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Research Paper

Differentiation of the C_3 and C_4 dicot (Centrospermeae) species along the altitudinal-aridity gradient and theirecological implications inbioproductivity paradigm in Kenya.

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ABSTRACT: *Centrospermeae specieswere collected at different sites along gradient of altitudes and aridity. Climatic data were obtained from meteorological research stations. Kranz leaf syndrome, $\delta^{13}C$ values and carbon dioxide compensation points were used to examine for C_3 or C_4 photosynthesis. Results show C_4 photosynthesis is a trait of modern dicotyledonae species and is of multiple evolutionary origins. C_4 species occur mainly in lowland habitats characterized by high temperature, low precipitation and high rates of evaporation. The areas were often associated with salinity and high $\delta^{13}C$ values of the species. C_4 dicots were further differentiated into biochemical types NAD-me type and NADP-me type. NAD–me dicot type tended towards drier region than NADP-me dicot type. NADP-me type preferred more moisture indexed habitats. With increasing aridity, the percent C_4 dicot abundance in the flora also increased. Inverse relationship does exist between rainfall (precipitation) and C_4 percent abundance distribution ($r= -0.91$, $R^2= 0.83$) along altitudes. C_3 species dominate moist and colder habitats, especially at higher altitudes. A few species C_4 species occur at high altitudes (3000-4000m a.s.l.) namely Sagina gallica, Silene abyssinica and Melandrium nordiflorum. The transition zone between C_3 and C_4 dicot species is rather narrow between 1500 to 1700m and thus much lower than recorded for the monocots (2000-2200m a.s.l.). The general pattern of $\delta^{13}C$ values distribution along the altitudinal gradient show that the values of -10.60 to -16.55, -17.75 to - 18.87 and -18.89 to 32.4‰ corresponds to altitudinal ranges 0-1500, 1550-1700 and 1800-4200m a.s.l., respectively. The occurrence of different transition range between C_3 and C_4 of the dicots compared to the recorded transition range of the monocots augur well for ecological photosynthetic mechanisms partition. The C_4 dicot species can be cultivated to occupy the cool shade canopy whereas C_3 dicot species occupy open canopy for photosynthetic efficiency per unit area. Variation of the Kranz leaf anatomy lend credibility to the manipulation of hybridization of the Kranz and non-Kranz leaf anatomy without fear that new structural leaf anatomy can limit performance of the biochemical and physiological processes and bioproduction , for example in the intermediate Mollugo species. Comparison of the C_3 and C_4 rates of CO_2 assimilation show that C_3 dicot species are much placed to utilize more CO_2 molecules than the C_4 species when CO_2 concentration is not limiting factor in space and time. Therefore, C_3 are well suited as possible control models in the rising CO_2 scenario and global warming conditions. Implications are that more indigenous C_3 are encouraged for afforestation in agroforestry management systems. The low altitudes are associated with drought and high temperatures. C_3 andC_4 dicot species can be intercropped to increase bioproductivity for betterment of the flora and fauna in the semi-arid and arid ecosystem. The proposed C_3 and C_4 species paradigm for both monocots and dicot intercropping along the altitude defined by aridity index is in the order of C_3 monocots-C_3 dicots-NADP-me monocot-NAD-me monocot-NADP-me dicot-NAD-ME dicot to sequentially partition the bioproductivity. The study is relevant for better understanding of species photosynthesis and diversity change in relation to herbivory, climatic and vegetation dynamics.*

Keywords: *Dicot species, C_3 C_4 photosynthesis, Climatic factors, Altitude, Transition zone, Bioproductivity*

I. INTRODUCTION

Plants are differentiated into three types of photosynthesis: C_3, C_4 and CAM pathways, both in monocots and dicots. The pathways are distinguished based on their unique anatomical, biochemical and physiological parameters. There is consensus that the C_3 pathway evolved first and is wide spread in the terrestrial and aquatic habitats (Sikolia, Onyango, Beck and Kinyamario, 2009[1]; Ehleringer, Cerling and

Hellicker, 1997[2]). The C_4 syndrome exhibit recent phylogenetic development and might have evolved independently several times in monocots and dicots[1]. The NADP-malic type, NAD-malic type and PEP-Carboxykinase are the biochemical subtypes of the C_4 pathway. Also, C_3-C_4 intermediate species were recorded. Climatic factors influence the distribution of the monocot species (Tieszen and Imbamba, 1976[3]; Ueno and Takeda, 1992[4]) and dicot species [1] along the altitude. Climatic factors that influence species distributioninclude rainfall or precipitation, evaporation, temperature and relativehumidity [1][2][4]. They further, determine the occurrence and relative abundance of the species in their habitats. The factors affect stomatal conductance and gaseous exchange and therein photosynthesis. The C_4species possess Ribulose-1,5 bisphosphate carboxylase/oxygenase (Rubisco) that is primary carbon dioxide fixing enzyme in plants. Rubisco is a slow catalyst with low affinity for its substrate carbon dioxide. Rubisco discriminate poorly between CO_2 and oxygen (O_2). Oxygenase activity of Rubisco occurs during high oxygen (by-product of the light reaction of photosynthesis and atmospheric oxygen) concentration and less carbon dioxide fixation. This initiate series of reactions of the photorespiration making photosynthesis less efficient process.

C_4plants make significant contribution to the world’s carbon budget and C_4 crops, like,maize, sorghum, millet and wheat are central to the current and future global security and safety ([2];Brown, 1999[5]). Furthermore, C_4 plants predominate in semi-arid, arid and saline habitatsprone to frequent drought. This observation is worsened by global climate change in various ways: global warming and changes in precipitation patterns are likely to expose many ecosystems, including C_4 dominated habitats to increasing soil and atmospheric water stress and scarcity(IIPP,2007[6]);ii) the impact of rising atmospheric carbon dioxide concentration on the productivity of C_4 plant species is much influenced by soil moisture aridity index ([2]; Ghannoum *et al*, 2006[7]) and global warming may lead to an increase in the proportion of land area covered by C_4 plants, especially in grasslands and rangelands (Crimp *et al*, 2002[8]).

It is important to understand the role of environmental factors, anatomical (structural) organization, physiological and biochemical processes in influencing the kinetics of the primary processes of carbon dioxide fixationin plants. This determines relative abundance and distribution of the dicot species in the partitioning of productivity along the altitude gradient. Therefore, therate of photosynthesis becomes benchmark in thebioproductivityin different ecological ecosystems. An exception cannot be in Kenya.

The paper attempts to i) correlate the distribution of the C_3 and C_4 species to different climatic variables along the altitudinal gradient, ii) determine the main factors that influence the distribution of the species, iii) describe the C_3 and C_4 habitats, iv) provide the climatic specifications in the transition phase between C_3 and C_4 dicot plant species, v) and show changes in bioproductivity in different plant species at different growth stages.

II. MATERIALS AND METHODS

Sampling Sites and Climatic Data.

Sampling sites were randomly selected along North West-North East belts transect. The belt transect was about 30km wide between 36° 30’E and 34°30’E, ran from south-west of Mt. Elgon to Mt. Kulal near Lake Turkana. It was about 365km long rising from 670m at Lodwar to 4200m at Mt. Elgon through 250m in Kerio valley up to around 2,415m to 2293m Mt. Kulal, 950m Samburu game reserve and Kapedo-Nginyang. Ten-year climatic data were sourced from meteorological stations in the area of study. Field climatic data was also measured. The means for each climatic variable was calculated. The variables included temperature, rainfall, relative humidity, radiation and potential evaporation. Twenty-fivequadrats were placed at 10m interval random sites along the belt transect. Percentage frequency of occurrence of each species sampled quadrats was determined. Thus, the total number of each species divided by the total species in the sampled in the quadrats times 100% was worked out.

Identification of the Plant Species

Identification was done both in the field and laboratory. Unknown species were sent to the East African Herbarium or Chiromo Campus Herbarium, University of Nairobi, Kenya for verification. Healthy floral organs and leaves organs were collected for plant identification and Kranz leaf anatomy studies, respectively. Leaves were dried in natural conditions between 25-30°C in the field.

Anatomical Studies

Microtome sections for Kranz leaf anatomy (presence/absence) were prepared and studied. C4 and C3 species exhibited Kranz leaf anatomy and non-Kranz leaf anatomy. Hattersley and Watson (1975) modified anatomical description of 0-3cells or 5-15 cells or 4-5 cells for the lateral cell count was adopted.

Measurement of the □^{13}C Data

Leaves were dried with circulating air in the oven at 25-30°C until there was no change in weight. Dried leaves of each species were milled into minute grains used for the determination of $^{13}C/^{12}C$ isotopic analysis of the species. Dried leafy-milled grains of each species were analyzed using an elemental analyzer (HERAEUS CHN.O RAPID) for Dumas combustion of the samples, a FINNIGAN MAT Delta (δ) gas isotope mass spectrometer with a dual inlet system, a method of Gebauer and Schulze (1987)[9]. Standard gas carbon dioxide was calibrated with respect to international standard (CO in Pee Dee Belemnite) by use of the reference substance NBS 16 to 20 for carbon isotopic ratio provided by the 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 using the formula equation below:

$$\delta_x = R_{sample}/R_{standard} - 1)\chi 1000(‰)$$

where, δ_x is the isotope ratio of carbon in delta units relative to the international standards andR_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ ratios of the samples and standards, respectively [9]. The $\delta^{13}C$ values were assigned against each species investigated.

Measurement of the Carbon Dioxide Compensation Points

Six week old plant species in enclosed in gas-airtight cover using Vaseline oil just before the experiment to prevent gas exchange with the soil, was put in an airtight 19litre fan stored glass chamber at 20°C controlled temperature. The carbon dioxide concentration (ppm) were continuously measured by pumping a stream of air through a closed, oxygen tight, circuit with an Infra-Red Gas Analyzer (Biros 1.1, Leybold, Hanau, Germany) for carbon dioxide compensation points measurements. A constant light intensity of 350µmol/m2/sec was used. The carbon dioxide concentration in the chamber was arbitrary set by injecting small amount carbon dioxide with a calibrated syringe through a small rubber plug in the jar lid, at a time to avoid fluctuations on the scale recorder. Experiments were run in atmospheres ranging from 1000ppm to 60-40 or 20-8ppm carbon dioxide (Tolbert, Benker and Beck, 1995)[10]. Sodium hydroxide pellets were used to remove excessive transpired moisture from the gas chamber. The carbon dioxide bind effect was nullified because it was used in each of the experiment carried out.

III. RESULTS

More than two hundred species of the Centrospermeae families were investigated for their climatic factors along the altitude in Kenya. The frequency of the species distribution along an altitudinal gradient from200-4,200m a.s.l. is shown in Figure 1. High degree of species diversity occurred between 900-2300m. Interesting *Melandrium nordiflorum, Silene abyssinica* and *S. gallica*, which are C_4 species, thrive at high altitude (>4000m a.s.l.). Low moisture, high diurnal temperature fluctuations, high relative humidity and high rates of potential of evaporation the C_4 habitats. Species of Amaranthaceae had broad ecological range of spatial distribution. Basellaceae has the least spatial distribution. The distribution of the species was mainly genera specific.

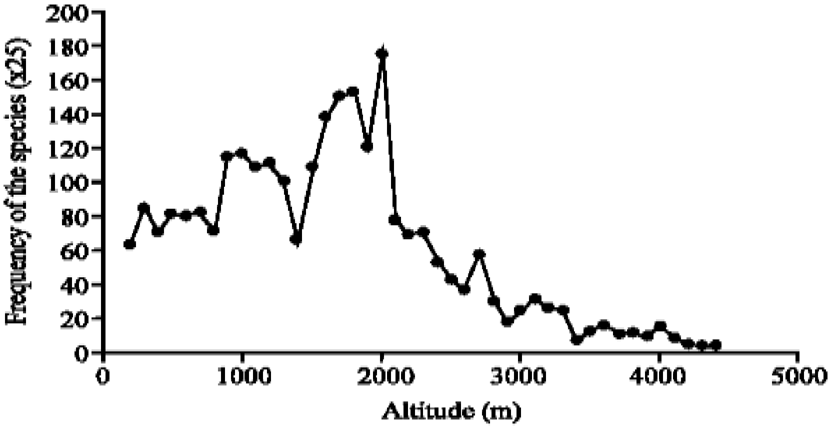

Figure 1: Distribution of the Centrospermeae species along the altitudinal gradient.

The $\delta^{13}C$ values of the species show three characteristic functional groups of the C_3, C_3-C_4 intermediate and C_4 photosynthetic types (Fig. 2). The species of the group were biotyped as follows: i) 68 species fell between -10.60‰, ii) 174 species between -21.16‰ to -30.93‰, respectively. Intermediate fell between -17.79‰-

25.89‰. *Chenopotium capitatum* showed an exception value of -32.42‰. *Mollugo nudicaulis* exhibited C_3-C_4 intermediate syndrome. No species of C_4 was recorded in the Basellaceae and Phytolacaceae families.

Correlation distribution percent of the C_4 and C_3 species exhibited different relationships with the climatic parameters: mean annual temperature (Fig.2), mean annual rainfall (Fig.3),mean annual rainfall(Fig. 4), mean annual evaporation (Fig. 5) along the elevational gradient; and their correlation coefficients recorded as r=0.94, r=-0.91,r=0.92, r=0.87, respectively.

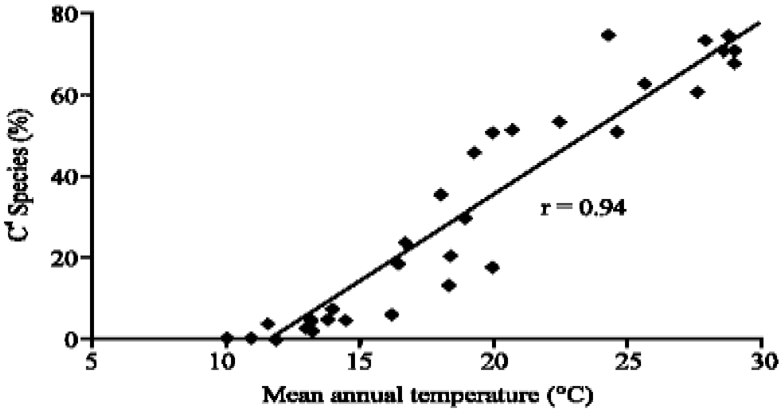

Fig. 2: Correlation distribution percent of C_4 species and mean annual temperature along the elevational gradient.

The C_4 pathway was inversely correlated to increasing annual rainfall (Fig.3) and vice versa for C_3 pathway (Fig.4). The mean annual evaporation was a promoter factor rather than a critical determinant variable for the distribution of either type of species. Relative humidity was the least of the determinant factors; was weakly correlated to species distribution with r^2 of 0.097 and 0.27 for C3 and C4 species, respectively.

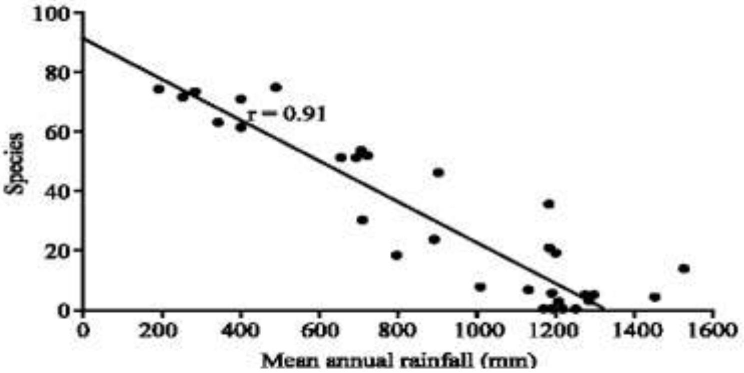

Fig. 3: Correlation distribution percent of C_4 species and mean annual rainfall along the elevation transect

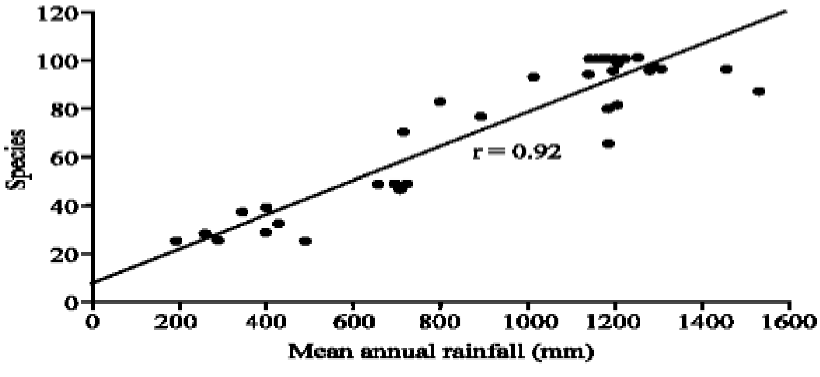

Fig. 4: Correlation distribution percent of C_3 species and mean annual rainfall along the elevation transect

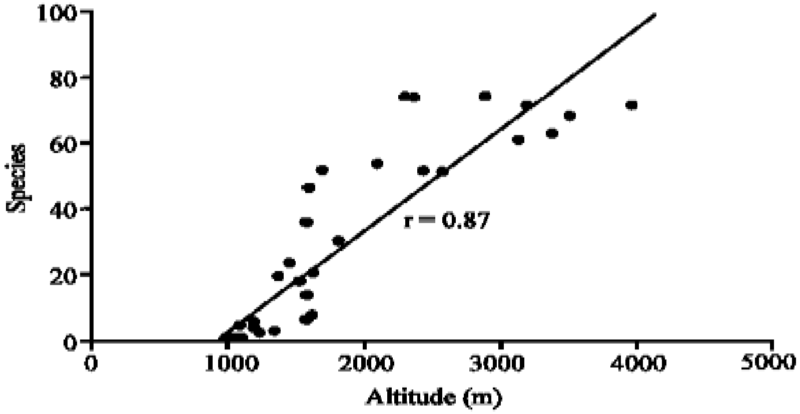

Fig. 5: Correlation distribution percent of C_3 species and mean annual evaporation along the elevation transect.

The correlation coefficient of the C_3 and C_4dicot species in relation to the climatic variables is summarized below (Table. 1). Note the inverse relation between C_4species and rainfall.

Table 1: shows the correlation coefficients between the climatic factor against the relative abundance of the C_3 (first row in the table) or C_4 (second row in the table) photosynthetic species, in Kenya.

Climatic Factor Type of Photosynthetic	Mean annual Temperature	Mean annual Rainfall	Mean annual Potential Evaporation	Mean annual Rel. Humidity
C_3 Photosynthetic Type	r^2=0.85 r =0.91	r^2=0.84 r =0.92	r^2=0.723 r =0.85	r^2=0.097 r =
C_4 Photosynthetic Type	r^2=0.89 r =0.94	r^2=0.83 r=-0.91	r^2=0.76 r =0.87	r^2=0.27 r =0.

Figure 6 shows the transition zone between relative C_3dominance and C_4 dominance species along the altitude. It is occurs within the range of 1,500-1700m a.s.l. This transition zone was defined by climatic parameters as mean minimum annual temperature (15.7 °C), mean annual temperature (25.6 °C), mean annual rainfall (700-950mm), mean annual potential evaporation (1575-1650mm^3 m^{-2}), mean annual radiation (450-500Jm^{-2}) and mean annual relative humidity (50-55%), respectively. Mean annual temperature range of 20.7 to 25.6 °C is the temperature for the transition shift from C_3 to C_4 dominance, regardless of the elevation or latitudinal gradients.

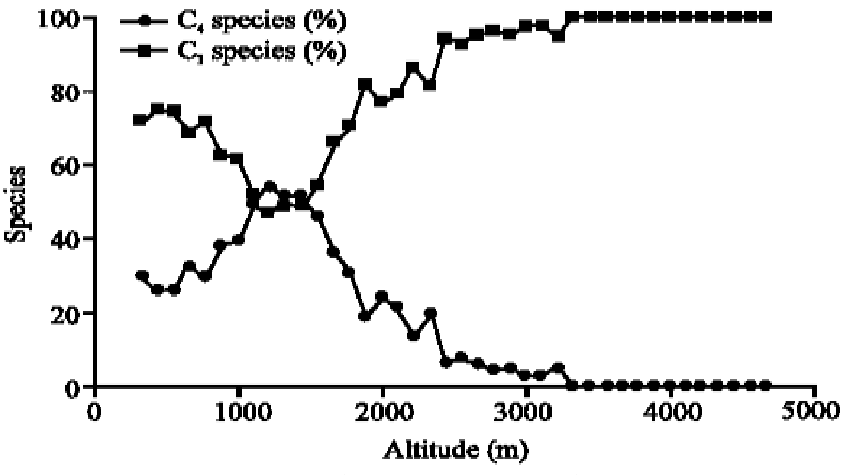

Fig. 6: Distribution percent curves of $C_3$and C_4 species of the Centrospermeaealong the altitudinal transect.

The figures below (Figs.7a and 7b) represent time course for net carbon dioxide uptake in various photosynthetic species under air tight gas chamber. Further, the species have different weight which is reflected in their different CO_2 uptake rates. This simulates the phenomenon of the species in the field under the current rising CO_2 concentrations.

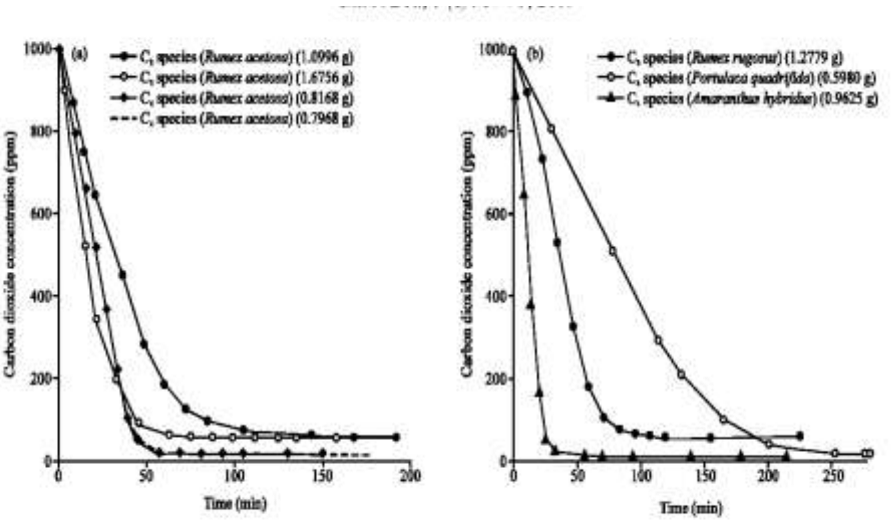

Fig. 7a/b: (7a- on the left and 7b on the right): Time course of net CO_2 uptake in different photosynthetic species carried out in air tight gas chamber.

IV. DISCUSSION

Distribution of C_3 and C_4 dicots species along the altitude

Global latitudinal distribution of C_4 grass species richness has been linked to different ecological drivers. Studies have demonstrated a strong decline in the richness, relative abundance and biomass of C_4 species with increasing altitude, but in all cases, the contribution of C_4 species to the floral or total biomass has been shown to correlate with some index of temperature[2]. The indices aremean annual temperature (Hattersley, 1983[11]) and climate of July (mean daily high temperature and month's total rainfall), (Teeri and Stowe, 1976[12]; Von Fischer *et al*, 2008[13]).

The present data represent the largest study of C_3 and C_4 dicots distribution in East Africa. The results showed that mean temperature determines the distribution of C_4 dicot species along the altitudinal gradient. This is modified by mean rainfall, mean annual evaporation and mean relative humidity as secondary ecological drivers. Strong correlation coefficient of r^2=0.89, r^2=0.83 and r^2=0.76 between mean annual temperature, mean annual precipitation and mean annul rates of evaporation and percent C_4 dicot species were observed. Positive correlation between climatic factors and percent C_4 dicots species was recorded except inverse for precipitation. Tieszen *et al* (1979) [14]found minimum temperature, irradiance and available soil moisture to be selective forces for the observed grass distributions in open grassland vegetation transect. The distribution and abundance of C_4 monocots andC_4 dicots respond to the same climatic parameters with varying intensity and behavior in similar ecological regions. Generally, temperature and evaporation are the main ecological drivers for C_4 dicot species distribution. This can be interpreted as aridity index ecological driver.

The distribution percent relationship between the relative abundance of the C_3/C_4 dicots species and temperature along altitudinal gradients is partitioned three times. The first partition corresponds to low altitude associated with high temperatures (>26.5 °C), C_4dicot species dominance without significant competition from high-temperature intolerant C_3species. The second partition reveals C_3 and C_4 transition versus competition zonation associated with moderate range temperature (20.7-25.6 °C). Some C_4 dicot species exhibit shade tolerant phenomenon in the transition phase, for example, *Tribulus terrestris*. Finally, below 20 °C, C_4 dicot species are rare, for example, *Melandrium nordiflorum* but C_3 dicot species pre-dominate, partly forming the leafy canopy.

The transition temperature was critical switch between C_3 and C_4 dominance in the present study. Here, transition temperature was defined as a point at which C_4 abundance fell below 50% based on the taxonomic basis. Most of the studies converge on the day time temperature range of 20-28 °C as the temperature for the shift in C_3-C_4 dominance, either based on elevation or latitudinal gradients[2]. The transition zone between C_3 and C_4 dicot groups is rather abrupt for the dicots and occurs at 1500-1,700m a.s.l along the altitude, less behind that recorded for monocots in Java (Hofstra *et al*, 1979)[15] and Kenya [14] at 2,000-2,300m a.s.l. altitude. The transition zone was defined by climatic variables of mean annual minimum temperature(°C), mean annual maximum temperature (°C), mean annual rainfall (mm),mean annual potential evaporation (mm m^{-2}), mean annual radiation (cal m^{-2}) and mean annual relative humidity(%) of 15.7,25.6,700-950mm, 1575-1650mm m^{-2}, 450-500Jm^{-2} and 50-55%, respectively. Mean annual temperature range of 20.7 – 25.6°C is the temperature for the transition shift from the C_3 to C_4 dominance, regardless of the elevation.

The C_4 subtypes, NAD-me, for example, *Portulaca oleracea* and NADP-me, for example *Portulaca grandiflora, P. quadrifida* and *P. pilosa* showed decreasing relative abundance gradation along the altitude as temperature increased, respectively. Within grasslands, there is a gradual transition from domination by C_4 NAD-me-type grasses in drier regions to domination by C_4 NAD-me-type grasses in regions of increased precipitation ([11]Schulze*et al*, 1996[16]; Ellis *et al*, 1980[17])

C_3, C4 and Bioproductivity

Differences in the C_3 and C_4 photosynthesis are relevant to global changes in atmospheric carbon dioxide concentration and changes in temperature. Further, the kind of photosynthetic pathway influences the magnitude of carbon fixation by the ecosystem, the quality of the plant food resource available to animals, and the isotopic composition of carbon dioxide released to the atmosphere (Sikolia, 2016[18]).

C_3 species fix CO_2 using Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) that has poor kinetic properties. Compared with other enzymes, Rubisco is a slow catalyst with low affinity for its substrate CO_2. During low CO_2 concentrations, oxygenase activity of Rubisco takes place at the expense of carboxylase activity. By reacting RuBP with oxygen, Rubisco fixes less carbon dioxide and initiates a series of reactions, photorespiration, which culminates in the release of carbon dioxide back to the atmosphere. Here, phosphoglycerate and unwanted phosphoglycolate are released. The oxygenase reaction results in less net carbon fixation and eventually leads to the production of CO_2 during photorespiration. Under the current atmospheric carbon dioxide concentrations and temperature of 25°C, photorespiration runs at about 20-30% of photosynthesis in C_3 leaves(Sage, 2004[19]). With increasing temperature, photorespiration increases faster than photosynthesis (Sage and Kabien, 2007[20]). Thus, C_3 photosynthesis becomes inefficient and wasteful.

The development of the CO_2-concetrating mechanism in C_4 leaves solves this problem. Carbon dioxide hydration forms bicarbonate which reacts with phosphoenolpyruvate with the aid of phosphoenolpyruvate carboxylase to produce oxaloacetate, a C_4 acid, in the mesophyll cells. The C_4 acid is converted into other acids like aspartate which diffuse into the bundle sheath cells where they are decarboxylated to release carbon dioxide for fixation by Rubisco and the rest of the C_3cycle. Thus, the C_4 cycle function as a concentrating mechanism because PEPC is faster than Rubisco and insensitive to O_2 and the bundle sheath presents a significant gaseous diffusion barrier. The whole process concentrates CO_2 in the bundle sheath suppressing apparent photosynthesis in air as well as the saturation of C_4 photosynthesis at ambient carbon dioxide concentrations than for the C_3 plants. Thus, C_4cycle becomes efficient in fixing carbon dioxide during photosynthesis. Regeneration of PEP from pyruvate requires additional cost of ATP in the C_4 cycle which makes it slightly inefficient. However, this is almost compensated by concentrating released C_3-CO_2 into more useful oxaloacetate Therefore, balance between the two pathways simulating the environmental conditions is very critical in achieving higher carbon fixation, both primary productivity and secondary productivity. Secondary productivity because the mammalian migration depends on the primary producers and grazer for their survival. This defines the course, nature and degree of bioproductivity.

Advantages of C_4 photosynthesis under lower atmospheric and or higher temperature environments, where photorespiration rates are relatively high in C_3 plants is significant for carbon gain and therein productivity. Under this environmental condition, the efficiency of C_4 photosynthesis is greater than that of the C_3 photosynthesis. However, under elevated CO_2 concentrations or cool temperatures, the efficiency of photosynthesis is greater in the C_3 photosynthesis because photorespiration is reduced and the additional ATP cost of C_4 photosynthesis makes it less efficient.

During recent glacial-interglacial cycles, an atmospheric CO_2 concentration has fluctuated between 180-280ppm [2]. But industrial revolution has led a reversal effect, where atmospheric CO_2 has dramatically increased since the 1950-todate. Until mankind's for fossil fuel is satisfied /or alternative source is put in place, atmospheric CO_2 will likely continue to rise to levels not yet known. The C_4 syndrome will likely loose in the competitionto the C_3 species due to reduced photorespiration and enhanced light-use efficiency. Certainly, increased bioproductivity will ensue. Humans will continue to grow C_4 crops as a farming culture of today, planting C_4 plants e.g. maize, millet, corn and sorghum. This demands novel methods to acquire hybrid of C_3/C_4species developed. May be a good reason to have successful C_3-engineered crop with C_4 syndrome like rice/or enhance search and promote C_3-C_4 intermediate crops.

REFERENCES

[1]. Sikolia, S., Onyango, J.C., Beck, E and Kinyamario, J.I., The distribution of C_3 and C_4 photosynthetic species of the Centrospermeae along an altitudinal gradient in Western Kenya. International Journal of Botany, 5(1), 2009, 47-57.

[2]. Ehleringer, J.R., Cerling, T.E. and Hellicker, B.R., 1997: C_4 photosynthesis, atmospheric CO_2 and climate. Oecologia, 112, 1997, 285-299.

[3]. Tieszen, L.L. and Imbamba, S.K., Photosynthetic systems and their significance in East African ecology and agriculture. Kenya Promot. Sci. Technol. (POST), 11, 1976, 24-28.

[4]. Ueno, O. and Takeda, T.,Photosynthetic pathways, ecological characteristics and the geographical distribution of the Cyperaceae in Japan. Oecologia, 89, 1992, 195-203.

[5]. Brown, R.H.,Agronomic implications of C_4 photosynthesis: In Sage, R.F. and Watson, R.R., Eds. C_4 Plant Biology(San Diego, CA: Academic Press, 1999) 473-507.

[6]. IPCC ,Technical summary. In: Solomon, S., Qin, D. and Manning, M., et al, (Eds.). Climate Change 2007: The physical science basis. Contribution of working Group to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.(Cambridge: Cambridge University Press, 2007).

[7]. Ghannoum, O. and Searson, M.J. and Conroy, J.P., Nutrient and water demands of plants under climate change. In: Newton PCD, Edwards, Carran, A., Nikluas, P., Eds. Agroecosystems in a changing climate. Advances in Agroecology Series, Vo., 12 Boca Raton, F.L.: CRC Press, 2006, 55-85.

[8]. Crimp,S.J., Flood, N.R., Carter, J.O., ConroyJ.P.and McKeon, G.M.,Evaluation of potential impacts of climate change on native pasture production- implications for livestock carrying capacity: Report to the Australian Greenhouse Office, 2002.

[9]. Gebauer, G.B., Schubert, M.I., Schuhmacher, H., Rehder, and Ku, M.S.B.,C_3-C_4 intermediate photosynthesis in plants. Bioscience, 3, 1984, 563-574.

[10]. Tolbert, N.E., Benker,C. and Beck, E., The oxygen and carbon dioxide compensation points of the C_3 plants: Possible role in regulating atmospheric oxygen. Proc. Natl. Acad. Sci., 92, 1995, 11230-11233.

[11]. Hattersley, P.W., The distribution of C3 and C4 in grasses in Australia in relation to climate. Oecologia (Berlin), 57, 1983, 113-128.

[12]. Teeri, J.A. and Stowe, L.G.,Climatic patterns and the distribution of C_4 grasses in North America. Oecologia, 23, 1976, 1-12.

[13]. Von Fischer, J.C., Tieszen, L.L. and Schimel, D.S.,Climate controls on C_3 vs. C_4 productivity in North American grasslands from carbon isotope composition of soil organic matter. Global Change Biology, 14, 2008, 1141-1155.

[14]. Tieszen, L.L., Senyimba, M.M., Imbamba, S.K. and Troughton, J.H., The distribution of the C_3 and C_4 grasses and carbo isotope discrimination along an altitudinal and moisture gradient in Kenya. Oecologia (Berlin), 37, 1979, 337-350.

[15]. Hofstra, J.J., Aksornkoe, S., Atmowidjojo,S, S Banaag, J.F., Santosa,R., Sastrohoetomo,A. and Thu,L.T.N., A study on the occurrence of plants with a low CO_2 compensation point in different habitats in the tropics. Ann. Bogoriensis, 5, 1972, 143-157.

[16]. Schulze, E-D, Ellis, R., Schulze, W., Trimborn, P. and Ziegler, H., Diversity, metabolic types and $\delta^{13}C$ carbon isotopic ratios in the grass flora of Namibia in relation to growth form, precipitation and habitat conditions. Oecologia, 106, 1996, 352-369.

[17]. Ellis, R.P., Vogel, J.C. and Fuls, A., Photosynthetic pathways and geographical distribution in the South Africa/Namibia. South African Journal of Science, 76,1980, 307-314.

[18]. Sikolia, S.F.,C_3 and C_4 photosynthetic species (Centrospermeae - Dicots) along the altitudinal Aridity Gradients and their Ecological Implications in Bioproductivity Paradigm, in Kenya. Proc. of the Alexander Von Humboldt Kolleg, Naivasha-Kenya, 2016, 59-60.

[19]. Sage, R.F., The evolution of C_4 photosynthesis. New Phytologist, 161,2004, 341-370.

[20]. Sage, R.F. and Kabien, D.S.,The temperature response of C_3 and C_4 photosynthesis. Plant, Cell and Environment, 30,2007,1086-1106.