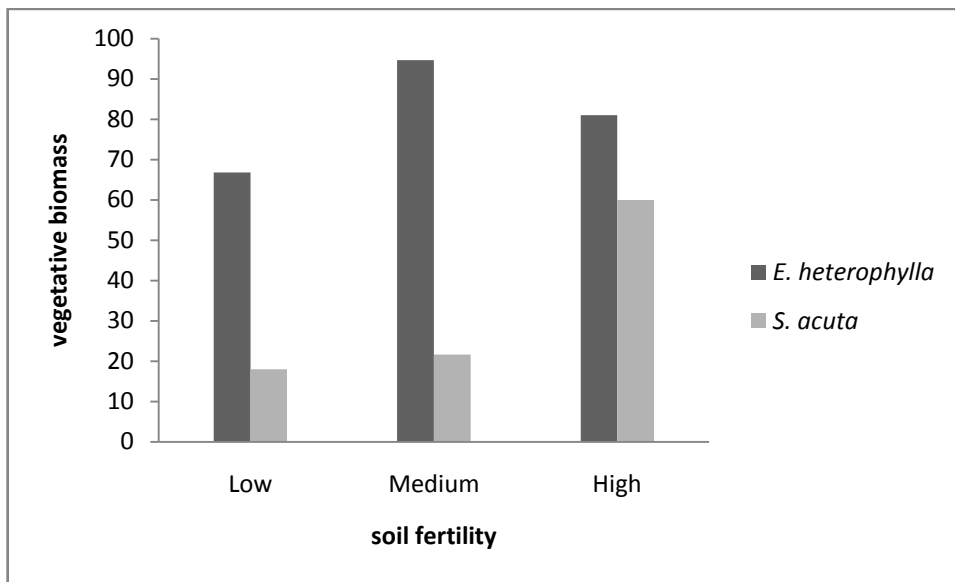


Figure 2. Vegetative biomass of *E. heterophylla* and *S. acuta* in response to soil fertility status

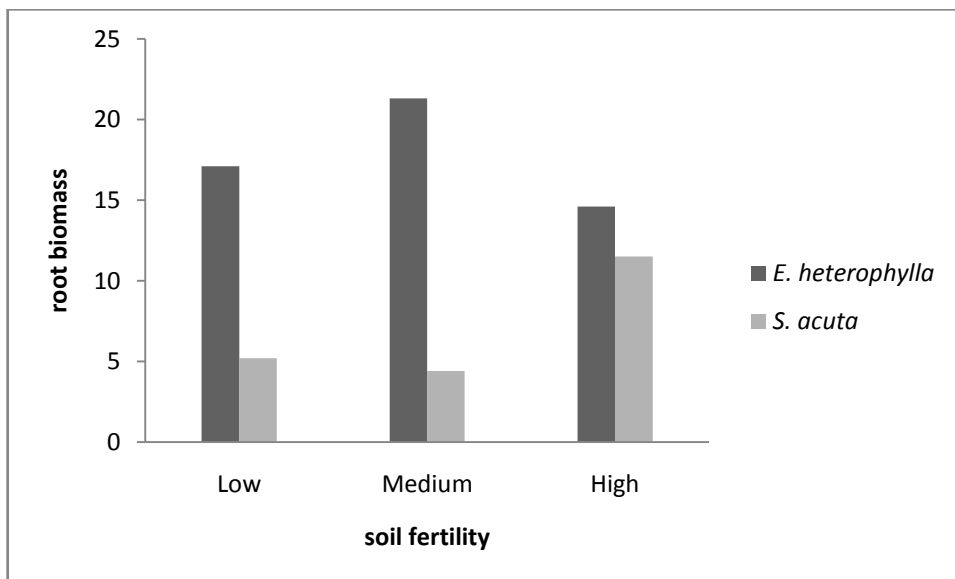


Figure 3. Root biomass of *E. heterophylla* and *S. acuta* in response to soil fertility status

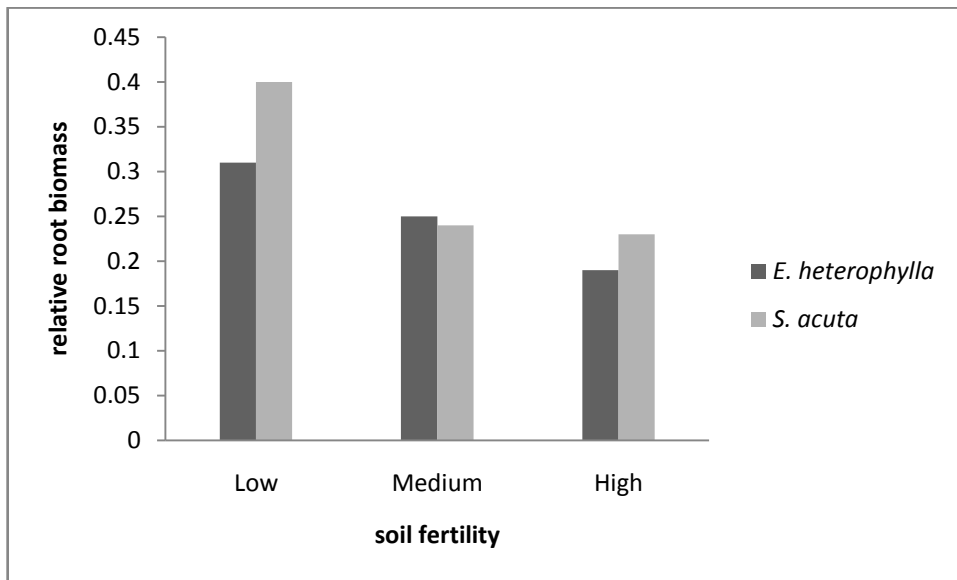


Figure 4. Relative root biomass of *E. heterophylla* and *S. acuta* in response to soil fertility status

The root shoot ratio (RSR) values increased with decreasing soil nutrient. The RSR values of *E. heterophylla* in the soil with high fertility was 0.19g which was lower than that of medium and low fertile soil (0.25g and 0.31g) respectively. Similarly, the RSR values of *S. acuta* in the low fertile soil was 0.40 which was 1.70 times higher than the RSR values in medium and high fertility soil (0.24g and 0.23g) respectively. This indicated that for both species soil fertility had significant effect on above and below-ground biomass allocations (Figure 5). However, the RSR of both species was not significantly different in the medium and high soil fertility.

Variation in soil fertility condition had no significant effect on relative biomass allocation of stem (RS) for each of the two weed species (Figure 6). The RS of *E. heterophylla* was significantly higher for each of the soil fertility level than for *S. acuta*. Relative leaf biomass of *E. heterophylla* (RL) was not significantly affected by soil fertility, likewise, no significant difference for *S. acuta* (Figure 7). Relative reproductive biomass allocation (RRE) was highest in the medium soil fertility, followed by high and then low fertility soil. RRE of *E. heterophylla* were significantly higher in all soil fertility levels than *S. acuta*.

The three-way analysis of variance showed that both soil fertility and plant density had a significant effect on relative stem biomass (RS), relative leaf biomass (RL), and relative reproductive biomass (RRE); however, irrigation interval had no significant effect on RL and RRE, only on RS (Table 4.7) ( $p < 0.01$ ). Also, relative root biomass (RRO) was significantly affected by plant density. A number of interactions had a significant effect on biomass allocation. Among the interactions  $S \times Sp$  had a significant effect on all the biomass allocation traits.  $S \times D$  and  $Sp \times D$  had a significant effect on RS and RRE. This indicated that there was significant difference on the plasticity between the two species (Table 4.7).

Correlation analyses indicated that, in all different treatments, reproductive biomass (BRE) showed a positive relationship with the vegetative biomass (BV) for both species (Table 4.8).

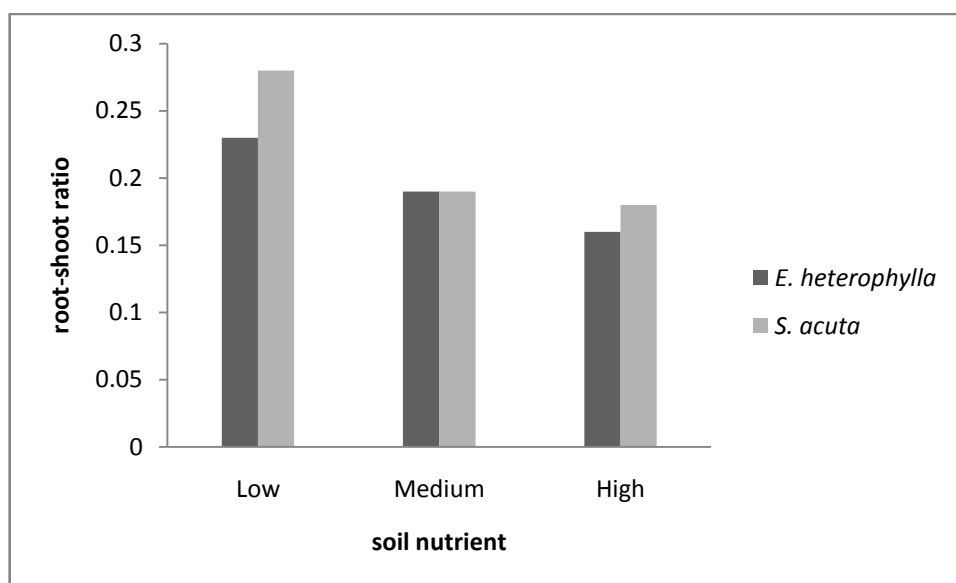


Figure 5. Root-shoot ratio of *E. heterophylla* and *S. acuta* in response to soil fertility status

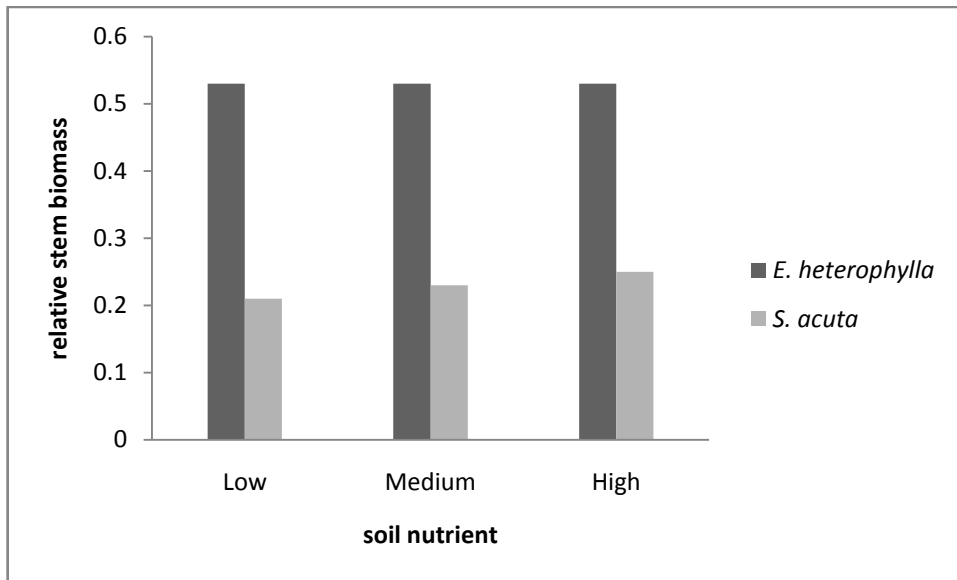


Figure 6. Relative stem biomass of *E. heterophylla* and *S. acuta* in response to soil fertility



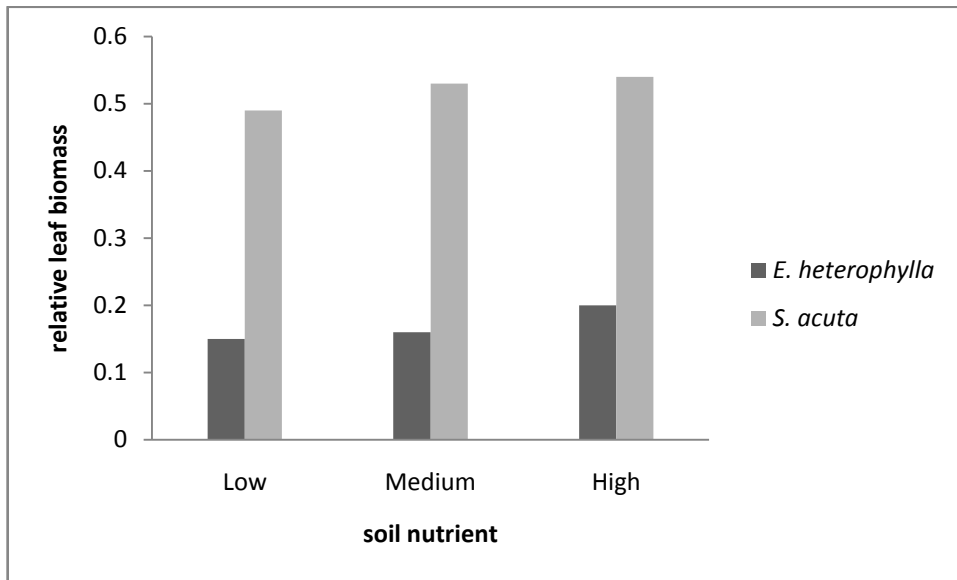


Figure 7. Relative leaf biomass of *E. heterophylla* and *S. acuta* in response to soil fertility

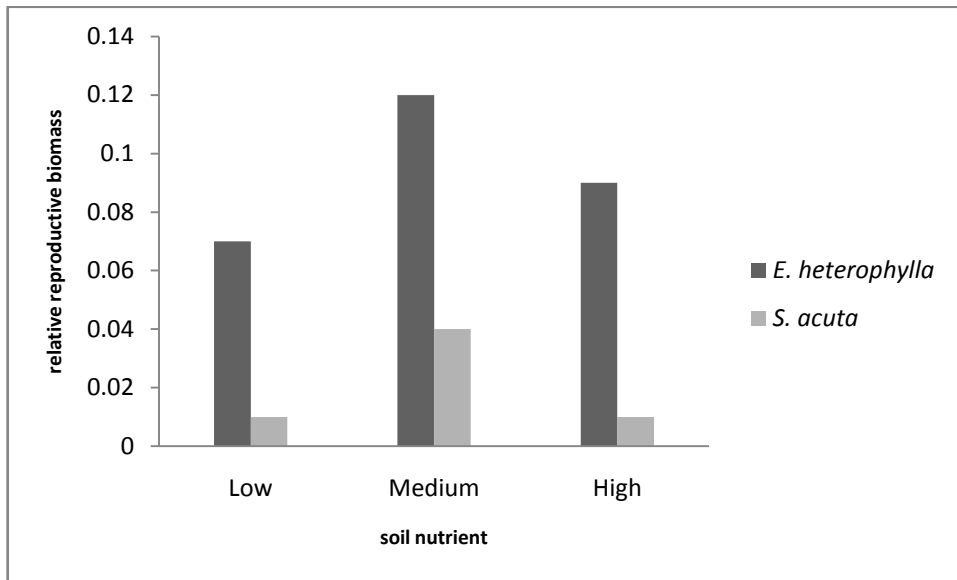


Figure 8. Relative reproductive biomass of *E. heterophylla* and *S. acuta* in response to soil fertility

Table 4.7: Analysis of variance for traits of *E. heterophylla* and *S. acuta* under soil fertility, water (irrigation interval) and plant density

Sources of variation	DF	RRO	RS	RL	RRE
Soil (S)	2	2.23	54.82**	92.25**	7.19**
Species (Sp)	1	173.36**	1927.45**	7.13**	84.15**
Density (D)	2	16.39**	35.97**	21.53**	5.42*
Water (W)	2	1.69	11.76**	0.89	0.57
S×Sp	2	24.95**	39.29**	41.56**	6.41**
S×D	4	1.25	17.77**	0.29	4.39*
S×W	4	1.05	2.08	0.36	1.64
Sp×D	2	2.16	7.33**	2.04	8.59**
Sp×W	2	0.39	4.53*	4.26	0.00
D×W	4	1.44	1.07	0.68	0.37
S×Sp×D	4	6.53**	25.77**	2.73	0.00
S×Sp×W	4	2.42*	3.52*	1.59	0.00
Sp×D×W	4	0.67	2.02	0.93	0.69

Significance at  $p < 0.05$  (\*),  $p < 0.01$  (\*\*), RRO = Relative root biomass, RS = relative biomass of stem, RL = relative biomass leaves, RRE = relative reproductive biomass

Table 4.8: Result of Correlation Analyses of Reproductive Biomass (Y) and Vegetative Biomass (X) in different Soil treatments.

Group	Soil fertility level	N	R <sup>2</sup>	Intercept
<i>E. heterophylla</i>	Low	36	0.369	-0.414
<i>E. heterophylla</i>	Medium	36	0.921	-0.209
<i>E. heterophylla</i>	High	36	0.835	-1.582
<i>S. acuta</i>	Low	36	0.788	-0.301
<i>S. acuta</i>	Medium	36	0.700	-0.148
<i>S. acuta</i>	High	36	0.488	0.101

## CHAPTER 5

### 5.0

### DISCUSSION

#### 5.1. Phenotypic Plasticity of *Euphorbia heterophylla* and *Sida acuta* Morphological Traits.

As with previous studies (Elberseet *al.*, 2003 and Huang *et al.*, 2009), the response of morphological traits to environmental variation was investigated here. This study clearly demonstrated that both species exhibited significantly increase plant height, leaves and higher biomass under high soil fertility and frequent irrigation interval, and low plant density, this trend was similar to earlier report (Huang *et al.*, 2009a). This might be as a result of the availability of nutrients, water and space, and also less competition.

It was observed that *E. heterophylla* exhibited a generalist strategy and was superior to *S. acuta* for most of the measured traits in response to the different soil fertility treatment suggesting a greater response to resource availability, hence, greater plasticity. However, *S. acuta* shows a specialist strategy and greater plasticity with its opportunistic response under high soil fertility. This could be as a result of different maturity period, because, *E. heterophylla* has a very short life cycle compared to *S. acuta* (CABI, 2014a,b). Van Kleunen *et al.*, (2010) reported that most trait differences between species are robust with respect to phylogeny.

Significant difference was observed between the two species in response to irrigation interval. *E. heterophylla* was better able to increase its fitness under frequent irrigation condition, while *S. acuta* maintained fitness at all irrigation regimes. This could be as a result of their differences in photosynthetic pathway, because *E. heterophylla* is a C<sub>4</sub> plant, while *S. acuta* is a C<sub>3</sub> plant. And, it has been reported that C<sub>4</sub> plants are more sensitive to water stress and have higher water-use-efficiency than C<sub>3</sub> plants (Ozturket *al.*, 1981). This agrees with Huang *et al.*, (2009b), where they found that species increase their fitness under increase water. Thus, patterns of plasticity in *S. acuta* could be said to be an example of an idealized scenario: “Master-of-some” better able to

increase fitness in favourable environments (Richards *et al.*, 2006); while *E. heterophylla* shows a complex strategy by exhibiting “Jack-of-all-trade” pattern that is maintaining fitness in unfavourable environment and also “Master-of-some” (Richards *et al.*, 2006). Based on this study, *E. heterophylla* was better able to increase fitness in some traits and maintain fitness for other traits, therefore *E. heterophylla* could be said to exhibit “Jack-and-Master” strategy (Richards *et al.*, 2006). In contrast, both species performances decline with increasing plant density. This might be as a result of competition for nutrients and space. This is in line with the findings of Japhet *et al.*, (2009), where they investigated phenotypic plasticity and found that a number of morphological traits (mean values) of *Fagopyrum esculentum* decreased as density increased. Similar results had been reported by Huang *et al.*, (2009a) on *Corispermum macrocarpum* and *Salsola collina* that density has significant influence on biomass allocation.

Plant density had significant influence on morphological traits of the two weeds. For instance, the interactions of soil fertility and plant density showed mean values for both species decreased with increase in plant density. The decreased ratio of height in high soil fertility – low plant density, compared to low soil fertility – low plant density, was 56% for *E. heterophylla* and 66% for *S. acuta*. This indicates significant plasticity for both species, and it is in line with the findings of Huang *et al.*, (2009a, 2012). This might be as a result competition for space and nutrient, with a corresponding loss of energy (Aerts *et al.*, 1991).

Similarly trait means increased with increased soil fertility and frequent irrigation. For example *E. heterophylla* had taller plants under high soil fertility and frequent irrigation interval condition compared to its performance at low soil fertility and frequent irrigation interval. However, the plants are shorter at high plant density regardless of irrigation frequencies. The interactions between species and environmental factors (treatments) varied across morphological traits, which imply shift in plasticity. Thus, the average performance of *E. heterophylla* was better than for *S.*

*acuta*, and the effect of interactions between species and environmental factors is significant. This agrees with the findings of Huang *et al.*, (2012) where they found out that plants do not have a uniform strategy in their response to environmental variables which could be as a result phylogenetic differences and ontogenetic drift.

## **5.2. Plasticity of Biomass Traits and Allocation**

The idea that individuals can adaptively adjust their behaviour, development and allocation of resources to competing demands is a cornerstone of behavioural ecology (Krebs and Davies, 2009). Total biomass (BT) increased at high soil fertility condition, while biomass of root (BRO) decreased. This agrees with “optimal partitioning theory (OPT)” in which it was reported that plant should allocate relatively more biomass to the organs that acquire the most limited resources (Bloom *et al.*, 1985). The root-shoot ratios (RSR) of both species were affected by different treatment regimes and there were significant differences in the RSR between the species. It was observed that both species had higher RSR values in the low fertility soil compared to the higher fertility soil. This result contrasts the Huang’s study on *Agriophyllum squarrosum*, in which the RSR of *A. squarrosum* was not affected by soil fertility because the variation of RSR in response to different soil fertility was balanced by plant body size (Huang *et al.*, 2009b). However, it agrees with (Moriuchi and Winn, 2005; Monyet *et al.*, 2007). Moriuchi and Winn’s (2005) study found plants in the lower-quality environment allocated proportionately less biomass to above-ground, and more to roots and rhizomes than those in the better environment this is consistent with Bloom *et al.*, (1985) optimal partitioning theory. This high RSR values under low soil fertility had been interpreted as evidence of a plastic response by a plant in order to capture more of a limiting resource (Kobe *et al.*, 2010).

The relative biomass of stem (RS) for *E. heterophylla* and *S. acuta* were unaffected by soil fertility levels. This is contrary to previous study of Poorter and Nagel (2000), which suggests that plants

allocate more biomass to stems at high soil fertility condition. This suggested that no plasticity occurred for stem biomass allocation with regard to soil fertility. These results were contrary to previously reported findings of Müller *et al.*, (2000) who reported that the “fraction of biomass in stems and, to a lesser extent, in leaves, was usually higher under soil fertility condition than in the low soil fertility condition. However, it agrees with Huang *et al.*, (2009c) in which they reported that RS was not influenced by soil fertility and plant density, and it was caused by plant size.

Relative leaf biomass (RL) of *E. heterophylla* and *S. acuta* was not affected by soil fertility conditions. In contrast to the findings of Poorter and Nagel, (2000), which reported that at different soil fertility levels leaf plasticity will be altered. This is because at low fertility conditions the decrease in nutrient uptake per unit root mass reduced the transpiration per unit leaf dry mass and hence low leaf plasticity corresponding to lower biomass (Hermans *et al.*, 2006).

Reproductive effort could vary according to different treatments (van Kleunen *et al.*, 2001). It can either increase (Hickman, 1977) or decrease (Snell and Burch, 1975) in response to increase in population density. In the present study, irrigation interval had no significant effect on biomass allocation and relative reproductive biomass (RRE). However, under high nutrient availability, plants allocate more biomass to other organs rather than to reproductive organs at the same plant size (Huang *et al.*, 2009a). In this study, it was observed that both *E. heterophylla* and *S. acuta* allocate more biomass to reproductive organ under medium soil fertility condition. This is because under high resource levels plants may postpone reproduction (Weiner *et al.*, 2009). Such a postponement in reproduction can be interpreted as developmental plasticity in the direction predicted by optimal allocation theory, which predicts that plants should devote 100% of their resources towards growth, and then switch to 100% allocation to reproduction (Cohen 1968; Ellner 1987).



Plants clearly have sophisticated methods of detecting dynamism of the environment they live in. This study showed that significant differences were found among different morphological traits of the two species, and were affected by environmental (treatment) conditions. Similarly, biomass allocation patterns of *S. acuta* and *E. heterophylla* differed in response to water and soil nutrients levels. On the whole *E. heterophylla* allocated proportionally more biomass to root and reproductive organ. In addition the biomass allocation pattern of *E. heterophylla* was consistent with optimal partitioning theory (OPT) which indicated that when resources are limited, allocation is channelled to relevant organs more resources to such organs. In contrast, *S. acuta* allocated more biomass to leaves and the root-shoot ratio also increases with decreases in soil nutrient. This is in line with Monyet *al.*, (2007) where they reported that Biomass production increased with fertilization and changes either in allocative ratios in response to nutrient availability. Although the total biomass of root, stem and leaves of *S. acuta* increased as soil fertility increases, *S. acuta* proportionally trade-off biomass between roots, stems and leaves. Also it was observed that plant density has a very significant effect on both vegetative and reproductive biomass, however, it contradicts Huang *et al.*, (2009b) findings where they reported that plant density has no significant effect on biomass allocation.

Correlation analysis indicated that in all different environmental factors (treatment) reproductive biomass showed a positive relationship with the vegetative biomass that is, as vegetative biomass increases, the reproductive biomass also increases. This is in line with previous findings (Li *et al.*, 2001; Sultan, 2001). These findings have suggested that plants increased reproduction in response to environmental stress (Li *et al.*, 2001), or that plants maintain reproductive output in resource poor environments. This indicates the ability of plants to maintain fecundity at low resource levels or as previously stated 'make the best of a bad job' (Sultan, 2001).

The variations observed in the present study also do not negate the value of mean traits as strategy indicators, but rather suggest that trait variation could be equally informative about plant response to environment, whether to resource availability as analysed here, or to various disturbances such as climate change and neighbourliness. The consequences of different responses to the same environmental change for coexisting species with contrasted strategies needs to be clarified. The assessment of vegetation vulnerability and climate change resilience require understanding of the diversity among plants species and their growth strategies in response to fluctuating resource availability (Nicotra *et al.*, 2010). Thus it is necessary to identify plant functional traits in which plasticity is likely to be a determinant in plant response to environmental changes contributing to predict species distribution changes and shifts (Dawson *et al.*, 2009).

## CHAPTER SIX

### 6.0 CONCLUSION AND RECOMMENDATION

#### 6.1. Conclusion

It was observed that the two weed species responded differently to soil fertility, and it was observed that *E. heterophylla* exhibited higher performance than *S. acuta* over a range of experimental conditions.

Trait variation responses of the two weed species were not related to their plasticities. *E. heterophylla* demonstrated a 'generalist' behaviour by maintaining fitness under environmental stress and enhancing performance under favourable condition, hence, greater plasticity. While *S. acuta* shows less plasticity with greater response to high resource availability.

This study demonstrated that the higher trait means and biomass recorded for some performance indices of both species might influence their capacity to outcompete others. Additionally, the ability of both species to increase fitness under favourable conditions might also influence their abundance.

#### 6.2. Recommendations

It is recommended that future studies should examine the combined effects of reproductive plasticity and vegetative plasticity on colonization success. Also to expand the range of traits and

environments, especially with regard to mimicking probable future conditions under climate change, and comparing traits and fitness between co-occurring species.

What still needs to be done, however, is to disentangle more of the underlying mechanisms and the genes responsible. Research on phenotypic plasticity in plants needs to turn away from the phenomenological approaches that largely ignore molecular mechanisms responsible for changes in development, and focus on the benefits from genomic and proteomic methods. Also the consequences of different responses to the same environmental change for coexisting species with contrasted strategies needs to be clarified.

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## APPENDICES

### Appendix A: Tables

Table 4.11: Show Biomass allocation of the *Euphorbia heterophylla* and *Sida acuta*

Species	Soil	BT	BV	BRO	RRO	RSR	RS	RL	RRE
<i>E. heterophylla</i>	S1	72.3	66.8	17.1	0.23	0.31	0.53	0.15	0.07
<i>E. heterophylla</i>	S2	107	94.7	21.3	0.19	0.25	0.53	0.16	0.12
<i>E. heterophylla</i>	S3	89.8	81	14.6	0.16	0.19	0.53	0.20	0.09
<i>S. acuta</i>	S1	18.21	18	5.2	0.28	0.40	0.21	0.49	0.01

<i>S. acuta</i>	S2	22.7	21.7	4.4	0.19	0.24	0.23	0.53	0.04
<i>S. acuta</i>	S3	61.1	60	11.5	0.18	0.23	0.25	0.54	0.01

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BT = total biomass, BV = total vegetative biomass, BRO = total root biomass, RRO = Relative root biomass, RSR = root-shoot ratio, RS = relative biomass of stem, RL = relative biomass leaves, RRE = relative reproductive biomass

Table 4.7a: Morphological Traits of *E. heterophylla* In Response to Soil fertility, Plant density and Irrigation interval

Species	Soil fertility status	Plant density	Irrigation interval	Stem height	Stem girth	Number of leaves
<i>E. heterophylla</i>	Low	3	7	20.60±2.08 <sup>d</sup>	1.09±0.06 <sup>b</sup>	9.44±0.72 <sup>c</sup>
<i>E. heterophylla</i>	Low	3	3	26.71±3.34 <sup>c</sup>	1.11±0.09 <sup>b</sup>	9.00±0.50 <sup>c</sup>
<i>E. heterophylla</i>	Low	3	2	31.77±3.88 <sup>b</sup>	1.11±0.05 <sup>b</sup>	9.89±0.82 <sup>c</sup>
<i>E. heterophylla</i>	Low	5	7	27.42±3.03 <sup>c</sup>	1.01±0.06 <sup>b</sup>	9.44±0.41 <sup>c</sup>

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<i>E. heterophylla</i>	Low	5	3	33.40±4.44 <sup>b</sup>	1.14±0.04 <sup>b</sup>	10.78±0.73 <sup>b</sup>
<i>E. heterophylla</i>	Low	5	2	42.77±5.29 <sup>a</sup>	1.23±0.05 <sup>ab</sup>	10.00±0.89 <sup>bc</sup>
<i>E. heterophylla</i>	Low	10	7	27.70±3.29 <sup>c</sup>	1.08±0.04 <sup>b</sup>	7.78±0.54 <sup>cd</sup>
<i>E. heterophylla</i>	Low	10	3	26.39±2.88 <sup>c</sup>	1.00±0.06 <sup>b</sup>	7.22±0.66 <sup>cd</sup>
<i>E. heterophylla</i>	Low	10	2	33.11±3.05 <sup>b</sup>	1.01±0.07 <sup>b</sup>	8.56±0.65 <sup>c</sup>
<i>E. heterophylla</i>	Medium	3	7	26.64±4.13 <sup>c</sup>	1.28±0.14 <sup>a</sup>	11.17±1.90 <sup>b</sup>
<i>E. heterophylla</i>	Medium	3	3	32.33±5.74 <sup>b</sup>	1.18±0.11 <sup>ab</sup>	17.50±3.38 <sup>ab</sup>
<i>E. heterophylla</i>	Medium	3	2	39.40±6.79 <sup>ab</sup>	1.20±0.11 <sup>ab</sup>	15.92±3.59 <sup>ab</sup>
<i>E. heterophylla</i>	Medium	5	7	26.54±4.31 <sup>c</sup>	1.08±0.12 <sup>b</sup>	8.75±1.08 <sup>c</sup>
<i>E. heterophylla</i>	Medium	5	3	35.35±5.32 <sup>b</sup>	1.23±0.10 <sup>ab</sup>	17.67±2.69 <sup>ab</sup>
<i>E. heterophylla</i>	Medium	5	2	33.22±5.08 <sup>b</sup>	1.21±0.11 <sup>ab</sup>	11.67±1.49 <sup>b</sup>
<i>E. heterophylla</i>	Medium	10	7	28.94±3.67 <sup>c</sup>	0.99±0.07 <sup>bc</sup>	8.58±0.86 <sup>c</sup>
<i>E. heterophylla</i>	Medium	10	3	26.22±3.85 <sup>c</sup>	1.01±0.08 <sup>b</sup>	8.17±0.75 <sup>c</sup>
<i>E. heterophylla</i>	Medium	10	2	30.73±4.12 <sup>bc</sup>	1.04±0.07 <sup>b</sup>	7.42±0.53 <sup>cd</sup>
<i>E. heterophylla</i>	High	3	7	45.78±7.29 <sup>a</sup>	1.43±0.12 <sup>a</sup>	16.83±2.13 <sup>ab</sup>
<i>E. heterophylla</i>	High	3	3	46.12±6.53 <sup>a</sup>	1.21±4.93 <sup>ab</sup>	20.00±2.96 <sup>a</sup>
<i>E. heterophylla</i>	High	3	2	47.25±6.39 <sup>a</sup>	1.38±0.10 <sup>a</sup>	16.00±1.76 <sup>ab</sup>

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<i>E. heterophylla</i>	High	5	7	30.01±4.24 <sup>bc</sup>	1.10±0.09 <sup>b</sup>	10.58±1.04 <sup>bc</sup>
<i>E. heterophylla</i>	High	5	3	32.45±5.08 <sup>b</sup>	1.02±0.08 <sup>b</sup>	9.75±0.91 <sup>c</sup>
<i>E. heterophylla</i>	High	5	2	37.07±5.50 <sup>ab</sup>	1.08±0.07 <sup>b</sup>	9.75±0.78 <sup>c</sup>
<i>E. heterophylla</i>	High	10	7	32.71±4.17 <sup>b</sup>	1.06±0.08 <sup>b</sup>	8.41±0.42 <sup>c</sup>
<i>E. heterophylla</i>	High	10	3	37.23±4.26 <sup>ab</sup>	1.06±0.06 <sup>b</sup>	10.41±0.91 <sup>bc</sup>
<i>E. heterophylla</i>	High	10	2	42.56±5.69 <sup>a</sup>	1.14±0.07 <sup>b</sup>	10.08±0.83 <sup>bc</sup>

P<0.01, Mean values with same superscripts along column are not significantly different.

Table 4.7b: Morphological traits of *S. acuta* in response to Soil fertility, Plant density and Irrigation interval

Species	Soil level	Density level	Water level	Height	Width	No. of leaves
<i>S. acuta</i>	Low	3	7	5.23±1.16 <sup>e</sup>	0.50±0.07 <sup>c</sup>	8.75±1.29 <sup>c</sup>
<i>S. acuta</i>	Low	3	3	7.42±1.93 <sup>c</sup>	0.40±0.07 <sup>c</sup>	8.50±1.59 <sup>c</sup>
<i>S. acuta</i>	Low	3	2	9.18±1.96 <sup>d</sup>	0.36±0.05 <sup>c</sup>	6.33±0.96 <sup>d</sup>
<i>S. acuta</i>	Low	5	7	2.43±0.29 <sup>f</sup>	0.25±0.03 <sup>d</sup>	4.25±0.83 <sup>e</sup>

<i>S. acuta</i>	Low	5	3	2.84±0.19 <sup>f</sup>	0.26±0.03 <sup>d</sup>	3.75±0.33 <sup>e</sup>
<i>S. acuta</i>	Low	5	2	3.95±0.62 <sup>f</sup>	0.26±0.03 <sup>d</sup>	4.50±0.43 <sup>e</sup>
<i>S. acuta</i>	Low	10	7	2.90±0.25 <sup>f</sup>	0.25±0.02 <sup>d</sup>	4.08±0.36 <sup>e</sup>
<i>S. acuta</i>	Low	10	3	3.57±0.42 <sup>f</sup>	0.28±0.02 <sup>cd</sup>	4.00±0.30 <sup>e</sup>
<i>S. acuta</i>	Low	10	2	4.53±0.66 <sup>f</sup>	0.30±0.03 <sup>c</sup>	4.83±0.51 <sup>e</sup>
<i>S. acuta</i>	Medium	3	7	6.73±1.44 <sup>e</sup>	0.33±0.03 <sup>c</sup>	9.17±1.98 <sup>c</sup>
<i>S. acuta</i>	Medium	3	3	8.61±1.98 <sup>de</sup>	0.34±0.03 <sup>c</sup>	9.58±1.75 <sup>c</sup>
<i>S. acuta</i>	Medium	3	2	6.97±1.77 <sup>e</sup>	0.32±0.04 <sup>c</sup>	6.67±0.74 <sup>d</sup>
<i>S. acuta</i>	Medium	5	7	5.81±1.34 <sup>e</sup>	0.30±0.04 <sup>c</sup>	7.50±0.94 <sup>cd</sup>
<i>S. acuta</i>	Medium	5	3	6.08±1.28 <sup>e</sup>	0.30±0.03 <sup>c</sup>	6.67±0.92 <sup>d</sup>
<i>S. acuta</i>	Medium	5	2	7.18±1.78 <sup>e</sup>	0.34±0.05 <sup>c</sup>	6.83±1.07 <sup>d</sup>
<i>S. acuta</i>	Medium	10	7	4.47±0.59 <sup>f</sup>	0.28±0.02 <sup>cd</sup>	6.08±0.62 <sup>d</sup>
<i>S. acuta</i>	Medium	10	3	4.87±0.98 <sup>ef</sup>	0.28±0.03 <sup>cd</sup>	6.83±0.72 <sup>d</sup>
<i>S. acuta</i>	Medium	10	2	5.94±0.95 <sup>e</sup>	0.29±0.03 <sup>cd</sup>	5.42±0.86 <sup>d</sup>
<i>S. acuta</i>	High	3	7	10.95±2.32 <sup>d</sup>	0.44±0.06 <sup>c</sup>	8.58±0.92 <sup>c</sup>
<i>S. acuta</i>	High	3	3	10.83±2.59 <sup>d</sup>	0.36±0.05 <sup>c</sup>	8.50±1.31 <sup>c</sup>
<i>S. acuta</i>	High	3	2	11.26±2.43 <sup>d</sup>	0.39±0.05 <sup>c</sup>	8.50±1.54 <sup>c</sup>

<i>S. acuta</i>	High	5	7	7.73±1.66 <sup>e</sup>	0.33±0.04 <sup>c</sup>	10.67±2.15 <sup>bc</sup>
<i>S. acuta</i>	High	5	3	10.08±2.23 <sup>d</sup>	0.33±0.05 <sup>c</sup>	10.41±1.62 <sup>bc</sup>
<i>S. acuta</i>	High	5	2	10.53±2.42 <sup>d</sup>	0.37±0.06 <sup>c</sup>	8.58±1.22 <sup>c</sup>
<i>S. acuta</i>	High	10	7	5.38±1.01 <sup>e</sup>	0.29±0.03 <sup>cd</sup>	7.42±1.19 <sup>c</sup>
<i>S. acuta</i>	High	10	3	5.98±1.16 <sup>e</sup>	0.29±0.03 <sup>cd</sup>	8.08±1.68 <sup>c</sup>
<i>S. acuta</i>	High	10	2	6.63±0.96 <sup>e</sup>	0.30±0.02 <sup>cd</sup>	6.75±1.91 <sup>d</sup>

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P<0.01, Mean values with same superscripts along column are not significantly different.

Appendix B: Showing the physicochemical analysis of the experimental soil

Sample No.	PRACTICAL SIZE- DISTRIBUTION CORRECTED TO 20°C (%)				PH. Ratio 1:2.50		(%)		(ppm)	(cmol/kg					
	CLAY	SILT	SAND	TEX. CLASS	H <sub>2</sub> O	0.01M CaCl <sub>2</sub>	OC	TN	AP	Ca	Mg	K	Na	H+Al	CEC
UPPER MOST	22	22	56	SANDY CLAY LOAM	6.7	6.3	0.78	0.35	3.33	5.2	0.84	0.2	0.304	0.4	7.6
MIDDLE/SLOPE	20	16	64	SANDY CLAY LOAM	6.8	6.4	0.94	0.098	5.78	5.6	2.06	1.28	0.321	0.4	7.4
BOTTOM/BASE	24	22	54	SANDY CLAY LOAM	7.2	6.5	1.66	0.049	12.6	6.8	2.86	1.69	0.304	0.2	13.5