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Carbon Dioxide Compensation Points of Some Dicots of the Centrospermeae Species and Their Ecological Implications for Agroforestry

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Abstract: The present studies on carbon dioxide compensation point (Γ) considered species from tropical semi-arid, snowline and saline ecosystems. The aim of the study was to establish the ecological range of the CO₂ compensation point of species in the semi-arid/arid, snowline/or saline conditions. Secondly, to determine the effect of biomass on the rate of carbon dioxide assimilation in relation to the ecological efficiency of the C₃ and C₄ photosynthetic pathways. Four and six-seven week old plants were used to assimilate carbon dioxide in the gas chamber until a constant reading was attained by Infra Red Gas Analyzer (IRGA). The carbon dioxide uptake concentrations (assimilations) were continuously measured by pumping a stream of the air through a closed gas tight, circuit with IRGA while temperature and light intensity and previous growth conditions were maintained constant. The dry weight of the plant was measured using a digital balance after the experiment. The CO₂ compensation points of the C₄ plants vary between 8-20 ppm. The CO₂ compensation points of the C₃ plants vary between 40-60 ppm. The age and biomass of the plant influenced the rate of carbon dioxide assimilation in the C₄ species and C₃ species. The C₄ plant attained the CO₂ compensation point faster than C₃ plant under the same physiological conditions. The C₄ plant photosynthesized below 40 ppm of carbon dioxide concentration. The C₃ plant ceased carbon dioxide assimilation below 40 ppm of carbon dioxide concentration. Thus, an ideal ecological canopy set-up should consist of a C₄ over storey and a C₃ under storey for efficient photosynthetic performance and yield. Potential C₄ overstorey species including *Amaranthus* species and *Kochia scoparia*, should be intercropped with potential C₃ understorey species like *Chenopodium album* and *Phytolaca dioica* by farmers and horticulturalists in Agriculture. The intercropping practice is economical, viable and apt in agroforestry systems, especially in the semi-arid and saline conditions socialized by nomadic tribes in Kenya. Perkerra irrigation project can act as satellite agroforestry research station, including Kerio valley and Turkana regions.

Key words: Carbon dioxide compensation points, Centrospermeae species, biomass, C₃ and C₄ photosynthetic pathways, agroforestry

INTRODUCTION

The present study investigated the rates of carbon dioxide assimilation, carbon dioxide compensation points of some Centrospermeae dicot species. Secondly, the effect of biomass on the rate of carbon dioxide assimilation was also measured.

Studies of the C₄ photosynthetic pathway has continuously been centre of scientific attention from the time of its discovery in the mid-sixties. Suffice with progressive immense literature reported. Quest for species with C₄ carbon metabolism, ecological comparison, biochemical differentiation, anatomical structural differentiation and physiological characterization and their phylogenetic distribution have yielded profuse literature (Ehleringer *et al.*, 1997). The photosynthetic types are easily differentiated as:

- Fix carbon dioxide by Crassulacean Acid Metabolism (CAM) (Cushman, 2001)
- Produce 4-carbon compounds as their first stable products (C₄ plants)
- Produce phosphoglyceric acid as the first stable products (C₃ plants)

These interrelated characteristics of the C₃ and C₄ systems have ecological importance. They are basic in determining maximum rates of photosynthesis and productivity as well as in determining the responses to a variety of environmental factors. The characteristics are also important in establishing the spatial distributions of the species and in determining what species or photosynthetic types should perform best in different agroforestry systems (Tieszen, 1981).

Earlier studies on CO₂ compensation point were carried out in the temperate species (Moss *et al.*, 1969) for ecological reasons. However, studies on the tropical/subtropical species especially semi-arid, arid and saline ecotypes are minimal. This may be due to logistic reasons. Furthermore, more emphasis was placed on the grasses because of agricultural and economic advantages.

Quest for biological understanding of the ecological significance(s) of the advantages of the compensation points in different species is emerging. For example, intercropped C₄ over storey canopy with C₃ under storey canopy can produce high bioproductivity (Tieszen, 1981; Ehleringer *et al.*, 1997). High yield and economic returns aptly urge in favour of agroforestry management practices by applying partitioning of the photosynthetic species in agriculture. Furthermore study models of the CO₂ compensation points of different species from varied ecological condition should offer possible explanations in understanding major selective forces for the expansion of the C₄ ecosystems at the end of Miocene period.

Ehleringer *et al.* (1997) suggested that in a reasonable range of growing season the C₄ species could have expanded and adapted to different climatic and growth conditions during pre-industrial, industrial present times and post-industrial carbon dioxide concentration levels of about 280 ppm V (at 17°C of daytime), approximately 350 ppm V (at 21°C of daytime), respectively. These models offer possible explanations for the dominant conditions and prevalent dominance of C₄ species during the past, present and in future. The study models could be used either to understand the recent geological record evidence for the changing proportions of C₃ and C₄ biomass during periods of both higher and lower CO₂ levels compared to the present (Ehleringer *et al.*, 1997; Cerling *et al.*, 1997a, b; Quade and Cerling, 1995). This could explain the fact that C₄ species should be favoured in reduced atmospheric CO₂ (Ehleringer *et al.*, 1997). Further, past sequence of the C₄ expansion pattern in relation to CO₂ concentration threshold regimes can be understood.

A central feature of photosynthetic carbon assimilation is the enzyme Ribulose Bisphosphate Carboxylase-Oxygenase (Rubisco) activity. It shows low efficiency as a catalyst due to its low turnover rate for CO₂ fixation as well as a lack of specificity for reacting both with carbon dioxide and oxygen (Edward *et al.*, 2004). Plants respond by producing large amounts of Rubisco to compensate for its low turnover rate. This dual specificity of the enzyme in using CO₂ and O₂ as substrate presents a different problem in plants that respond differently under different relative CO₂ and O₂ concentrations. Thus,

the functions of Rubisco as a Carboxylase and Oxygenase using the substrate Ribulose-1,5-Bisphosphate (Rubp) can be investigated using CO₂ and O₂ compensation point models (Tolbert *et al.*, 1995) under varying concentrations of CO₂ and O₂. Further, relative rates of CO₂ and O₂ assimilation can be investigated in different C₄ species with remarkable ecological results in relation to the efficiency of photosynthesis and yield.

This could explain the evolution and development of the dual catalytic activity of the Rubisco enzyme during photosynthesis and under what environmental conditions photosynthesis first evolved (Edward *et al.*, 2004). This process determines the carbon dioxide compensation point of a species. The carbon dioxide compensation point was defined as the point where there was no net change in the carbon dioxide concentration uptake by the plant at 20/15.7°C temperature, 350 μE light intensity (kept constant) under normal growth conditions.

Studies of CO₂ compensation point modules would provide a possible role of C₄ plants and C₃ plants in the current scenario of global warming caused by carbon dioxide emissions, among other gases. Possible remedial measures are recommended to be undertaken using the C₃ species and C₄ species intercropping ecosystems.

MATERIALS AND METHODS

This study was done in the Department of Plant Physiology, University of Bayreuth, Germany, 2000.

Plant culture for carbon dioxide compensation point studies: The species in various families of the Centrospermeae were randomly selected and used for carbon dioxide compensation point investigations. The species varied in growth habits and biomass and occurred in different ecotypes defined by altitudinal gradient. Ten to fifteen seeds of each species were germinated in 0.5 L pots on vermiculite nutrient rich soils in the growth chamber under controlled growth conditions (automatic irrigation system, 20-25°C temperature and normal bulb light system). The seedlings were ready for transplanting 2-3 weeks after germination. Plants infected by fungus were isolated from the rest of the germinating species. An 18 h monitoring duration was carried out on a daily basis.

The plant species were irrigated daily until they were 6-7 weeks old, then used for the CO₂ compensation point experiments. Four week old plants were also used to determine the effect of age on the rate carbon dioxide assimilation.

CO₂ compensation point and biomass determination: The biomass of 4 and 6 week old plants were used determine

the carbon dioxide compensation point of each species. A closed photosynthetic chamber for experimental measurements of changes in the atmospheric CO₂ was constructed for the tests. A 4 or 6 week old plant in a pot was enclosed in a gas-tight cover using Vaseline just before the experiment to prevent gas exchange with the soil. It was put in an air tight 19 L glass chamber at a controlled temperature of 20°C. A fan was used to mix the air. The carbon dioxide concentrations was continuously measured by pumping a stream of the air through a closed, gas-tight, circuit with an Infra Red Gas Analyzer (IRGA) (Binos 1.1, Leybold, Hanau, Germany) for carbon dioxide measurements.

The carbon dioxide contents of the air in the chamber was arbitrarily set by injecting CO₂ with a calibrated syringe through a small rubber plug in the jar lid. Only a little amount of carbon dioxide was injected at a time to avoid varied fluctuation on the scale-recorder. According to the IRGA recordings, additional volumes of CO₂ were only supplied after attaining a constant CO₂ compensation point, for a second replicate experiment. Experiments were run in air ranging from 1000 parts per million (ppm) to 8 ppm carbon dioxide concentrations. Excess transpired moisture was removed using sodium hydroxide pellets placed in the glass chamber. At the end of an experiment, the plant was dried in an oven at 65-75°C for 3-5 days to reach constant weight. The dry weight was determined using a digital balance. Three replica plants for each species were used in each experiment and this took three days.

Three physiological variables that would alter photorespiration were kept constant in the glass chamber, for instance, temperature, light intensity and previous growth conditions (Tolbert *et al.*, 1995). A constant light intensity and temperature of 350 μmol/m²/sec from fluorescent/incandescent bulbs and 20°C were used, respectively. Thirty minutes duration was allowed for the apparatus set-up to acclimatize and standardize the internal conditions in a closed photosynthetic chamber before next plant species was placed in it for CO₂ compensation point measurements. The plant was removed from the pot, washed and dried using hot air steam. Immediately, the dry weight was measured. The replicate experiment results were represented in the graphs, showing the course of net CO₂ uptake in a given plant species over time.

RESULTS

Carbon dioxide compensation points: An initial carbon dioxide concentration of 1,000 parts per million (ppm) was assimilated by the plant over time until a constant carbon

dioxide concentration was recorded over time (min), when the graph normalized (Fig. 1a-i, 2). Less time to reach CO₂ compensation point was achievable with a well spread expanded leaf of a mature (6-7 week old) plant unlike a young plant (less than six-week old) or a very old plant (more than seven weeks). Correspondingly, a 6 week old plant with high relative biomass reached the compensation point faster. Similarly, a C₄ plant achieved a short duration to reach CO₂ compensation point than a C₃ plant. The carbon dioxide compensation points for different species are presented in Table 1.

The time course of net carbon dioxide uptake was variable in different species of the Centrospermeae. The C₄ species had carbon dioxide compensation points between 10-18 ppm and C₃ species varied between 40-60 ppm as shown in Table 1. The rate of carbon dioxide uptake with time varied within species depending on the age and the corresponding biomass of the C₃ species and the C₄ species. Younger (4 weeks of growth) C₃ plants had lower rates of carbon dioxide uptake for example *Rumex acetosa* (1.0996 g) compared to the *Trianthema triquetra* (0.7968 g) (Fig. 1a), a C₄ species. *Rumex acetosa* weighing 1.0996 g achieved carbon dioxide compensation point (l) later than that of *R. acetosa* weighing 1.6756 g, a course not observed in *Trianthema triquetra* of 0.7968 g to that of 0.8168 g (Fig. 1a). This was the general trend in the species studied (Fig. 1a, e).

The C₄ dicot species attained low carbon dioxide compensation points compared to the C₃ dicot species, regardless of the duration of growth and biomass of the species (Fig. 1a-d).

Table 1: Carbon dioxide compensation points (l) for different species

Species	Carbon dioxide compensation points
C₄ species	
<i>Amaranthus lividus</i>	11
<i>Amaranthus hybridus</i>	12
<i>Amaranthus retroflexus</i>	10
<i>Amaranthus patulus</i>	11
<i>Amaranthus spinosus</i>	11
<i>Amaranthus dubius</i>	11
<i>Kochia scoparia</i>	11
<i>Portulaca oleracea</i>	16
<i>Portulaca quadrifida</i>	18
<i>Trianthema triquetra</i>	15
C₃ species	
<i>Chenopodium album</i>	54
<i>Chenopodium ambrosioides</i>	55
<i>Chenopodium capitatum</i>	56
<i>Phytolaca americana</i>	59
<i>Phytolaca dioica</i>	52
<i>Rumex acetosa</i>	54
<i>Rumex rugosus</i>	58
<i>Rumex triangulivalvis</i>	58
<i>Pleuropetalum darwinii</i>	54
<i>Mirabilis jalapa</i>	53
<i>Fagopyrum tataricum</i>	58
<i>Silene dioica</i>	60
<i>Silene vulgaris</i>	59

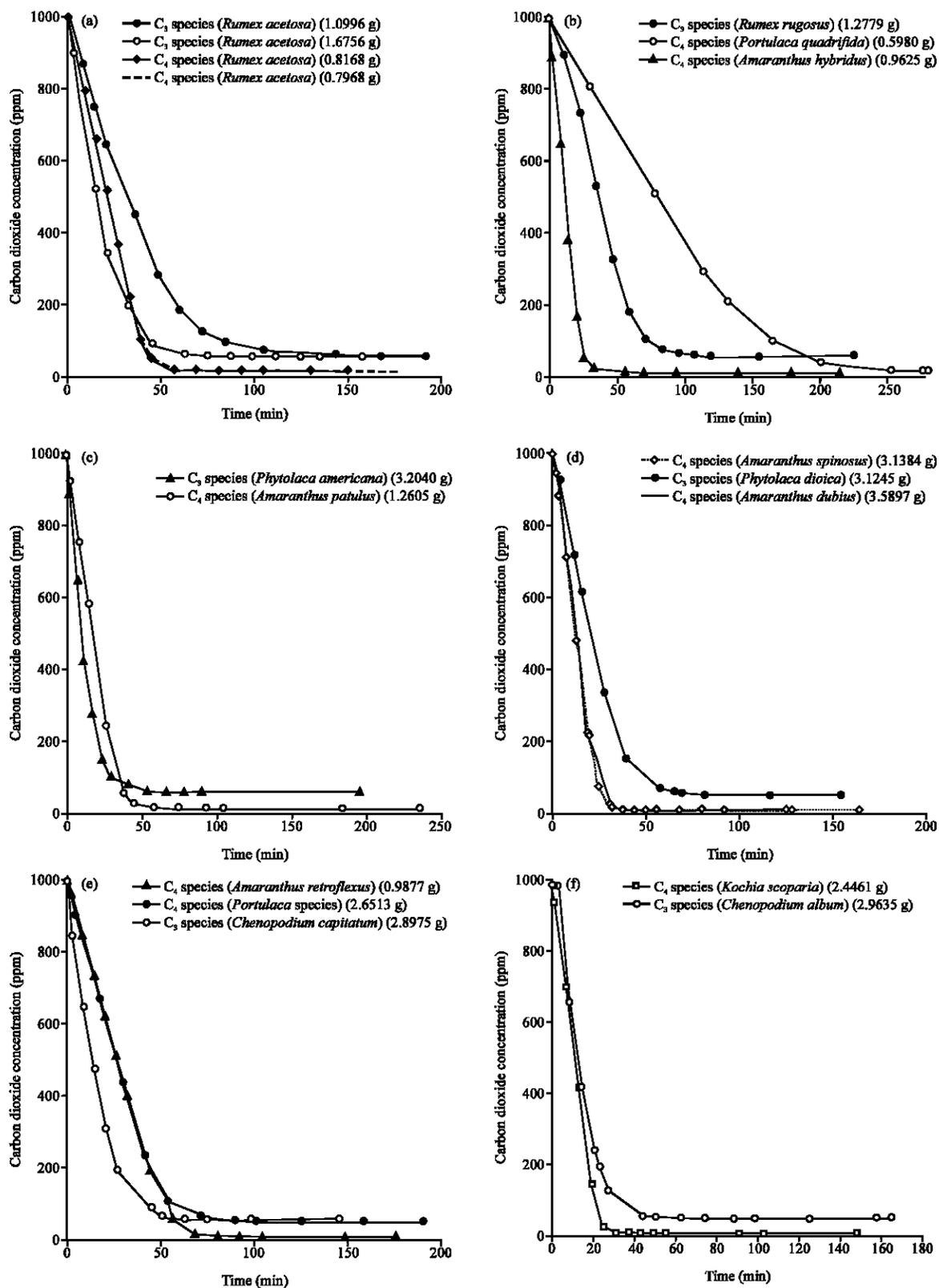


Fig. 1a-i: Continued

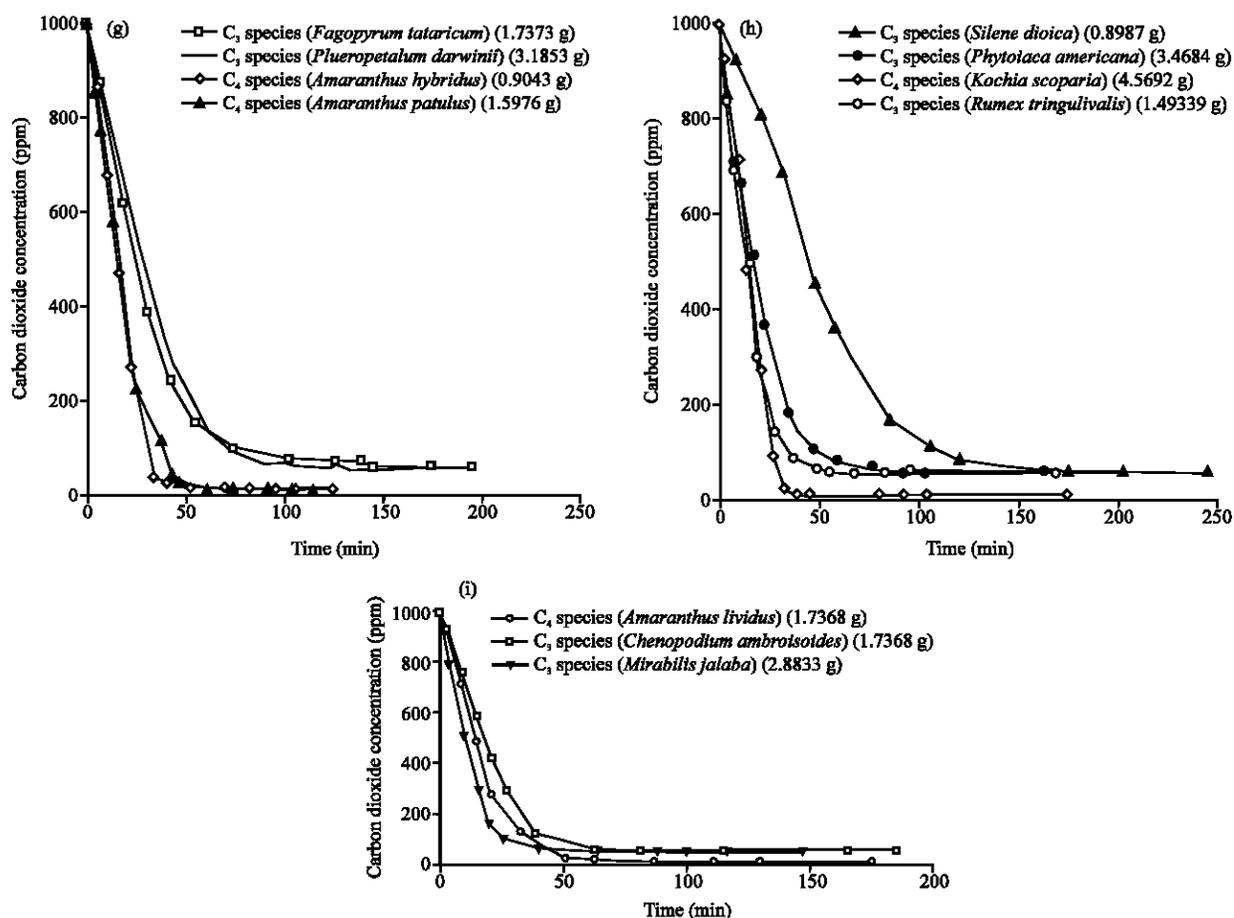


Fig. 1a-i: Time course of net carbon dioxide uptake in different photosynthetic species carried out in air tight gas chamber

The graph of C_4 species tended to be the left of that of the C_3 species based on the same growth duration of the species (Fig. 1a-h), exception occurred in the high biomass *Chenopodium capitatum* (2.8975 g) (Fig. 1e).

Trianthema triquetra C_4 species of dry weight 0.8168 g has a higher rate compared to *Rumex acetosa*, a C_3 species of dry weight 1.6756 g (Fig. 1a). Furthermore, the effect of biomass on the net CO_2 uptake differentiation

In a different study, *Chenopodium album* (2.9635 g) had its initial rates of CO_2 assimilation pronouncedly tending closer to the C_4 species-*Kochia scoparia* (2.4461 g) until a CO_2 concentration of 165 ppm, when the C_4 activity achieves its photosynthetic efficiency (Fig. 1f). A high biomass C_3 species *Pleuropetalum darwinii* (3.1853 g) show a C_4 -like course of carbon dioxide uptake of the C_4 species-*Amaranthus hybridus* (0.9043 g) and *Amaranthus patulus* (1.5976 g) compared to that of low biomass C_3 species *Fagopyrum tataricum* (1.7373 g) (Fig. 1g) as carbon dioxide concentration tends towards 145 ppm.

The biomass and age effects were observed in *Silene dioica* (0.8987 g) (4 week young stage) relative to mature *Phytolaca americana* (3.4864 g) (6 week old) and *Rumex trigulivalvis* (1.4939 g) (7 week old) where the course of CO_2 uptake in *Rumex trigulivalvis* showed a C_4 -like effect close to that of *Kochia scoparia* (4.592 g) (Fig. 1h).

Similar observations were recorded between C_3 species-*Chenopodium ambrosioides* (1.7368 g), *Mirabilis jalapa* (2.8833 g) and a C_4 species, *Amaranthus lividus* (1.9204 g) species (Fig. 1i). The rate of CO_2 uptake ($\mu mol/m^2/sec$) in the C_3 species *Chenopodium schradernum* and a C_4 species *Amaranthus patulus* of the Centrospermeae were studied and showed a higher rate in the C_4 species at a given carbon dioxide concentration (Fig. 2). The rate of carbon dioxide assimilation in a C_4 species (*Amaranthus patulus*) had a steeper gradient compared to a C_3 species, *Chenopodium schradernum*. The rate of carbon dioxide ($\mu mol/m^2/sec$) of the C_4 species is considerably high (Fig. 2) compared to C_3

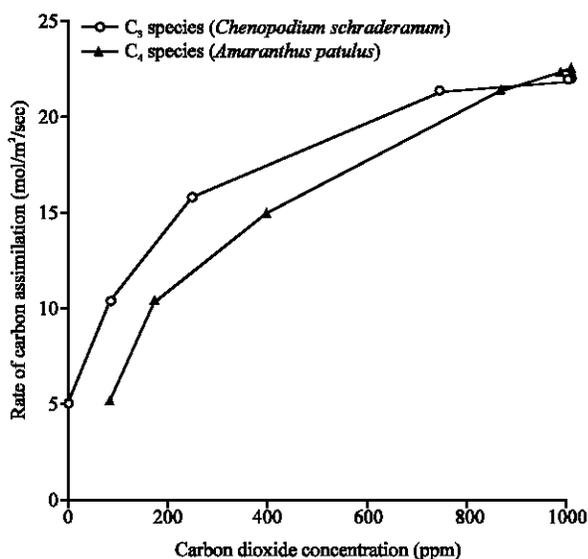


Fig. 2: Analysed rate of carbon dioxide assimilation in a C₃ species *Chenopodium schraderanu* species and C₄ species *Amaranthus patulus* at varying carbon dioxide concentration in air tight gas chamber

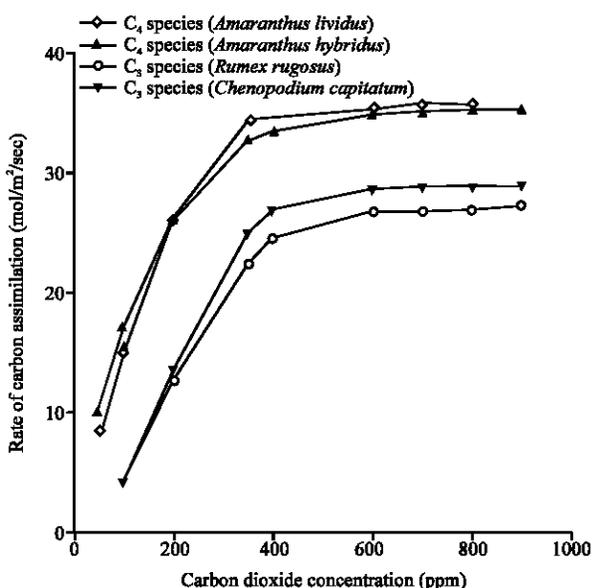


Fig. 3: Rates of carbon dioxide assimilation (mol m² sec⁻¹) in different photosynthetic species: *Amaranthus hybridus*, *Amaranthus lividus*, *Rumex rugosus* and *Chenopodium capitatum*

species *Chenopodium schradernum*. Similar studies carried out using narrow range of biomass and age of the species show that in the C₄ species-*Amaranthus hybridus* (1.8750 g) and *Amaranthus lividus* (1.9204 g) have higher

rates of carbon dioxide assimilation compared to C₃ species-*Rumex rugosus* (1.9775 g) and *Chenopodium capitatum* (2.1055 g), measured under the same air tight gas chamber conditions (Fig. 3).

Analysis of the rates of carbon dioxide assimilation in different C₄ species were different under same growth conditions. Similar rate of intervals in the C₃ species, *Chenopodium capitatum* and *Rumex rugosus* exist and are species dependent (Fig. 3).

DISCUSSION

The net effect of PEP carboxylase serving as the primary carboxylase enzyme and decarboxylation in the parenchyma bundle sheath cells is to create a system capable of high rates of photosynthesis even at low intercellular CO₂ concentrations. This photosynthesis as a function of CO₂ concentration shows a different response curve in C₄ plant species compared to the C₃ plant species. C₄ plant species possess a net positive uptake of CO₂ concentrations in the absence of photorespiration. The rate of CO₂ uptake with time is also greater in the C₄ plant species.

In the species so far examined C₃ and C₄ plants saturate with respect to CO₂ concentrations (Krenzer *et al.*, 1975; Tolbert *et al.*, 1995). Different C₄ plant species, with relatively higher biomass show compensation points between 10-18 ppm while C₃ dicot species show carbon dioxide compensation points between 40-60 ppm, under normal atmospheric conditions of oxygen concentrations. Tolbert *et al.* (1995) have pointed out that the O₂ and CO₂ compensation points of plants in a closed system depend on the ratio of CO₂ and O₂ concentrations in air and in the chloroplast and the specificities of Ribulose Biphosphate Carboxylase Oxygenase (Rubisco). Photosynthetic metabolism is a competition between CO₂ and O₂ for the dual activities of Rubisco, based on the ratio of CO₂ and O₂ concentrations in the chloroplast and the specificities of Rubisco for its gaseous substrates. As a consequence, the distribution of carbon flow around the C₃ and C₂ cycles is proportional to the ratio of atmospheric CO₂ and O₂ and to processes for CO₂ import and export. At a low CO₂ and high O₂ ratio that inhibits the Carboxylase activity of Rubisco, much Malate accumulates. This suggests that the oxygen-insensitive Phosphoenol Pyruvate carboxylase activity occurs in the C₃ photosynthetic pathway where such Malate product does not form.

Different species of the Centrospermeae possess variable time course of net carbon dioxide uptake. The net CO₂ uptake over time varies within a species depending on the age and corresponding biomass of the vegetative

photosynthetic material. The younger plant species about 4 weeks old show a lower rate of carbon dioxide uptake. The rate relates to the net amount of carbon being invested in a given plant species. C₄ plant species become saturated at CO₂ concentrations only slightly higher than ambient levels, compared to the C₃ plant species which compensate at high CO₂ concentrations. Thus, at higher CO₂ levels, C₃ plants photorespire and the enzyme system does not saturate.

The carbon dioxide compensation point (Γ) of the C₄ species show the functional role of the enzymes in the parenchyma sheath cells that concentrate carbon dioxide for photosynthetic carbon reaction cycle such that photosynthesis still occur below 40 ppm of carbon dioxide but above 20 ppm. At 40 ppm of carbon dioxide concentration the C₃ species photosynthetic carbon reduction reaction is inhibited. This observation supports the proposed explanation for the expansion of the C₄ ecosystems at the end of the Miocene as due to the declining atmospheric carbon dioxide concentration as a major selective force (Ehleringer *et al.*, 1997). Using quantum yield for carbon dioxide uptake in the C₃ species as a function of both temperature and carbon dioxide concentration and applying basic equations and parameters to describe leaf-level photosynthesis, Ehleringer *et al.* (1997) have indicated that the quantum yield at any specified temperature should increase with carbon dioxide concentrations. In contrast to the C₃ species, the quantum yield of the C₄ species do not change with the temperature and carbon dioxide concentration over biologically relevant range of temperatures. Further, the transition temperature between C₃ and C₄ species show that both the atmospheric carbon dioxide and temperature are functions of a specific photosynthetic type (Ehleringer *et al.*, 1997).

Recently, Sikolia *et al.* (2008) reported that distribution and abundance of the C₃ and C₄ dicot species occur in the transition region defined by climatic factors: mean annual temperature, mean annual maximum temperature, mean annual rainfall, mean annual rate of potential evaporation, mean annual radiation and mean annual relative humidity of 15.7, 25.6°C, 700 mm-1650, 450-500 j m⁻² and 50-55%, along the altitude, respectively. Similar, studies in monocots had been done by Tieszen *et al.* (1979). The mean annual temperature range for the cross-over region between the C₃ species and C₄ species abundance is 20.7-25.6°C. Under conditions of sufficient soil moisture, a C₃ plant have greater potential for carbon gain at low temperatures while a C₄ plant has carbon gain at high temperatures

with cross-over point at approximately 25-30°C (Ehleringer *et al.*, 1997). This implies that a C₄ plant metabolism would be disadvantaged at cool low light habitats such as the understory canopies of temperate and tropical forest. But, C₄ plant will selectively perform efficiently in overstorey canopies associated with high temperatures, high light intensities of tropical grassland of western region inhabited predominantly by nomadic tribes. Here, C₄ plants will be particularly advantageous in the semi desert habitats where little shading of the photosynthetic organs occurs in the plant stands. Thus, increased capacity for photosynthesis at high light intensities and high quantum yield at high temperatures which enhance the significant advantage. The photosynthetic efficiency being the results of the ability of the C₄ pathway to increase the concentration of CO₂ at the site of fixation of RuDP Carboxylase-Oxygenase.

The C₄ species have low CO₂ Γ and function independent of CO₂ intracellular concentration. Conversely, C₃ plants have high CO₂ Γ and require high CO₂ concentration, low O₂ concentration, or both, which selectively favour C₃ pathway due to its low intrinsic quantum requirement for CO₂ fixation. The O₂ inhibition of the quantum yield in C₃ plants offsets the extra ATP requirement of the C₄ pathway at 25-30°C, resulting in similar quantum yields. Therefore, a C₄ overstorey canopy and C₃ understory canopy is an ideal logical plant stratification plan for maximum photosynthetic efficient and high bioproductivity system for agricultural adoption by farmers in the semi arid and saline ecosystems in western Kenya. Already the native C₃ and C₄ species exist in these areas. It is a question of adopting improved agroforestry systems of intercropping of the C₃ and C₄ species to enhance agricultural yield in these inhabitable ecosystems. Some of the recommended economical crop plants for agroforestry systems include: most of the C₄ dicots that are found to be vegetables (*Amaranthus hybridus*, *A. patulus*, *A. dubius* and *A. lividus*), fodder (*Kochia scoparia*, *Amaranthus* species and *Trianthema triquetra*), soil erosion control species (*Portulaca oleracea*, *P. quadrifida*) and green yard mature source (*A. retroflexus*). The C₃ species were found to be medicinal (*Phytolaca dioica*, *Rumex acetosa*), livestock fodder (*Silene vulgaris*), soil binders (*Chenopodium album*, *C. ambrosioides*, *Mirabilis jalapa* and *Rumex rugosus*). Some C₄ species were found to be the most noxious, aggressive and stubborn weeds during planting season, especially in Perkerra irrigation scheme, Baringo district Kenya. It is recommended that intercropping of the understory C₃ and overstorey

C₄ canopies should be undertaken to maximize on photosynthetic efficiency within a limited field area to improve on the yield of the species for the dependants.

Variation in the C₃/C₄ cross-over temperature occurs because of the dependence of C₃ quantum yield on both temperature and [CO₂]/[O₂] ratio (Ku and Edward, 1978). Thus, the inherent differences in quantum yields among C₄ monocots and C₄ dicots leads to the fundamentally different combinations of carbon dioxide and temperature favouring C₄ monocots over C₃ plants or C₄ dicots over C₃ plants. In this case, given a rationalized growing-season temperature regime the carbon dioxide assimilation or quantum yield possibilities, both C₄ monocot species and C₄ dicot species should be a rare phenomenon under high carbon dioxide concentrations globally relative to the C₃ species and/or its pathway phenomenon. However, the C₄ photosynthesis pathway would continue with the expansion as the atmospheric carbon dioxide levels decrease. The carbon starvation which inhibit C₃ photosynthetic metabolism will be available as carbon substrate in increased concentration (Ward *et al.*, 2005). The only limiting factor will be increased season temperature.

Increasing aridity index and carbon dioxide concentration should draw attention to the significance of the CAM pathway and/or species and C₃-C₄ intermediate species evolution and mesoscale partition and their roles in the semi-arid and arid ecosystem. With the lowest past recorded levels of CO₂ (\approx 220 ppm), the O₂ \uparrow with an isolated C₃ plant is \approx 23% near current atmospheric levels of O₂ and with increased CO₂ to $<$ 350 ppm today the O₂ \uparrow increases to \approx 27%. From the global carbon and oxygen cycles and to allow plant growth, atmospheric CO₂ levels must be $>$ CO₂ \uparrow of a C₃ plant and the O₂ levels must be $<$ O₂ \uparrow . The global atmospheric 0.03% CO₂ and 21% O₂ equilibria appears to be limits set by the mean specificity properties of Rubisco from plant. The present study predicts that increasing atmospheric carbon dioxide concentration greater than 450-550 ppm will favour the expansion of the C₃ ecosystem under most global conditions and show enhanced bioproductivity. The C₄ dicots will thrive well in warmer, disturbed (due to grazing/or fire) and often saline ecosystems.

The CO₂ \uparrow is the carbon dioxide concentration at which net carbon dioxide is zero at a given O₂ level and temperature (Moss *et al.*, 1969; Tolbert *et al.*, 1995). The specificity of Rubisco seems to establish both a CO₂ \uparrow and O₂ \uparrow , which depend on the ratio of CO₂ and O₂ concentration. Earlier when the CO₂ level was $>$ 1000-15000 ppm CO₂ and the O₂ level lower, Rubisco

functioned primarily only as a carboxylase and the CO₂/O₂ ratio for the dual activities of Rubisco was not a controlling factor on plant growth. However, once the level of oxygen increased and that of carbon dioxide decreased, the Oxygenase activity of Rubisco limited the CO₂ removal and the CO₂/O₂ ratio became a governing factor on net photosynthesis, plant growth and the atmospheric composition. Thus, there is the potential of carbon dioxide \uparrow to rise with increased oxygen concentration to maintain a CO₂/O₂ ratio based on the average Rubisco specificity for the two substrates. Further, it is proposed that C₄ dicots may have not been advantageously selected until carbon dioxide concentrations had their lowest measures during the glacial maxima in the quaternary.

There is a need to investigate oxygen \uparrow in different C₃ and C₄ species to establish the behaviour of Rubisco specificity in varying carbon dioxide and oxygen concentrations. This would provide scientific prospects on the photosynthetic efficiency and bioproductivity in the ever increasing carbon dioxide scenario.

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