The Distribution of C₃ and C₄ Photosynthetic Species of the Centropermeae Along an Altitudinal Gradient in Western Kenya

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Abstract: Two hundred and seventy eight species of the Centropermeae were collected at different sites in Western Kenya representing gradients of altitude and aridity. Climate data were obtained from meteorological research stations. Species were examined for C₃ or C₄ photosynthesis using the anatomical Kranz syndrome, δ¹³C values and carbon dioxide compensation points. C₄ photosynthesis is a feature of modern members of dicotyledoneae of multiple evolutionary origins. It evolved independently in members of the same family and was found in one to several genera and then often only with two to three species. C₄ species are concentrated in lowland habitats subjected to high temperature, low precipitation and high evaporation. High δ¹³C values is associated with low water availability which is a physiological syndrome and also a feature of saline habitats. The C₄ representatives of the Centropermeae dominate in more moist and colder habitats, especially at higher altitudes. Only a few C₄ species occur at high altitudes (3000-4000 m) namely Sagina gallica, Silene abyssinica and Melandrium nortiflorum. The transition zone between C₃ and C₄-dicot is rather narrow between 1500 to 1700 m and much lower than that recorded for the monocots (2000-2200 m). The general pattern of δ¹³C 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 -32.42% that corresponds to altitudinal ranges, 0-1500, 1550-1700 and 1800-4200 m, respectively. The low altitudes are associated with drought and high temperatures. C₃ and C₄ dicot species can be intercropped to increase bioproducitivity for the betterment of the flora and fauna in the semi-arid and arid ecosystem. C₄ species are potential candidates for exploitation in the agroforestry systems especially for long-term management programmes. The present study may also be relevant for better understanding of global change with respect to the diversity of photosynthetic pathways, herbivory and vegetation dynamics.

Key words: C₃ and C₄ photosynthetic species, climatic factors, altitude, transition zone, ecological significances

INTRODUCTION

The coexistence of diverse plant species with different photosynthetic pathways is now well established (Ehleringer et al., 1997; Wang, 2004). The groups are characterized as CAM, C₄ and C₃ plants. There is consensus that the C₃ pathway evolved first and is widespread in terrestrial and aquatic habitats. The C₃ syndrome is a phylogenic younger achievement and apparently evolved independently in monocots and dicots perhaps as many as twenty times (Smith et al., 1976). This interpretation is corroborated by the existence of different types of the C₃ syndrome, namely the NADP-malic type, the NAD-malic type and the PEP-Carboxykinase type (Hatch, 1987). C₄ photosynthesis: a unique blend of modified biochemistry, anatomy and ultrastructure. Nevertheless, 40% of the taxa in the Poaceae show the C₄ syndrome (Tieszen, 1978). A No. of genera contain both C₃ and C₄ species but only very few species in the Paniculoides and of the genus Flaveria are C₃-C₄ intermediates (Drinovich et al., 1998; Edwards et al., 2001). Thus, most species are clearly either C₃ or C₄ and are not interconvertible.

The C₃ and C₄ species possess different structural, physiological and biochemical features resulting in different water use efficiency and adaptation to climate (Ehleringer et al., 1997; Wang, 2004) has been demonstrated in the Gramineae and Cyperaceae families. As C₃ plants are better adapted to higher temperatures and arid or saline conditions, knowledge of the C₃ syndrome and its occurrence in the plant kingdom is also required for the understanding and prediction of vegetation change during global climatic change and for the conservation and restoration of natural ecosystems (P'yankov et al., 2000). Similar ecological studies of the dicots are too few for a sound assessment of a correlation

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between their occurrence and environmental variables. Centrospermeae group has been proposed to possess different photosynthetic types (Tieszen, 1981). But the proportion of the photosynthetic types has not been studied. Furthermore, ecological significances associated with C_3 and C_4 systems should be characterized in detail, especially in the dicot families. The objective of this study is to present data on the mesoscale distribution of the C_3 and C_4 syndrome in the Centrospermeae choosing gradients of altitude and aridity. Western Kenya was selected as sampling area because of its wide altitudinal range (up to 4200 m) broad range of air temperature, evaporation, precipitation in different rainfall regimes and even radiation, in habitats varying from open grassland to semi-arid/or arid deserts with intermittent saline habitats.

MATERIALS AND METHODS

This study was carried out in the 2000-2003 duration.

Geographical description of the gradient(s) and collection of the ecological data of the sampling sites: The studies were carried out in the semi-arid and saline areas. Sampling sites were randomly distributed along North West-North East belt transect. The transect about 30 km wide between 36°30'E and 34°30'E, ran from South-West of Mt. Elgon to Mt. Kalal near Lake Turkana. It was about 365 km long rising from 670 m at Lodwar to 4200 m at Mt. Elgon through 250 m in Kerio Valley up to around 2,415 to 2293 m Mt. Kalal, 950 m Samburu Game reserve and 900 m at Kapedo-Nyiang. Sites were sampled in a broad range of vegetation types from semi-arid regions to near snowline. Attempt was made to sample at least some communities from each of the regions of available soil moisture as defined for Kenya by Woodland (1981). This annual index is based upon soil water storage, precipitation and Penman estimates of water surplus divided by the annual total evaporation. Climatic data were sourced from meteorological stations in the area of study. Ten-year climatic data were obtained from meteorological stations at the area of study - North West Kenya and their means calculated over the time period. Field climatic data was also measured. The stations included: Rohet, Lokori, Perkerra, Lodwar, Chewoyet and Kitale, Nginyang, Chemelatingot, Lokichogio and Marigat areas. The mean annual values of the climatic variables collected included: maximum and minimum temperature (°C); monthly rainfall; relative humidity (%); daily radiation (J m⁻²); monthly potential evaporation (mm m⁻²) and altitude (m), measured by a thermometer, maximum-minimum thermometer, rain gauge, thermopile pyranometer, litre pan water drying per meter area in a day and altimeter, respectively. Twenty-five Quadrats were placed at 10 m interval random sites along the belt transect. Percentage of frequency of occurrence of each taxon of the sampled Quadrats was determined. Thus, the total number of each species divided by total species in the sampled quadrats times 100%.

Identification of the specimens: Identification was made in the field. Difficulty specimens were identified in the East African Herbarium or the Chiromo Campus herbarium, University of Nairobi, Kenya for verification. Nomenclature followed by Clayton (1974), Beentje (1994), Blundell (1992), Loischert and Beese (1994) and Oleombo et al. (1995), system of identification and documentation, respectively. Healthy leaves and desirable floral organ of the species were collected from different sites and enclosed in wet toweling paper in Jar(s). Enclosed containers for short transportation to the laboratory or brief storage were used. Leaves of species were dried in natural conditions between 25-30°C in the field.

Anatomical investigations: The classification of the dicot species into C_3 or C_4 or CAM groups was made on the basis of the structural Kranz anatomy (or, more specifically, the 0-3 cells or 5-15 cells or 4-5 cells for the maximum lateral cell count of the modified method of Hattersley and Watson (1975), δ¹³C values and CO₂ compensation points.

Determination of the δ¹³C data: Air oven at 25-30°C circulation dried leaf or vegetative organ until there no change in weight. Dried specimens were used for δ¹³C/¹²C isotopic analysis of species at Bayreuth Universitat, Germany. Dried leafy-milled grains of each species were analyzed using an elemental analyzer (HERAEUS CHN.O RAPID) for Dunas 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). Standard gas of carbon dioxide was calibrated with respect to international standard (CO₂ 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 δ¹³C/¹²C isotopic ratios (denoted as δ values or δ¹³C/¹²C values), were calculated according to the following equation:

\[ \delta = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \]%

where, δ is the isotope ratio of carbon in delta units relative to the international standards and R_{\text{sample}} and R_{\text{standard}} are the δ¹³C/¹²C ratios of the samples and standards, respectively (Gebauer and Schulze, 1987). The δ¹³C values were recorded against each species studied.
Measurement of the carbon dioxide compensation points:
Six week old species in a pot enclosed in a gas-tight cover using Vaseline oil just before the experiment to prevent gas exchange with the soil, was put in an airtight, 19 L fan stored glass chamber at 20°C controlled temperature. The carbon dioxide concentrations (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 point measurements. A constant light intensity of 350 μmol/m²/sec was used. The carbon dioxide concentration in the chamber was arbitrarily set by injecting small amount CO₂ 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 1000 parts per million to either 60-40 or 20-8 ppm CO₂. Sodium hydroxide pellets were used to remove excessive transpired moisture from the gas chamber. The carbon dioxide-sodium hydroxide bind effect was nullified because it was used in each of the experiment carried out.

RESULTS

Elements of climate for the ecological study area temperature (°C), rainfall (mm), relative humidity (%), radiation (cal cm⁻² or J m⁻²) and rates of potential evaporation (mm m⁻²) had their mean annual values worked out. Climatic elements were correlated to the abundance of either the C₃ or C₄ species along the altitude.

The vegetation consists of drought resistant species. High percentage of the region is bare especially in dry spell. Annual grassland, with or without dwarf shrub lands, nbusa grassland, scattered woody plant species such as Acacia reficiens may exist. Perennial grassland which is mostly ephemeral appears after a downpour especially during the April long rains. Afro-Alpine belt has groundsel, Lobelia, Alchemilla, dominated with Podocarpus-Juniperus and large pasture. Sometimes Podocarpus-Juniperus is mixed with Arundinaria alpina and the subnival tussock grassland (Festuca-Agrostis). At low end of the mountain ends of valleys are pastures and partly replaced by Dendrosenecio-Festuca-Agrostis. Sometimes small forests of small ericaceous-leaved trees (Erica-Philippi) occur.

Distribution of the species along the altitude: In total more than two hundred species of the Centrospermae families were studied. Figure 1 shows the frequency of Centrospermae species along an altitudinal gradient from 200-4,200 m. The highest diversity of Centrospermeae species was recorded between 900 and 2300 m. A dramatic decrease in species richness was observed above 2000 m and only very few species were recorded above 3500 m. Nevertheless even Sagina gallica, Silene abyssinica and Melandrium nordiflorum species were found on the top of Mt. Elgon at an elevation of 4,200 m. The habitat exhibit high degree of aridity. The habitat was characterized by high diurnal temperature fluctuations, low moisture availability, high relative humidity and high rates of potential of evaporation.

Figure 2 and 3 show the representation of the Centrospermae families along the gradient. Portulaceaeae, Caryophyllaceae and Polygonaceae had the widest range of distribution reaching from 200-4,200 m and the species diversity of latter two families exhibited several pronounced peaks between 1500 and 3000 m. The highest species diversity was found with the Amaranthaceae, the Phytolaceae and the Polygonaceae. The species in the families are typical lowland. Biodiversity was an adaptation to environmental factors, especially temperature.

The patterns of distribution of the species along the altitude in different families were very variable.
Species of Amaranthaceae had broad range spatial distribution. Species of the Polygonaceae, Caryophyllaceae, Aizoaceae, Chenopodiaceae and Portulacaceae had average spatial distribution. Low species spatial distribution was associated with Nyctaginaceae, Phytolacaceae and Caryophyllaceae, Basellaceae.

The distribution of the species was predominantly genera specific. At the altitude less than 1300 m: Gisekia, Mollugo and Trianthema of Aizoaceae, Aerva, Celosia, Digera and Aamaranthus of Amaranthaceae, Polygonum and Stellaria of Caryophyllaceae, Oxygonum and Polygonum of Polygonaceae, Calyptrotheca, Portulaca and Talinum of Portulacaceae had high frequency compared to the species of Basellaceae and Phytolacaceae. At the altitude less than 1400 m: Gisekia and Mollugo were almost not available, Delosperma and Limnium showed low frequencies (with Trianthema at 1800 m) for the Aizoaceae, Achyranthes, Aerva, Cynanthis, Aamaranthus of Amaranthaceae, Cerastium, Comes, Drymaria, Policha and Polygonum had good ecological cross-over (GECO), Silene (Very-GECO), Sagina of Caryophyllaceae, Chenopodium and Sueda (GECO) and Gyroptera of Chenopodiaceae and most genera of Polygonaceae (GECO). At altitude 1500-2500 m, individual species in the genera mentioned occurs in almost even frequency. Individual species in the genera: Sagina (at 3,500 m), Stellaria (at 1400 m and then towards 3300 m) and Melandrium of Caryophyllaceae (at 4,000 to 4,200 m mostly) and Trianthema of Aizoaceae (at 1800 m), are of ecological significance because deviate from the expected distribution trend. Too, they occur at almost snowline sites associated with high precipitation, very low temperatures, high radiation, increased moisture and relative humidity indices. Further, individual species of Oxygonum, Polygonum and Ramex of Polygonaceae does well at high altitudes whereas that of Tribulus of Zygophyllaceae least occur or not at all above 1400 m of the sampled sites.

Carbon ($^{13}$C/$^{12}$C) isotope discrimination: The $^{13}$C values of the species show three distinct groups of the C$_{4}$, C$_{3}$-C$_{4}$ intermediate and C$_{4}$ photosynthetic types. The $^{13}$C values of the groups are summarized as follows: (i) 68 species fall between -10.60 and -16.55% with a mean of -13.65% and standard deviation of 1.8; (ii) 171 species between -21.16 to -30.93% with a mean of -26.40% and standard deviation of 1.94, respectively. An exception case of -32.42% value for Chenopodium capitatum was significant variation. Intermediate species, Mollugo nudicaulis (Aizoaceae) and CAM species: Basella alba and Basella paniculata (Basellaceae) had $^{13}$C values as -25.89, -18.75 and -17.79%, respectively, with a mean of -20.81% and standard deviation of 4.4. The first cluster is characteristic of C$_{4}$ species, the second for the C$_{3}$ species, the third for the C$_{4}$-C$_{3}$ intermediate species and/or CAM species with $^{13}$C values which fall between -10.60 to -17.79%, -21.16 to -30.93% and -17.79 to -18.75%, respectively.

C$_{4}$-C$_{3}$ intermediate species occurred in the Aizoaceae (Mollugo nudicaulis) and CAM species in Basellaceae (Basella alba and Basella paniculata).

The C$_{4}$ species were conspicuously not recorded in two families - Basellaceae and Phytolacaceae. Basellaceae exhibit C$_{4}$-C$_{3}$ intermediate status but Phytolacaceae possess C$_{4}$ pathway. C$_{4}$-C$_{3}$ intermediate metabolism could be due to the transition evolution process in the Centrospermeae group. C$_{4}$-C$_{3}$ intermediate species included Mollugo nudicaulis, Portulacaria afra and Portulaca sp. Nov. The C$_{4}$-C$_{3}$ intermediate percent frequency of occurrence was approximately 1.25% of the Centrospermeae species. The C$_{4}$ type occur in the Amaranthaceae (16.7%), Caryophyllaceae (9.9%), Chenopodiaceae (70%), Nyctaginaceae (33.3%), Polygonaceae (11.1%), Portulacaceae (12.5%), Zygophyllaceae (50.00%) and Elatineaceae (25%) (Table 1). Amaranthaceae possess fewer C$_{4}$ species than Chenopodiaceae with almost similar growth habit and habitat. About 28.5% of the total species investigated were C$_{4}$ species, 70.3% C$_{3}$ species and 1.2% C$_{4}$-C$_{3}$ intermediate species. Concomitantly, in the C$_{4}$, a photosynthetic pathway whose distribution is both taxonomically rare and phylogenetically wide dispersed among the species occurs.

C$_{4}$ and C$_{3}$ species occurred in the genera: Mollugo, Melandrium, Alternanthera, Trianthema (Aizoaceae), Aerva (Amaranthaceae), Silene (Caryophyllaceae), Gyroptera (Chenopodiaceae) and Dianthus.
Table 1: Distribution of the C₃ pathway and C₄ pathway in the Centrospermeae group

<table>
<thead>
<tr>
<th>Genera (%)</th>
<th>Specie (%)</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>C₃-species</td>
</tr>
<tr>
<td>Aizoaceae</td>
<td>63.6 (7)</td>
</tr>
<tr>
<td>Amaranthaceae</td>
<td>16.7 (3)</td>
</tr>
<tr>
<td>Caryophyllaceae</td>
<td>9.5 (3)</td>
</tr>
<tr>
<td>Chenopodiaceae</td>
<td>70.0 (7)</td>
</tr>
<tr>
<td>Nyctaginaceae</td>
<td>33.3 (1)</td>
</tr>
<tr>
<td>Phytolaccaceae</td>
<td>0.0 (0)</td>
</tr>
<tr>
<td>Polygonaceae</td>
<td>11.1 (1)</td>
</tr>
<tr>
<td>Portulacaceae</td>
<td>12.5 (1)</td>
</tr>
<tr>
<td>Zygocephalaceae</td>
<td>50.0 (2)</td>
</tr>
<tr>
<td>Elatitaceae</td>
<td>25.0 (1)</td>
</tr>
</tbody>
</table>

Values in brackets are the total number species collected.

(Caryophyllaceae), Sesuvium sesuvioideae (-12.21%), of Aizoaceae, Silene abysinica (-10.9%), of Caryophyllaceae, Gyroptera gilletii (-12.12%), Salsola pestifera (-10.60%) of Chenopodiaceae, Tribulus terrestris (-10.68%) of Zygophyllaceae, Boerhavia elegans (-11.99%) of Nyctaginaceae had their δ¹³C values less negative than -12.22%. These δ¹³C values are occurred in the extreme dry habitats and could be an indicator of dryness of the habitat. The same is true for C₃ species with δ¹³C values that are more positive just outside the δ¹³C values range of C₄ species which is -22.40 to -30.34%. These C₃ species were Pandiaka lamarginosa of Amaranthaceae (-21.42%), Lychnis viscaria of Caryophyllaceae (-21.84%), Polygonum amphibium of Polygonaceae, Talinum cuneifolium and P. paniculatum of Portulacaceae. These six species have been found in the dry habitat and saline soils of Baringo and Turkana regions in Kenya. Salsola pestifera (-10.60%) and Tribulus terrestris (-10.68%) having a less negative δ¹³C values are widely distributed mostly in extremely dry habitat ecotypes. T. terrestris is related to the more δ¹³C negative value species of -12.56 and -13.40%, for the species, T. parvispinus and T. cistoïdes, respectively. These regions show high degree of dryness. Most of the Amaranthus species were C₃ species showing wide distribution up to the transition zone for the C₃ species and C₄ dicot species along the altitude.

The distribution abundance of the C₃ and C₄ Centrospermeae species showed different relationships with the climatic variables: mean annual temperature (Fig. 4), mean annual rainfall (Fig. 5, 6), mean annual minimum temperature (Fig. 8) and mean annual evaporation (Fig. 7). The percentage of C₃ species and C₄ species were plotted against the climatic variables and their correlation coefficients, provided. The present studies showed correlation coefficients of r = 0.94, r = 0.91, r = 0.87, r² = 0.27 for the percentage of C₃ species against mean annual temperature (Fig. 4), mean annual rainfall (Fig. 5), mean annual evaporation (Fig. 7), relative humidity, respectively. The correlation coefficient,
Mean annual evaporation was a promoter factor rather than the critical determinant factor for the abundance of the C₃ dicot species (Fig. 7) or C₄ dicot species. Mean annual relative humidity was neither a critical nor a promoter parameter. Therefore, mean annual temperature is the dominating determinant parameter correlated with the abundance of C₃ dicot species and its effects on the C₄ dicots species distribution increased with increasing aridity indices in the present study. Probably, relative humidity act as a synergistic factor with the major climatic determinant factors for example mean annual temperature and precipitation and evaporation.

The transition zone associated with the switch between C₃ dominance and C₄ dominance of abundance occurs between 1,500-1,700 m. Here, the transition zone was defined as the point at which C₃ abundance fell below 50%, based on the taxonomic basis and not necessarily on a percent C₄ biomass basis. This transition zone was defined by climatic variables as mean annual minimum temperature (°C), mean annual maximum temperature (°C), mean annual rainfall (mm), mean annual potential evaporation (mm² m⁻²), mean annual radiation (J m⁻²) and mean annual relative humidity (%) of 15.7, 25.6°C, 700 to 950 mm, 1575-1650 mm² m⁻², 450-500 J m⁻² and 50-55%, respectively. Mean annual temperature range of 20.7 to 25.6°C is the temperature for the transition shift from the C₃ to C₄ dominance, regardless of elevation or latitudinal gradients. High temperatures, high evaporation and low moisture (rainfall or precipitation) are characteristic of aridity associated with the abundance of C₃ dicot species contrasting C₄ dicot species. The distribution and abundance (%) of the C₃ and C₄ species along the altitude show a transition phase as rather abrupt and sharp (Fig. 8).

**DISCUSSION**

**Phylogenetic distribution:** The taxonomic distribution of species exhibiting C₃ pathway and C₄ pathway attained 70.4 and 29.4% amongst the Centrospermeae group, respectively. Aizoaceae and Chenopodiaceae have high percentage of 63.6 and 70% of the genera exhibiting C₃ pathway. Similar phenomenon at the species level attained 50, 53.6 and 53.6% of the C₃ pathway in the Aizoaceae, Chenopodiaceae and Portulacaceae, respectively. Amaranthaceae, Basellaceae, Caryophyllaceae, Chenopodiaceae, Nyctaginaceae, Phytolaccaceae, Polygonaceae, Portulacaceae, Zygophyllaceae and Elatinaceae recorded 30.4-69.6%, 0.0%, 8.3.91.7%, 53.6: 46.4%, 33.3:66.7%, 0.100%, 57.94.3%, 53.6:46.4%, 50:50% and 16.7:83.3% for C₄ species: C₃ species proportion percentages, respectively. C₃ and C₄ type (interspecific)
species occurred in the genera- *Sesuvium*, *Trianthema*, *Alternanthera*, *Melandrium*, *Silene*, *Clypeastera*, *Portulaca* and *Zygophyllum*. This suggests interesting and perhaps recent evolutionary origins in the C₄ photosynthesis restricted to advanced members of the Centrospermeae. Multiple evolutionary origins of the C₄ pathway were evidently recorded in 25 of the 98 genera of the Centrospermeae. This is calculated at 28.6% of the genera studied. C₃-C₄ intermediate pathway occurs in the *Mollugo nudicaulis*, *Portulacaria afra* species.

Monson *et al.* (1984) reported the occurrence of the super-orders of the dicotyledonae and monocotyledonae. Most of the species exhibiting the C₃ pathway are quite separated from each other and belong to different genera. The finding reinforces the notion that the C₄ pathway must have evolved independently multiple times. This view is held by Monson (1989), Ehleringer and Monson (1993) and Ehleringer *et al.* (1997). Within the monocots, C₃ photosynthesis is quite common among the Poaceae and Cyperaceae that are closely related taxonomic groups (Hattersley, 1987; Hattersley and Watson, 1992). Lack of occurrence of the C₃ syndrome in the Phytolacaceae suggests its old ancestral lineage and greater phylogenetic diversity among the Centrospermeae group. But, Caryophyllaceae and Polygonaceae could be the initial point of phylogenetic development based on the low percentage of the C₃ syndrome occurrence.

According to Ehleringer *et al.* (1997), the C₄ syndrome in the dicots occurs in only 16 of the approximately 400 families. The present study reveals that in each family, C₄ pathway occur in only one to several genera and then often only within two to three species. Exception to this trend occurred in the Aizoaceae, Amaranthaceae and Portulaceae, where C₄ pathway is common among the genera. This is not the trend in Phytolacaceae. Furthermore, C₃-C₄ intermediate metabolism can exist in the genus that does not possess C₄ pathway, for example *Portulacaria afra*. The C₃ photosynthesis occurs in all the families of the Centrospermeae and shows high degree in the Caryophyllaceae (90.5%), Nyctaginaceae (66.7%), Phytolacaceae (100%), Polygonaceae (78.8%) and Portulaceae (85.7%) families. This taxonomic distribution pattern is consistent with the fact that C₃ photosynthesis may has evolved recently in the tropical dicots (Ehleringer *et al.*, 1997).

**Climatic variables and distribution of species:** The photosynthetic species are influenced by climatic differences. Species at low altitudes are associated with high temperature, relative humidity, potential rates of evaporation, radiation and low degree of precipitation. The group consists of a higher percentage of the C₄ species. High temperature and low precipitation played a dominant and synergistic causal role, whereas the other factors modified the frequency percent distribution of the species. These variables associated with aridity reveal the C₄ syndrome is arid-adaptive. Similar studies in Poaceae of the Northern Saharan Desert (Winter *et al.*, 1976), in Kenya (Tiuszen and Imbamba, 1976), in Java (Hofstra *et al.*, 1972), Ireland (Collins and Jones, 1985), Cyperaceae in Japan (Ueno and Takeda, 1992), Gramineae in North Argentina (Cavaganaro, 1988) and Poaceae in Australia (Hattersley, 1983), Israel (Vogel *et al.*, 1986) and salty areas of Hungary (Kalap et al., 1997), are also consistent with the present observation. In contrast, C₃ dicot species occur in high frequencies at high altitudes. The CAM species- *Basella alba* and *B. paniculata* and C₃-C₄ intermediate species- *Mollugo nudicaulis* and *Portulacaria afra* occur in the range between the extremes of the climatic factors.

The C₃ dicot species- *Melandrium nordiflorum* thrive in areas with the mean annual minimum temperature below 8°C. Similarly, Teeri and Stowe (1976) reported few or no C₃ species in habitats where July minimum temperatures were below 8°C.

Generally, the C₃ biochemical pathway concentrates carbon dioxide at the site of RUBP carboxylation (Hatch, 1976; Doliner and Jolliffe, 1979) that is selective advantage whenever internal carbon dioxide concentration becomes low. These conditions occur under high light intensities, periods of water stress and stomatal closure. The sites at low altitudes are subjected to serious water stress, high temperatures, high evapotranspiration and high irradiances. The C₃ species are selectively adapted to the four climatic factors and therefore have competitive advantage against the C₄ species.

**Ecological features of lowland habitats that allow the occurrence of C₄ species:** There are few exceptions to the present general distribution pattern, which helps provide insight into the factors controlling distributions. The few C₃ dicot species at low altitudes were found mainly in the understorey of closed forests and their families often consisted of the C₄ species. Also, some of the C₃ dicot species exhibit short timing life cycle synchronized with the rainfall spell. Under these conditions irradiances would be quite low and leaf temperatures would only uncommonly exceed 32°C. Ehleringer (1978) and Ehleringer and Bjorkman (1977) showed that temperature below 32°C provide higher quantum yield for C₄ compared to the C₃ plants. Thus, all factors being equal, the C₄ species should have carbon balance advantage in the shaded environments and maximum leaf temperatures.
below 32°C. The present studies support this view. Furthermore, most of the $C_3$ dicot annuals dominated some of the lowland or aquatic areas. Polygonaceae and Caryophyllaceae species formed a higher percentage of the understorey communities at low altitudes.

**C$_3$ species growing at high altitudes:** Few of the $C_3$ dicot species thrive at the high altitudes. The species include *Sagina gallica*, *Silene abyssinica* and *Melandrium nordiflorum* (4,000 m), *Calyptrotheca* species (3000 to 3300 m) species. The species have thick epidermal layers that would resist low temperatures and may partly account for the $C_3$ dicots at high altitude. The species occur in low frequency and disappear above 4,000 m. The species belong to the following genera: *Giselia*, *Delosperma*, *Lineum*, *Mollugo*, *Aizoaceae*, *Aerva*, *Amaranthus Gomphrena* (Amaranthaceae), *Emex*, *Polyacarpa*, *Silene*, *Caryophyllaceae*, *Gyropteran* (Chenopodiaceae), *Fagonia tribulus*, *Zygophyllum* (Zygophyllaceae), *Calyptrotheca*, *Portulaca*, *Talinum* (Portulacaceae) were common at very low arid altitudes. But, some of the $C_3$ genera: *Silene*, (Caryophyllaceae), *Sueda* (Chenopodiaceae), *Emex*, *Fagopyrum* (Polygonaceae) were less common in more arid areas. The present distribution show that species of the Caryophyllaceae, Chenopodiaceae and Polygonaceae thrive in hot moist habitats, often associated with saline conditions. They commonly occur near lakes in the arid, for example *L. baringo* and *L. turkana*.

The $C_3$ dicot species are found at the warmer ending regions of the $C_3$ monocot species distribution pattern and often coexist with increasing $C_3$ dicot species. This frequency species-photosynthetic syndrome relationship, suggest high $C_3$ composition in the lowland understorey conditions compared to the $C_3$ composition at the high altitudes. There is monocot-dicot photosynthetic pathway relationship whereby at a given altitudinal range the frequency of the $C_3$ dicot syndrome overlaps $C_3$ monocot syndrome with decreased proportion and $C_3$ monocot syndrome overlaps $C_3$ dicot syndrome with increased proportion along the altitude. This is a good indicator system of the evolutionary process which is due to the synergistic effect of climatic factors in a given photosynthetic pathway at a given point. The net effect of the climatic factors influences the proportion of the photosynthetic species in the habitat along an elevation gradient.

The present studies shows that mean annual temperature and mean annual precipitation determines the distribution and percent frequency of the photosynthetic species in the semi arid and arid areas.

Current linear correlation coefficients between percent frequency of the species and altitude mean annual temperature, rainfall, potential rates of evaporation, radiation and relative humidity show good positive correlation, in this decreasing order. The $C_3$ dicot species show negative correlation coefficient with temperature, potential rates of evaporation parameters. The parameters are inversely related to the photosynthetic systems as altitude increases. This study confirms the observations of Tieszen et al. (1979) and Rundel (1980). At high altitudes (>4000 m) higher water availability also occur as a consequence of lower evapotranspiration and dewfall.

*Trilibus teres*, *T. cistoides* of Zygophyllaceae exhibited the shade tolerant phenomenon. The results indicate the potential for $C_3$ genotypes to adapt to shade conditions and acclimatize. The present data for relative distribution of $C_3$ and $C_3$ dicots demonstrate that patterns of the relative dominance of the photosynthetic systems along the climatic gradients is due to the synergistic degree of temperature, precipitation, shade and evapotranspiration. Further, the elevation transition zone between the $C_3$ and $C_3$ metabolic systems dominance is expected to be much sharper on the observed plant coverage compared to the floristic composition basis. The $C_3$ species susceptibility to low temperatures (Berry and Bjorkman, 1980) was mostly the NADP-ME type that may be related to Pyruvate Phosphatase Dikinase cold liability (Sugiyma et al., 1979). This cold acclimatization is known in various families (Caldwell et al., 1977; Jones et al., 1981; Winter, 1981; Hattersley, 1992). In general, $C_3$ dicot species like $C_3$ dicots increase in number with rainfall in their preferred temperature regime. The $C_3$ species are numerous where the area is hot and wet but the $C_3$ species in the cool and wet areas. The $C_3$ species decline with decreasing temperature and increasing seasonal rainfall whereas the $C_3$ species decline with increasing temperature and decreasing seasonal rainfall. Within the group of $C_3$ dicot the Malate-forming NADP-ME species favoured habitats where water stress was less severe.

Recently, some European $C_3$ plants have been observed extending towards northern latitudes, for example the *Spartina* species, *Salsola kali*, *Atriplex laciniata* (Long, 1983) and *Cyperus longus* (Jones et al., 1981). Therefore, unique occurrence of *Melandrium nordiflorum* dicot species at 4,000 m raises significant ecological questions, in the present study. Evolution and adaptations in the $C_3$ species is a continuous process. While precipitation is obviously essential to initiate plant growth, temperature is such a dominant factor in regression analyses that it explains more than 90% of the total $C_3/C_3$ monocot distribution.
variation across almost all geographic regions. Clearly, temperature has manifested itself as the critical determining factor in the distribution of the $C_4$ species.

The transition temperature was a critical switch between $C_4$ dominance and $C_3$ 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 daytime temperature range of 20-28°C as the temperature for the transition shift in $C_3$-to-$C_4$ dominance, either based on elevational or latitudinal gradients. The transition zone between $C_3$ and $C_4$ groups is rather abrupt and occurs at 1,500-1,700 m a.s.l. along the altitude, less behind that recorded for the monocots in Java (Hotstra et al., 1972) and Kenya (Tieszen et al., 1979) at 2,000-2,300 m a.s.l. altitude. This transition zone was defined by climatic variables as 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 cm⁻²) and mean annual relative humidity (%) of 15.7, 25.6°C, 700-950 mm, 1575 to 1650 mm m⁻², 450-500 J m⁻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 elevation.

 Earlier studies have shown that $C_4$ monocots might comprise well over half of the monocots taxa in a region. The present study has shown that the $C_4$ dicots constituted approximately 30% of the flora of the Centrospermae. Studies in the Sonoran hot desert with summer precipitation reported 4-4% (Stowe and Teeri, 1978; Wentworth, 1983). The present study showed that with decreasing degree of aridity index, the percent (or frequency) of $C_4$ dicot species decreased. In contrast, the $C_3$ dicot species increased. Similar observations have been reported in subtropical regions such as Florida (2.5%) and Texas (2.8%) (Ehleringer et al., 1977) Europe (Collins and Jones, 1985), Japan (Okuda and Furukawa, 1990). The abundance of $C_4$ NAD-MA dicots increases with decreasing aridity unlike $C_4$ NAD-ME dicots.

The present data analysis show that the percent of $C_4$ dicots does not follow the same climatic factor as for $C_4$ monocots but are closely related to the aridity characters such as summertime pan evaporation rates and annual dryness ratio (ratio of annual net rates of radiation to heat required to evaporation mean precipitation). Instead, there was a stronger correlation coefficient of $r^2 = 0.89$, $r^2 = 0.83$ and $r^2 = 0.76$ between mean annual temperature, mean annual precipitation, mean annual rates of evaporation and the % $C_4$ dicot species, respectively. However, there was an inverse relationship with the % $C_3$ dicot species. The conclusion is that the distribution and abundances of $C_4$ monocots and $C_4$ dicots respond to the same climatic parameters, with varying intensity and behaviour in similar ecological regimes.

REFERENCES


