Quest Journals
Journal of Research in Humanities and Social Science
Volume 6 ~ Issue 3 (2018) pp.: 10-22
ISSN(Online) : 2321-9467
www.questjournals.org

Research Paper

Adaptive Strategies of the Centrospermeae Species with Different Photosynthetic Systems in the Semi-Arid and Saline Areas in Mt. Kulal - Mt. Elgon Habitats in Kenya.

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ABSTRACT*: Centrospermeae species were collected at different sites along gradient of altitude and aridity in the semi-arid, saline and arid habitats in western region of Kenya. $\delta^{13}C$ values and Kranz leaf anatomy were used to examine for C_3, C_4 C_3-C_4 intermediate and Crassulacean metabolism (CAM) species photosynthesis. ^{13}C values and Kranz leaf anatomy were used to differentiate the C_3 plant species from the C_4 species. The C_4, C_3, C_3-C_4 and CAM species were confirmed to be present in the Centrospermeae group in different proportionate percentage. Interspecific species occur in the group. The morphological, anatomical, physiological and biochemical adaptive strategies of the C_3, C_4,C_3-$C_4$and CAM species of the Centrospermeae group are discussed.*

KEY WORDS: *Centrospermeae, C_4, C_3, C_3-C_4 species,$\delta^{13}C$ values, Kranz leaf anatomy,adaptive strategies*

I. INTRODUCTION

There is consensus that C_3 pathway evolved first and wide spread in terrestrial and aquatic species and habitats (Sikolia, Onyango, Beck and Kinyamario, 2009[1]). The C_4 syndrome is phylogenetic younger achievement and apparently evolved independently in monocots and dicot perhaps as many as twenty times (Quade and Cerling, 1995[2]; Edwards, Franceschi and Voznesenskaya, 2004[3]; Edward, Furbank, Hatch and Osmond, 2001[4] [1] Sikolia, 2016[5]). This interpretation is corroborated by the existence of different types of the C_4 syndrome, namely, the NADP-Malic type, the NAD-malic type and the PEP-Carboxykinase [1]. Phylogenetic distribution of the C_4 syndrome has been extensively investigated in the Gramineae and Cyperaceae families but few dicot species. Studies in the dicot do not provide comprehensive data for analysis of the taxonomic distribution of the plants possessing C_3 and C_4 photosynthetic pathway and their adaptive strategies. Furthermore, the few studies on the dicots have rarely been carried in the semi-arid and or saline tropical ecosystems. Exhaustive studies on theadaptive strategies of the species and their life forms are therefore warranted. Downton (1975) [6], Imbamba and Papa (1979) [7], Mateus-Andre's (1993) [8] and AKhana, Trimborn and Ziegler (1997) [9] have listed some of the investigated C_4 perennial species. However, in the Euphorbiaceae some of the C_4 tree forms do occur (Pearcy and Troughton, 1975) [10].

An exhaustive study in the Middle East and USSR (Winter, 1981) [11] has shown that most of the flora are C_4 species. They include trees or tall shrubs of high biomass with economic value, in that they are fast growing, sand binders, for fuel, medicinal use, honey, improved biodiversity, effective in carbon sequestration,restoration purposes and source of alkaloids. Clearly, there is need for more information on the occurrence and therein adaptive mechanisms of C_4 species, especially from semi-arid and arid regions outside North America [11] that equip them to survive in their ecological habitats. This missing gap and/or situation on the C_4 dicot studies and data availability have not changed much [5]. Similarly, there is little information about the relationships within the Sedges, Cyperaceae, and Centrospermeae and more so about their quantitative occurrence.

The relative causal factors that influence C_4 species partitioning in their ecosystem, whether monocots or dicots have recently were discussed in detail (Ehleringer *et al*, 1997[12] [5). However, the adaptive strategies have yet to give comprehensive explanations for their resilient survival apt. The current study will attempt to correct the imbalance in research and investigation bias more so against the dicot studies. Thus, in C_3, C_4, C_3-C_4 and CAM species, we havephotosynthetic systems whose quantitative data on morphological, anatomical, physiological and biochemical adaptive strategies are not completely described [1] but needs to be put in proper and exhaustive perspective. The studies should enable an evolutionary and adaptative strategies assessment of

the hierarchial dichotomous tree of the angiospermous species and across the families (Raghavendra, 1980[13]; Das and Raghavendra, 1973[14]). Further studies on the occurrence of interspecific differences and strategies in the operation of the photosynthetic pathwayswould provide biological lead to examine the close relationship between C_3 and C_4 species [13] and therefore the evolutionary selective forces and adaptive strategies for the variable photosynthetic ontogenies and phylogenies. Furthermore, the biodiversity of the photosynthetic species will be appreciated in the widespread distribution in different ecological habitats.

The occurrence and diversity of the C_4 pathway in the angiospermous group has been variously reported. For example, Takeda, Ueno and Agata (1980) [15] reported C_4 pathway in three of the seven tribes of Cyperaceae: Cyperdeae, Fimbristydeae and Rhynchosporeae, occurring in different habitats associated with different adaptations; and Brown (1977) [16] reported in the Poaceae. Further, C_4 syndrome is reported in the Poaceae (Hattersley and Watson, 1976[17]; Hattersley,1984[18]; Prendergast, Hattersley and Stone, 1987) [19], *Sueda monoica* (Shomer-llan, 1975) [20], *Arudinella hirta* (Crookston and Moss, 1973) [21], Asteraceae (Smith and Turner,1975) [22], *Eleocharis*, a sedge (Ueno, Samejima and Koyama, 1989) [23], *Scaevola* and *Euphorbia* (Robichaux and Pearcy, 1984) [24], *Flaveria* (Monson and Charles, 1991) [25], Chenopodiaceae [9], intermediate *Flaveria* (Ku, Monson, Littlejohn, Nakumaoto, Fischer and Edwards,1983) [26]; species that might be showing different adaptive mechanisms in different ecological habitats. The study is informed that there is little information on theeco-physiological mechanisms for the survival of C_3-C_4 intermediate species[26]. Further, no information is available on the characteristics of C_3-C_4 intermediates in their natural habitats. This lack of information has hindered the understanding of the adaptive and evolutionary characteristics of the C_3-C_4 intermediates [26], C_3, C_4 and CAM species in their habitats. Furthermore, these studies are useful in the postulation of phylogenetic affinities within a given family or families. Thus, this paper provides discourse on the adaptive strategies that enable the distribution and survival of the dicot species of the Centrospermeae families. The study involved Aizoaceae, Amaranthaceae, Basellaceae, Caryophyllaceae, Chenopodiaceae, Nyctaginaceae, Phytolacaceae, Polygonaceae, Portulacaceae, Zygophyllaceae and Elatinaceae families of the Centrospermeae. Further, the study provides the much required quantitative data on the C_3,$C_4$and C_3-C_4 intermediate dicot plant species in their semi-arid, arid and saline habitats.

II. MATERIALS AND METHOD

2.1. Study site and climatic conditions

The belt transect, 30km wide between 34° 30'E and 36° 30'E, ran from South-West of Mt. Elgon to Mt. Kulal. It was about 365km long rising from 670m a.s.l. at Lodwar to 4200m a.s.l. at Mt. Elgon through 250m a.s.l. in Kerio Valley up to 2415m a.s.l. to 2293m a.s.l. Mt. Kulal then 950m a.s.l. Samburu game reserve and 900m a.s.l. at Kapedo-Nginyang. The sampling sites were randomly selected in a wide broad range of vegetation types from semi-arid to near snowline.

Ten-year climatic data was sourced from meteorological stations in the area of study. Further, one-year data of climatic variable was taken in the field. The stations included Rohet (1538m a.s.l.), Lokori (830m a.s.l.), Kitale (2084m a.s.l.), Chemolingot (950m a.s.l.), Perkerra (1067m a.s.l.), Chewoyet (2134m a.s.l.), Lodwar (506m a.s.l.), Nginyang (908m a.s.l.), Lokichogio (1050m a.s.l.) and Marigat (250m a.s.l.). Also, the field climatic data was measured. The mean of the eleven year climatic data was then calculated. Mean annual values of the climatic parameters collected included: mean annual temperature, mean annual maximum temperature and mean annual minimum temperature, mean annual relative humidity, mean annual potential rates of evaporation, mean annual radiation, mean annual rainfall and altitude measured by thermometer, dew-point hygrometer, 1litre pan water drying per metre in a day, thermopile Pyranometer, rain gauge and altimeter, respectively. The Klimadiagramm of Walter, Harnickell and Mueller-Dombois (1975) [27] were used to describe the climate of the study sites (Sikolia, 2017) [28].

Twenty-five quadrats placed at 10m interval random sites along the belt transect were used. Plant species were collected, especially healthy leaves, vegetative organs and flowering organs from different sites and enclosed in a wet toweling jar(s). Enclosed containers were used to transport the plant material to laboratory for further studies. Species were identified in the field. Difficulty species were taken to East African Herbarium or Chiromo Campus, University of Nairobi, Nairobi, Kenya for further verification and identification. Nomenclature followed Clayton (1974) [29], Beentje (1994) [30], Blundell (1992) [31], Lotschert and Beese (1994) [32], Agnew (1974) [33], Olembo, Fedha and Ngaira (1995) [34] system of identification and documentation. The vegetative parts, especially leaves of the species were dried under natural conditions 25 °C - 30 °C in the field for carbon isotope analytical studies.

2.1.2. Kranz leaf anatomy

Leaves of individual species were collected and immediately fixed in formalin-Acetic acid-Ethyl alcohol (F.A.A.) for six hours. Specimens were then washed in tap water (2 hours) and preserved in 70%

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ethanol solution, renewed after three months in readiness for anatomical studies . The mid –leaf organs were dehydrated in the ethanol-xylol series and embedded in pure paraffin wax at 52℃ melting point. Transverse and longitudinal sections were prepared at 7-12µmm thick. Staining of sections in Heidehain's Iron Alum-Hematoxylin using erythrosin or Fast green in clove oil as counterstain, was done, a method of Sikolia and Onyango (2009)[35]. PDX mountant was used to prepare permanent slides. Other stains used included Safranin-fast green, and Crystal violet-Iodine, depending on the structures: vascularization (xylem and phloem), mestome sheath, parenchyma bundle sheath and the mesophyll sheath organelles. For histochemical studies, Crystal violet – Iodine staining was used to observe the distribution of the starch granules and concentration of chloroplasts, according to the method of Jensen (1962)[36].

The phase-contrast microscope and photomicroscope (Iroscope research microscope mounted with 35mm Reflex camera) were used to study the detailed Kranz leaf anatomy and take photomicrographs (Sikolia, 2005)[37]. The photomicrographs showed the distribution and abundance of chloroplasts, parenchyma bundle sheath (PBS), mestome sheath cells (MS) and mesophyll cells, size and number of PBS, mesophyll and chlorenchymatous cells.Kranz leaf anatomical characters scored included radiate mesophyll, presence or absence of well-defined PBS, PBS cells larger than the other mesophyll cells, number of the chlorenchymatous mesophyll cells between the PBS cells of laterally adjacent vascular bundle with emphasis on the maximum number seen in a given leaf (maximum lateral cell count [37]. The count made along straight line from the centre of one vascular bundle to the centre of the next, included the maximum cells distant count and the cell distant criterion was adopted[17].

2.1.3 Carbon Isotope Studies

Carbon isotope studies involved the following procedures. Air oven at 25 ˚C-30 ˚C circulation dried the leaves or

vegetative organs until there was no further change in weight. Dried specimen were used for $^{13}C/^{12}C$ isotope analysis at Bayreuth Universitat, Germany. Dried leafy-milled grains of each of the species were analyzed using an elemental analyzer (HEREAUS CHN.O RAPID) for Dumas combustion of the sample, a FINNIGAN MAT Delta (δ) gas isotope mass spectrometer with dual inlet system, a method of Gebauer and Schulze (1987) [38]. Standard gas of carbon dioxide was calibrated with respect to international standard (CO_2 in Pee Dee belemnite) by use of reference substance NBS 16 to 20 for carbon isotopic ratio provided by International Atomic Energy Agency (IAEA), Vienna. The $^{13}C/^{12}C$ isotopic ratios (denoted as δ values or $^{13}C/^{12}C$ values) were calculated according to the following equation:

$$\delta_x = (R_{sample}/R_{standard}-1)x1000‰,$$

where δ_x, is the isotope ratio delta unis relative to the international standards, R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ are the ratios of the samples and standards, respectively [38]. The $\delta^{13}C$ values were recorded for each species studied (Sikolia, Beck, Kinyamario, Onyango and Ouma, 2008) [39] and represented on graphs.

III. RESULTS

The life form of the species is variable. The frequency percentage of annuals, biennials and perennial was 55%, 8% and 37% in the studied semi-arid and arid habitats. 76% of the species exhibited succulent organs (leaves/stems) whereas 67% showed xerophytic characteristics. About 4% of the species exhibited hydrophytes characters whereas the 29% has mesophytic-like features. Most of the species depicts hairy leaves, stems and floral organs. The species possess strict life cycles whose vegetative cycle is associated with rainfall availability but fruiting with the dry conditions. Perennial species often bypassed the dry season as seeds and leaf fall phenomena. The seeds per ovule could be as much as fifty, small in size (1mm in diameter) and very light in the case of *Portulaca afra* species. Leaf fall was very conspicuous in the Amaranthaceae family.

The species of the Centrospermeae were differentiated into C_3 species, C_4 and C_3-C_4 intermediate species based on the $\delta^{13}C$ values, the presence of the Kranz leaf anatomy (K) or absence of the Kranz leaf anatomy(NK), and Kranz-non Kranz leaf anatomy (K-NK), respectively, as shown in the Table 1. CAM species were also recorded.

Table 1: $\delta^{13}C$ values and Kranz anatomy of the Centrospermeae species

FAMILY/SPECIES	$\delta^{13}C$ values	K, NK, N-NKor CAM species
AIZOACEAE		
Corbichonia decumbens	-12.5	K
Delosperma abyssinica	-13.73	K
Delosperma nakurense	_	K
Delosperma oehleri	_	K
Gisekia africana	-11.77	K

Gisekiapharnacoides	-11.99	K
Glinus lotoides	-26.79	NK
Glinus oppositifolius	-25.04	NK
Glinus seliflorus	-25.37	NK
Hypertelis bowkeriana	-23.32	NK
Limeum fruticosum	-26.82	NK
Limeum indicum	-24.51	NK
Limeum praetermissium	-23.75	NK
Limeum viscosum	-24.40	NK
Mollugo cerviana	-15.36	K
Mollugo nudicaulis	-25.89	K-NK
Sesuvium portulacastrum	-24.88	NK
Sesuvium sesuvioides	-12.21	K
Tetragonia acanthocarpa	-22.90	NK
Tetragonia tetragonoides	-23.84	NK
Tetragonia expense	-23.81	NK
Tetragonia ceratosepala	-23.66	NK
Trianthema portulacastrum	-12.48	K
Trianthema triquetra	-13.25	K
Trianthema salsoides	-13.86	K
Trianthema sedifolia	-13.86	K
Zelaya pentandra	-12.26	K
AMARANTHACEAE		
Achyranthes aspera L. var. *Pubescens*(Moq.)C.C. Townsend	-30.89	NK
Achyranthes aspera I. var. Sicula L.	-30.93	NK
Achyropsis fruticola	-25.13	NK
Achyropsis greenwayi	-25.18	NK
Aerva javanica	-14.41	K
Aerva lanata	-28.12	NK
Aerva leucura	-26.53	NK
Aerva peploides	_	NK
Alternanthera pungens	-14.75	K
Alternanthera sessilis	-25.51	NK
Amaranthus caudatus	-16.55	K
Amaranthus dubius	-15.14	K
Amaranthus graecizans	-15.83	K
Amaranthus hybridus	-14.70	K
Amaranthus lividus	-12.96	K
Amaranthus patulus	-13.12	K
Amaranthus retroflexus	-13.48	K
Amaranthus spinosus	-13.98	K
Amaranthus thurnebergii	-13.45	K
Amaranthus species	-13.48	K
Celosia anthelmintica	-25.66	NK
Celosia argentea	-25.42	NK
Celosia hastate	-28.22	NK
Celosia polystachya	_	NK
Celosia sweinfurthiana	-27.97	NK
Celosia trygina	-23.55	NK
Celosia rubra	-25.34	NK
Centemopsis gracilenta	-26.73	NK
Centemopsis kirkii	-27.97	NK
Centrostachya aquatica	-23.15	NK
Centrostachya coriacea	-28.35	NK
Centrostachya cylindrica	-27.42	NK
Centrostachya orthacantha	-27.99	NK

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Centrostachya polycephala	-28.24	NK
Centrostachya uncinulata	-26.91	NK
Digera muricata	-25.67	NK
Gomphrena celosioides	-13.08	K
Hermastaedtia gregori	-29.59	NK
Pandiaka lanunginosa	-21.42	NK
Psilotrichum elliotii	-23.30	NK
Puppalia grandiflora	-24.36	NK
Puppalia lappacea	-24.17	NK
Puppalia micrantha	-25.67	NK
Sericomposis hilderbandtii	-23.41	NK
Sericomposis pallida	-25.56	NK
Volkensinia prostrata	-25.26	NK
BASELLACEAE		
Basella alba	-18.75	CAM
Basella paniculata	-17.79	CAM
CARYOPHYLACEAE		
Arenaria foliacea	-24.83	NK
Arenaria montana	-25.66	NK
Cerastium adnivale	-27.53	NK
Cerastium afromontanum	-25.68	NK
Cerastium corymbosa	-27.67	NK
Cerastium indicum	-26.26	NK
Cerastium octandrum	-25.13	NK
Corrigola capensis	-25.78	NK
Corrigola litoralis	-27.47	NK
Comes abyssinica	-26.76	NK
Dianthus barbatus	-15.73	K
Dianthus plumarius	-30.92	K
Dianthus species	-25.86	K
Drymaria cordata	-28.69	NK
Gypsophila elegans	-26.82	NK
Gypsophila gillettii	_	NK
Gypsophila oldhamiana	-25.67	NK
Lychnis alba	-30.28	NK
Lychnis githago	-22.41	NK
Lychnis cororiana	-25.58	NK
Lychnis viscaria	-21.84	NK
Melandrium nordiflorum	-13.57	K
Melandrium rubrum	-13.11	K
Melandrium persicum	-26.75	NK
Minuartia elenbeckii	-27.57	NK
Minuartia juniperiana	-30.24	NK
Pollichia campestris	-25.75	NK
Polycarpea corymbosa	-13.12	K
Polycarpon prostratum	-27.23	NK
Polycarpon tetraphyllum	-28.00	NK
Sagina abyssinica	-27.09	NK
Sagina afroalpina	_	NK
Sagina apetala	_	NK
Silene abyssinica	-10.91	K
Silene burchelli	-26.76	NK
Silene dioica	-25.70	NK
Silene gallica	-25.72	NK
Silene longitubulosa	-25.79	NK
Silene nocteolens	-29.52	NK

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Silene macrosolen	-26.75	NK
Silene species	-26.85	NK
Silene vulgaris	-27.27	NK
Spercula arvensis	-25.94	NK
Stellaria mannii	-26.72	NK
Stellaria media	-27.69	NK
Stellaria sennii	-28.26	NK
Uebelinia abyssinica	-27.45	NK
Uebelinia cf *rotundifolia*	-25.01	NK
Uebelinia crassifolia	-24.75	NK
Vaccaria pyramidata	-28.75	NK
Saponaria vaccaria	-26.65	NK
Saponaria depressus	-26.56	NK
CHENOPODIACEAE		
Arthrocnemum indicum	-13.70	K
Atriplex coriacea	-14.35	K
Atriplex farinosa	-16.33	K
Atriplex halimus	-12.39	K
Atriplex semibaccata	-15.18	K
Atriplex muelleri	-14.68	K
Beta vulgaris	_	K
Chenopodium album	-26.70	NK
Chenopodium ambrosioides	_	NK
Chenopodium botryoides	-26.80	NK
Chenopodium capitatum	-32.42	NK
Chenopodium carinatum	-25.03	NK
Chenopodiumfasculosum	-27.44	NK
Chenopodium murale	-25.64	NK
Chenopodium opolifolium	-25.72	NK
Chenopodium procerum	-25.47	NK
Chenopodium pumilio	-27.70	NK
Chenopodium rubrum	-26.70	NK
Chenopodium schraderanum	-25.44	NK
Fadenia zygophylloides	-13.50	K
Gyroptera gillettii	-12.12	K
Gyroptera somalensis	-25.54	NK
Kochia indica	-12.54	K
Kochia scoparia	-12.94	K
Salicornia pachystachya	-26.70	NK
Salsola dendrites	-13.62	K
Salsola pestifera	-10.60	K
Sueda monoica	-14.92	K
PHYTOLACCACEAE		
Gallesia gorarema	-25.65	NK
Hilleria latifolia	-29.01	NK
Phytolaca americana	-28.37	NK
Phytolacca chilensis	-27.53	NK
Phytolacca dioica	-23.79	NK
Phytolacca dodecandra	-23.49	NK
Phytolacca octandra	-23.32	NK
POLYGONACEAE		
Antipogon leptopus	-28.62	NK
Coccoloba uvifera	-30.08	NK
Emex australis	-12.79	K
Emex spinosus	-12.36	K

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Fagopyrum esculentum	-13.53	K
Harpagocarpus snowdenii	-28.18	NK
Homacladium platycladium	-26.72	NK
Oxygonum atriplicifolium	-24.67	NK
Oxygonum sinuatum	-26.65	NK
Polygonum afromontanum	-26.11	NK
Polygonum ampibium	-21.46	NK
Polygonum aviculare	-25.37	NK
Polygonum capitatum	-29.84	NK
Polygonum chinense	-26.19	NK
Polygonum convolvulus	-29.76	NK
Polygonum equisetiforme	-29.91	NK
Polygonum nepalense	-27.32	NK
Polygonum pulchrum	-27.94	NK
Polygonum salicifolium	-26.67	NK
Polygonum senegalense	-27.04	NK
Polygonum setulosum	-27.18	NK
Polygonum strigosum	-23.99	NK
Polygonum tomentosum	-27.51	NK
Rumex abyssinica	-28.35	NK
Rumex acetosa	-30.15	NK
Rumex bequaertii	-27.30	NK
Rumex crispus	-27.66	NK
Rumex lunaria	-29.85	NK
Rumex nervosus	-27.04	NK
Rumex triangulivalvis	-27.76	NK
Rumex rugosus	-27.96	NK
Rumex ruwenzoriensis	-26.55	NK
Rumex usambarensis	-28.01	NK
PORTULACACEAE		
Calyptrotheca somalensis	-24.86	NK
Calyptrotheca taitensis	-23.34	NK
Montia fontana	-28.53	NK
Portulaca afra	-20.93	K-NK
Portulaca decorticans	-12.36	K
Portulaca fascicularis	-12.37	K
Portulaca foliosa	-12.29	K
Portulaca grandiflora	-12.33	K
Portulaca kermesina	-12.43	K
Portulaca oblonga	-13.11	K
Portulaca oleracea	-14.98	K
Portulaca parensis	-12.40	K
Portulaca petersii	-13.69	K
Portulaca pilosa	-13.68	K
Portulaca quadrifida	-15.66	K
Portulaca species (K)	-14.50	K
Portulaca species (T)	-11.48	K
Portulaca wightiana	-12.98	K
Ravina tinctoria	-30.11	NK
Talinum caffrum	-24.34	NK
Talinum crispatulatum	-23.41	NK
Talinum cuneifolium	-21.16	NK
Talinum paniculatum	-21.32	NK
Talinum patens	-28.18	NK
Talinum portulacifolium	-23.72	NK
Vallamila peruviana	-29.52	NK

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ZYGOPHYLLACEAE		
Fagonia indica	-25.25	NK
Fagonia isotricha	-24.82	NK
Fagonia paulayana	-23.20	NK
Fagonia schweinfurthii	-23.75	NK
Tribulus cistoides	-13.40	K
Tribulus cf *T. cistoides*	-14.68	K
Tribulus parvispinus	-12.56	K
Tribulus terrestris	-10.68	K
Zygophyllum cordifolium	-24.57	K
Zygophyllum simplex	-13.77	K
NYCTANGINACEAE		
Boerhavia diffusa	-12.20	K
Boerhavia elegans	-11.99	K
Commicarpus grandiflora	-25.10	K
Commicarpus pendunculosus	-25.03	K
Commicarpus plumbagineus	-27.70	K
Marabillis jalaba	-30.34	K
ELATINACEAE		
Bergia ammanioides	-24.42	K
Bergia decumbens	-25.17	K
Bergia suffructicosa	-23.99	K
Elatine triandria	-23.76	K

In the Table 1., K, NK,K-NK and CAM refers to the Kranz, non-Kranz, intermediate Kranz leaf anatomy and Crassulacean acid metabolism, respectively. The C_3-C_4 intermediate metabolism occurred in the Aizoaceae (i.e. *Mollugo nudicaulis* species) and CAM species in the Basellaceae family (i.e. *Basella alba* and *Basella paniculata*) in the Centrospermeae group. Further, *Dianthus* species are now placed under Caryophyllaceae family and not the Elatinaceae, according to plant list, released by the collaboration between the Royal Botanic Gardens, Kew and Missouri Botanical Garden enabled the creation of The Plant List by combining multiple checklist data sets held by these institutions and other collaborators, September,

2013)(http://www.theplantlist.org/)[40].

The Kranz leaf anatomical characters included Kranz parenchyma sheath showing centrifugal to median chloroplasts observed in the *Amaranthus hybridus, Sesuvium portulacastrum, Amaranthus species, Amaranthus spinosus, Portulaca oleracea, Carbiconia decumbens, Portulaca grandiflora, Portulaca quadrifida, Portulaca kermesina* and *Tribulus terrestris*; and Kranz parenchyma sheath showing centripetal chloroplasts observed in the *Tribulus cf T. cistoides, Tribulus cistoides* and *Portulaca fascicularis*[37]. Non-Kranz leaf anatomy was designated if the mesophyll cells intervening between any parenchyma sheath cells of the two vascular bundles were more than three to even more than twelve cells in *Polygonum salicifolium* to fifteen mesophyll cells in *Drymaria cordata* [37]. C_3-C_4 Kranz leaf anatomy was not quite regular but had less mesophylls cells than the C_3 species intervening between the between sheath cells of the two vascular bundles but more than three mesophyll cells of the C_4 species. CAM species were designated based on the $\delta^{13}C$ values, its succulent leaves whose cells were large than those of C_4 species and research data recorded (Chellappan and Gnanam, 1980) [41][1][39].

IV. DISCUSSION

Two groups of annual plants were recognized, the long rain annuals and short annuals. The long rains annuals consist of species that germinate and complete their life cycles between February to early June months of the year. The short rains annuals include species that germinate and complete their life cycles between the dry season and early wet season. Normally, the seasonal occurrences of these differentiations of species are highly predictable and are determined by specific temperature ($15.7^{\circ}C$ – $26.7^{\circ}C$) and moisture (700mm – 900mm) combinations for germination, especially in transition phase between C_3 and C_4 species (Rundel, 1980)[42][37].

The percentage C_4 species decrease with increasing altitudinal gradient and higher latitudes [1] in contrast to the C_3 species. The altitude and latitude elements define the minimum, maximum daily, monthly and

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annual temperatures as well as precipitation, radiation, hours of sunshine, annual mean evaporation, soil moisture index and growth or thermal index of the habitat that determine the availability of either the C_4 species or the C_3 species. Further, the adaptation modules of the C_4 species are then modelled against these variables. The modules are differentiated into biological clock, morphological, weedy behaviour to subdue the competitors, anatomical, physiological and biochemical parameters of the plant species to include life cycle timing activities, reduced leaf surface area, mechanisms to compart water stress and the different photosynthetic pathways, respectively.

The annuals are mesophytic in nature as exhibited by the genus *Portulaca, Portulacaria* and escape unfavourableconditions of soil water stress and high insolation by rapid completion of their life cycle during the short periods when temperature and moisture regimes are favourable for growth. They shed a lot of seeds at regular intervals per flower of seed-case and not at once, for example in *Portulaca grandiflora, Amaranthus patulus and Amaranthus spinosus,* amongst other species [37]. Germination takes place immediately after heavy showers and takes place through intermittent phases not once [37].

Many species are abundant on disturbed habitat and possess weedy characteristics. The foliage is mostly strikingly xerophytic and often showheavy pubescence, basal leaf or leaflets. The leaves are often succulent, simple, entire and often relatively small for example in *Portulaca oleracea, Kochia scoparia*but rarely pinnate compound, for example, *Tribulus cistoides and T. terrstris.*The basal, leaves characterize above soil surface plant features in contrast to long rain annuals like *Comes abyssinica, Pollichia campestris, Polygonum afromontanum, Oxygonum sinuatum, Silene burchelli, Sagina afroalpina, S. abyssinica,Cerastium afromontanum, Arenaria montana and Delosperma abyssinica*. The mostsophisticated adaptative strategy of semi-arid/arid long rain species is the life-cycle timing which ensures germination during the short rains periodic cycle define as August, September and October months of every year as shown in the *genera Portulaca, Delosperma, Gisekia, Mollugo cerviana, Sesuvuium, Zelaya, Aerva, Amaranthus, Gomphrena, Melandrium, Gypsophila, Polycarpea, Pollichia, Gyroptera, Tribulus.*Correspondingly, the annual species operating successfully under the high temperature stresses of the semi-arid/arid environments have evolved in relatively few genera, suggesting the difficulty of adaptation in these ecotypes, through the utilization of the C_4 pathways compared to the C_3pathways. Similar observations have been recorded in Mojave desert and Sonoran desert (Mulroy and Rundel, 1977)[43] and Turkana – Marsabit dry habitats (i.e. Mt. Elgon- Mt. Kulal) [37]. Long rain annuals require abundant moisture coinciding with favourable temperature regimes.

The annuals remain in vegetative rosette ortuft until stem elongation take place in March or early April of the year and can grow for five to eight months. Vegetative part has leaves with various structural dissections. For example, Leaves fleshy, alternate, obovate-spathulate or oblanceolate, glaucous; petiole wingedin *Corbichonia decumbens*, each leaf has five to eight pairs of unequal leaflets, the upper surface of the leaves, are green and sparsely pubescent while the lower surface is whitish and densely pubescent in *Terrestris cistoides*. However, growth can drop to six weeks or less during unfavourable times. Thus, the semi-arid/arid annuals exhibit morphological adaptations in growthform, leaf dissection and developmental plasticity to their short and unpredictable growing season. The growth forms include rosette leaves, bud phenology, pedicel elongation, developing buds are kept near the warm soil surface e.g.in *P. kermesina* to hasten development, and dissected leaves. Production of abundant vegetation growth during rainy season sufficient for germination is not followed by significant extra rainfall as shown *Chenopodium schraderanum, Pollichia campestris and Sagina abyssinica* species.

Perennial succulent shrub and arborescent species occur in the families of the Centrospermeae. Perennial succulent leaf includes *Basella alba* and*Basella paniculata.* Perennial leaf deciduous includes*Arthrocnenum indicum, Atriplexcoriacea, A. farinose, A. halimus, A. semibaccata, Salicornia pachystachya, Gallesia gorarema, Calyptrotheca somalensis,C. taitensis, Fagonia indica, and Fagonia isotricha* species. Perennial stem succulents include *Basella alba, B. paniculata, Arthrocnenum indicum, Atriplex faranosa, Salicornia isotricha, F. indica and Calyptrotheca taitensis, Polygonum carinatum, Phytolaca americana.*Perennial arborescent species in this study include*Calyptrotheca somalensis, which are also reported in Haloxylon aphyllum*species (Wang *et al,* 2004)[44].There are phanerophytes, chamaephytes and therophytes present in the Centrospermeae group. Yamori, Hikosaka and Way (2014)[45] observedthat differences in the inherent ability for temperature acclimation of photosynthesis exists: (1) among the C_3, C_4, and CAM species; and (2) among functional types within C_3 plants. Generally, the C_3 plants depict greater ability for temperature acclimation of photosynthesis across a broad temperature range, CAM plantsacclimated day and night photosynthetic process differentially to temperature, and C_4 plants was adapted to warm environments. An example of such CAM is the *Mesembryanthemum crystallinum.* Furthermore, within C_3 species, evergreen woody plants and perennial herbaceous plants showed greater temperature homeostasis of photosynthesis than deciduous woody plants and annual herbaceous plants, indicating that photosynthetic acclimation would be particularly important in perennial, long-lived species that would experience a rise in growing season

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temperatures over their lifespan [45]. A striking phenomenon of perennial C_4species in the semi-arid, arid orsaline habitats is their occurrence in areas with large daily and annual temperature fluctuations and low temperatures during the long rain seasons in the studied regions.

The C_4 dicots are the most noxious and aggressive time weeds in temperate, subtropical regions (Holm *et al*, 1977[46]; Elmore and Paul, 1983[47]). This was observed in the semi-arid and/or saline irrigated areas especially in Perkerra irrigation scheme in Baringo County, Kenya [1][37]. Researchers [45] reported that fourteen (14) of the eighteen (18) worst weeds globally had C_4 photosynthetic pathway. Further, researchers[46] calculated that the taxonomic fraction of C_4 weeds was seventeen (17) fold greater than would be expected based solely on a C_3/C_4 species basis. During carboxylation, the C_4 species discriminate in favour of the light isotope of carbon, ^{12}C, with the result that all plants contain relatively less ^{13}C than the atmosphere. Thus, the C_4 species show a higher $^{12}C/^{13}C$ isotopic carbon ratio than the C_3 species. In habitats of intensedegree of the abiotic factors, for example, disturbance, fire, deforestation, the C_4 species are more likely to comprise a significant component of the invaders. The C_4 dicot and C_3 dicot weeds have synchronized timing in their life cycle during the long rain season in their micro environmental attributes of disturbed sites that override climatical differences to abiotic and edaphic factors.About 29.5%, 0.5% and 70% of the Centrospermeae dicot species were found to be C_4 species, C_3-C_4 intermediate and C_3 species [1][39].

The C_4 species have been shown to exhibit the Kranz leaf anatomy. The C_4 Centrospermeae dicot species are no exception. A single bundle surrounded by non-chloroplast parenchyma sheath or double sheath cell layers was observed [37]; the mestome sheath cell layers were surrounded by parenchyma sheath cell layer which possess the chloroplasts as observed in *Amaranthus hybridus.* The Kranz of the enlarged cells have walls thicker than the mesophyll cell walls in *A. hybridus*; the chlorencyma cells are arranged more or less radially around vascular bundle and each cell has contact with Kranz sheath cell. The mesophyll is differentiated between successive bundles into radial mesophyll cells e.g. in *Corbichonia decumbens*, *Portulaca* species. The differentiation of biochemical activity between the mesophyll and bundle sheath cells indicate the functional difference from the non-Kranz species where this division of labour is not anatomically typed and reported [37]. The Kranz anatomy revealed subdivision into Kranz parenchyma sheath showing centrifugal to median chloroplasts[37]exemplified by *Amaranthus hybridus, Sesuvium portulacastrum A. spinosus, Portulaca oleracea, Corbichonia decumbens, Portulaca grandiflora, P. quadrifida, P. kermesina, Tribulus terrstris* and Kranz parenchyma sheath showing centripetal chloroplasts [37], for example shown in *Amaranthus dubius, Tribulus cistoides, Tribulus* cf. *T. cistoides.* The non-Kranz leaf anatomy lacks the above C_4 Kranz anatomical arrangement such thatit possess a "maximum lateral cell count of 5-15" cells in the estimated 70% dicot species of the Centrospermeae [39].For example, the "maximum lateral cell count" observed in the *Polygonum salicifolium, Drymaria cordata, Bougainvillea, Boerhavia* and *Polygonum pulchrum* was 10-15cells, 8-10cells7-12 cells, and 8-15 cells, respectively [37]. The C_4 species Kranz anatomy is organized such that themesophyll and bundle sheath cells cooperate to concentrate the carbon dioxide at the site of carbon assimilation in the bundle sheath cells. This mitigates the oxygenase reaction arising from the Photosynthetic Carbon Reduction (PCR or Calvin-Benson) cycle for CO_2 fixation in which Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) catalyzes the first step producing a three-carbon compound, phosphoglycerate (3-PGA).Oxygenase is suppressed at the expense of the carboxylation where photorespiration course is avoided during high and drought conditions, especially in the semi-arid/saline areas. The differentiation of mesophyll and bundle sheath cell types is fundamental for the functioning of C_4 photosynthesis. Further, the unique operationalization of the C_4 cycle within a single photosynthetic cell type has been reported in *Borszczowia aralocaspica* (Voznesenskaya, Edwards, Kiirats, Artyushevaand Franceschi, 2003)[48],*Bienertia cycloptera*(Voznesenskaya, Koteyeva, Choung, Akhani, Edwards, Franceschi, 2005)[49],*Bienertia sinuspersici***(**Akhani, Barroca, Koteeva, Voznesenskaya, Franceschi, Edwards, Ghaffariand Ziegler, 2005)[50], *Suaeda*and *Hydrilla verticillata* aquatic species (Edwards *et al.*, 2004[51]; Lara *et al.*, 2002[52]; Lara and Andreo, 2005[53]).The C_3-C_4 intermediate Kranz syndrome and/or metabolism was exhibited by *Mollugo nudicaulis*, an Aizoaceae [37].

The C_4 species blend the structural, physiological and biochemical parameters to thrive in ecological environments less inhabited by the C_3 species [28]. The C_4 species exhibit diverse decarboxylation enzymes as well as different transported metabolites. Thus, the decarboxylation process occurs in three diverse ways, mainly using one of the following enzymes: NADP-malic enzyme (NADP-ME), NAD malic enzyme (NAD-ME) or phosphoenolpyruvate Carboxykinase (PEP-CK). Therefore, C_4 plants are grouped into three biochemical subtypes depending on the major decarboxylase used (C_4-NADP-ME subtype; C_4-NAD-ME subtype or C_4-PEP-CKsubtype). Each C_4 subgroup possesses particular structural features, biochemistry and physiology, and also differences in the mechanism used to regenerate phosphoenolpyruvate (PEP), the substrate of PEP-carboxylase in mesophyll cells. Nevertheless, it is now becoming apparent that, in several cases, more than one decarboxylase operates at the same time (Drincovich *et al.*, 2011)[54]. Corresponding to the decarboxylation sub-types is the proposed anatomical sub-types as NAD-me dicot > NADP-me dicot > NAD-me monocot >

NADP-me monocot sequence of the adaptive metabolic and functional strategies in the angiosperm group from the lower altitude [37]. This sequence of thesub types corroborates the observation that,at the current CO_2 levels, C_4species (particularly dicots) generally require less water than C_3 because of the higher CO_2uptakes rates and greater stomatal resistance to water loss [12].

The C_4decarboxylation modules has enabled the C_4 species to increase their water use efficiency and nitrogen use efficiency relative to the C_3 species, especially during the high light and temperature conditions, where oxygenase reaction of Rubisco is greatly increased (Lara and Andreo, 2011)[55].Increased leaf and plant water use efficiency in C_4 plants is due to both higherphotosynthetic rates per unit leaf area and lower stomatal conductance, with the greater CO_2 assimilation contributing to a major extent (Ghannoum *et al*., 2011)[56][55]. Further, it has been shown that the C_4 species have greater rates of CO_2 assimilation than C_3 species for a given leaf nitrogen when both parameters are expressed either on a mass or an area basis [56]. Thus, the adaptive strategies found in the dicot species of the Centrospermeae group are morphological, anatomical, physiological and biochemical in nature and their occurrence is differentiated in different species and different families along the soil moisture, temperature, aridity indices and altitudinal gradient.

V. CONCLUSION

C_3, C_4, C_3-C_4 intermediate and CAM diverse photosynthetic pathways occur in different plant species of the Centrospermeae group. The species are distributed in different habitats showing varying soil moisture, aridity index, temperature and precipitation gradients. These environmental conditions demand certain adaptive strategies to be met for the survival of the plant species. The timing of the life-cycle of the plant species, the succulent nature of the vegetative organs and variable life forms constitute the morphological strategies. The wide spread distribution of the species from low altitude to high altitude habitats (approx. 4200m a.s.l.) show the ecological plasticity strategies functioning, including occurrence in the wet and dry conditions. The variation in the Kranz leaf anatomy is well structured to create a biochemical carbon dioxide pump that concentrate carbon dioxide (CO_2) at the site of Rubisco therebyreducing or avoiding the Rubisco oxygenase reaction. This due tothe differentiation of the mesophyll and bundle that allows spatial separation of the CO_2 fixation and assimilation at the Rubisco site. This C_4 Kranz leaf anatomy overcomes the limitation of the photorespiration, improving photosynthetic efficiency and minimizing the water loss in hot, dry environments. Thus, the C_4 Kranz anatomy, derived from the C3 anatomy, is a specialized anatomical strategy to overcome photorespiration during times of low carbon dioxide concentration at the rubisco site. This C_4 pathway is further differentiated into diverse decarboxylation enzymes as well as different transported metabolites.The three different decarboxylation enzymes areNADP-malic enzyme (NADP-ME), NADmalic enzyme (NAD-ME) or phosphoenolpyruvate Carboxykinase (PEP-CK) that organize biochemical subtypes , the C_4-NADP-ME subtype, C_4-NAD-ME subtype or C_4-PEP-CK subtype), respectively. Consequently, specialized structural features, biochemistry and physiology are unique to each decarboxylation subtype and even in the mechanism to regenerate the substrate of PEP-carboxylase in mesophyll cells, the phosphoenolpyruvate, required during decarboxylation. Thus, plant species of the Centrospermeae exhibit anatomical, biochemical and physiological adaptive strategies that are internally integrated, enhanced with the morphological strategy and modified by the ecological habitats.

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Stephen F. Sikolia "Adaptive Strategies of the Centrospermeae Species with Different Photosynthetic Systems in the Semi-Arid and Saline Areas in Mt. Kulal - Mt. Elgon Habitats in Kenya.." Quest Journals Journal of Research in Agriculture and Animal Science, vol. 06, no.3, 2018, pp. 10–22.