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REVIEW ARTICLE

Photosynthesis peculiarities in representatives of the Euphorbiaceae Juss. family

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Abstract

The article provides a literature analysis of the features and advantages of C_4 and CAM photosynthesis in Euphorbiaceae Juss. representatives compared to classic C_3 metabolism. It determines the prerequisites and possible stages in plants' transition from C_3 to C_4 and CAM photosynthesis. The C_4 photosynthesis is a convergent evolutionary system that emerged independently more than 62 times. It involves anatomical and biochemical modifications of the C_3 pathway and ensures high productivity under hot, dry conditions, tolerance to insolation, and metabolic intensity, serving as a key model of adaptive evolution. Its formation stages include the accumulation of preadaptations, the formation of proto-Kranz anatomy, the emergence of C_2 photosynthesis, the adjustment of photosynthetic components, and the development of a full-fledged C_4 pathway with simultaneous suppression of C_3 metabolism.

In CAM plants, CO_2 fixation occurs at night through the carboxylation of phosphoenolpyruvate, producing C_4 acids. Meanwhile, during the day, with stomata closed, the internal CO_2 reserve is used after C_4 acids decarboxylation, which ensures temporal process segregation. The C_2 photosynthesis type is considered an evolutionarily important intermediate stage between the classic C_3 and efficient C_4 pathways found in *Euphorbia* subg. *Chamaesyce* (i.e., *Euphorbia acuta* Engelm., *E. angusta* Engelm., and *E. johnstonii* Mayfield).

The Euphorbiaceae family also exhibits 'photosynthetic mosaicism', which combines different carbon fixation pathways, a phenomenon of great scientific interest and in need of in-depth study. The combination of C_3 and CAM pathways in *E. tirucalli* L. ensures resilience and rapid biomass accumulation, while the intermediate strategy of *E. milii* Des Moul. (C_3 with partial CAM cyclization) reduces water loss and illustrates the transition between C_3 and CAM. A typical tropical C_3 plant, *E. umbellata* (Pax) Bruyns, adapts to seasonal drought using morphological mechanisms (fleshy leaves and latex) without involving CAM. Improving crops with advanced C_4 photosynthesis can therefore increase yields of food, industrial, and energy plants and ensure efficient use of Ukraine's plant resources.

Keywords: Euphorbiaceae, photosynthesis types, Kranz anatomy, resilience, preadaptations, mosaicism

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Introduction

Modern realities encourage humanity to pause and realize that global climate change, combined with military actions, is extremely rapid and large-scale, posing the risk of further reductions in agricultural lands due to an increased number of droughts and floods, mechanical destruction, and pollution with heavy metals, oil products, explosives, and other toxic compounds. Abiotic factors (higher average temperatures, lack of moisture, rising levels of greenhouse gases, including CO₂, and weather anomalies) are accompanied by intensified biotic factors (pest infestations, bird predation), together causing a decrease in the yield of valuable food crops and sometimes their complete loss.

At the current stage, plants are known to demonstrate flexibility of a wide range of ecologically important features – morphological, physiological, anatomical, and ontogenetic ones, including reproductive processes. The implementation of comparative genetic and molecular approaches enables the determination of the adaptive nature of flexibility, the definition of its mechanisms, and the clarification of the role of plant resilience in preserving biodiversity (Kordyum et al., 2003).

Under global warming, only the most flexible species will have a possibility to survive. Their efficiency in utilizing CO₂ and their rate of net photosynthesis should be higher under changed environmental conditions, in the absence of sufficient moisture, the presence of salinity, and high temperatures. Plants with the C₄ and Crassulaceae Acid Metabolism (CAM) types of photosynthesis meet these requirements. Compared to the C₃ type, they have a greater chance of surviving and dominating plant diversity in the future.

Since plants of the Euphorbiaceae Juss. family fully satisfies these requirements, they are now of great scientific interest as a model research object. In particular, they have a cosmopolitan distribution across all climatic zones except Antarctica and use the C₂, C₃, C₄, and CAM types of photosynthesis. Moreover, certain species can switch carbon fixation strategies depending on environmental conditions, such as *Euphorbia tirucalli* L. and *E. tithymaloides* L.

The article aimed to conduct a literature review to determine the features and advantages of the C₄ and CAM types of photosynthesis in the family Euphorbiaceae representatives compared to the C₃ type; to summarize the factors affecting the efficiency and productivity of photosynthesis; and to trace the possible mechanisms of plants' transition from C₃ to C₄ and CAM photosynthesis, as well as suggest a model of transformation of these processes.

Results and discussion

The Calvin cycle, characteristic of C₃ species, is universal and the most ancient one in the plant world, as evidenced by its wide distribution. Hence, the C₄ and CAM types of photosynthesis can be considered modifications of the interaction between the photosynthetic cycle of carbon reduction and the autotrophic part of photosynthetic cell metabolism (Zaimenko, 1987).

There is a close relationship between the photosynthesis pathway of a plant and its growth environment conditions: CAM species are succulents, C₄ species are mainly annual plants of tropical origin developing in hot summer conditions, and C₃ species are annual and perennial plants of Mediterranean, European, or Arab-Saharan origin that bloom in winter in their native ranges. Plants with C₃ photosynthesis grow under better water supply and lower temperatures than C₄ plants, while most CAM and C₄ species are concentrated in the tropical zone, which features high temperatures (Batanouny et al., 1991).

Respiration is a key source of energy in plants. Its intensity varies depending on chemical composition and environmental conditions. In the course of adaptation to environmental changes, along with general fluctuations in respiration intensity, enzymatic systems are restructured. The final oxidation stage plays an important role here, and is catalyzed by oxidases that maintain catalytic activity at both low and high temperatures (Zaimenko, 1987).

C₄ photosynthesis, or the Hatch-Slack pathway (Hatch & Slack, 1966), has been found to be one of the most convergent and complex evolutionary phenomena. It involves a series

of anatomical and biochemical modifications to the typical C_3 pathway, accompanied by a significant increase in plant productivity under hot, sunny, and arid conditions. The C_4 type has independently evolved more than 62 times and is a crucial system for studying the mechanisms of plants' evolutionary adaptation (Sage et al., 2011a; Christin & Osborne, 2014; Lundgren et al., 2014).

However, the absence of C_4 origin in most plant phylogenetic groups and its presence in others, including the Euphorbiaceae family, clearly indicates that certain characteristics enhance the evolutionary emergence of C_4 in certain phylogenetic groups (Pascal-Antoin et al., 2012).

Today, C_4 plants are of particular interest to scientists. They enable researchers to study formation patterns of the physiological mechanisms of plant resilience to abiotic factors, as C_4 plants have several advantages over C_3 species. In particular, they dominate in the tropics, subtropics, and warm temperate zones under high temperatures, water scarcity, and excess sunlight, exhibit intense metabolic processes, and are tolerant of high insolation.

It is in such climatic conditions that these plants can successfully compete with C_3 species due to the absence of photorespiration (Wang, 2005). The two main climatic factors that control the number and share of C_4 species in the flora, and their distribution in certain areas, are annual precipitation dynamics and aridity (Wang, 2004).

The leaves of many C_4 plants differ from those of C_3 plants in their anatomical structure. Each vascular bundle in them is surrounded by a layer of rather large parenchymal cells. This is a so-called vascular bundle sheath, which in turn is surrounded by smaller mesophyll cells. Numerous plasmodesmata connect the mesophyll and lining cells. This type of structure is called 'Kranz anatomy', or wreath type (Musiyyenko, 2001).

The chloroplasts of the lining and mesophyll cells differ in structure. In the chloroplasts of lining cells, the grana are very small or absent, while in the chloroplasts of mesophyll cells, the grana are well developed. Very little starch accumulates in the chloroplasts of mesophyll cells, whereas numerous large starch grains accumulate in the chloroplasts of lining cells (Makrushin et al., 2006).

The C_4 photosynthesis is spatially separated, as plants use a two-celled system, where CO_2 assimilation into organic compounds occurs in the mesophyll cells of the leaf, and carbon reduction occurs via the Calvin cycle in the mesophyll cells of their C_3 ancestors, that is, in the vascular bundle lining (Pascal-Antoin et al., 2012). Mesophyll cells have higher activity of PEP carboxylase (phosphoenolpyruvate carboxylase), while lining cells demonstrate high activity of RuBP (ribulose-1,5-bisphosphate) carboxylase and other Calvin cycle enzymes. Thus, C_4 fixation acts like a pump supplying carbon dioxide to the C_3 photosynthesis pathway (Musiyyenko, 2001; Christin & Osborne, 2014).

The formation, functioning, and establishment of the appropriate physiology and biochemistry of C_4 plants requires preadaptations (Lundgren et al., 2014). Current scientific models consider the movement of glycine, one of the amino acids involved in photorespiration, to be central in the evolution of the C_4 pathway. Photorespiration is the so-called 'bridge' to the C_4 photosynthesis, as in the process of combating its consequences (significant losses of excess energy and overall carbon balance or a 30–50% decrease in the net productivity of photosynthesis in C_3 plants), numerous structural features necessary for C_4 photosynthesis evolved (Makrushin et al., 2006; Sage et al., 2014; Lundgren et al., 2019).

Thus, C_4 metabolism evolved in stages through a series of successive evolutionary changes. First, favorable preadaptations accumulated, then proto-kranz anatomy formed, after which full-fledged C_2 photosynthesis emerged. At stage four, based on these structural and functional preconditions, C_4 photosynthesis developed. During the fifth, final stage, optimization and fine-tuning of photosynthetic components for the most efficient operation of the C_4 pathway took place, together with a simultaneous decrease in C_3 processes in mesophyll tissues, which ultimately formed the full-fledged C_4 photosynthesis (Pascal-Antoin et al., 2012; Sage et al., 2012, 2014; Lundgren et al., 2019).

The C_4 pathway is speculated to have evolved in environments where photorespiration creates significant resistance to C_3 photosynthesis. Semi-arid landscapes are likely to have been the sites of the evolution

of C_4 photosynthesis in Euphorbiaceae (Sage et al., 2011a).

Most CAM plants have thick, dense leaves and are primarily epiphytes. These plants fix CO_2 at night via PEP carboxylation with the formation of dicarboxylic C_4 acids, and reduce CO_2 during the day with closed stomata using internal CO_2 reserves formed in the course of C_4 acids decarboxylation. The newly formed CO_2 is fixed again within the Calvin cycle. In CAM plants, carboxylation occurs twice in a single cell. Unlike C_4 plants, these processes are separated in time rather than space (Musiyenko, 2001; Makrushin et al., 2006). Thus, metabolism based on stomatal type is an adaptation enabling plants to survive in adverse conditions, namely, very dry and hot ones (Makrushin et al., 2006).

Many plants can use the C_3 pathway for carbon fixation during the day and the CAM pathway at night. Other species photosynthesize as C_4 species during the day and as CAM plants at night. This phenomenon of carbon dioxide fixation is called 'photosynthetic mosaicism' and is currently of great scientific interest, requiring in-depth study (Zaimenko, 1987).

For some species, CAM metabolism may be a facultative form of photosynthesis used only under severe, prolonged water stress (Zaimenko, 1987). With sufficient moisture, many CAM plants can behave like C_3 species, demonstrating a reverse transition when water supplies decrease. When C_3 plants switch to CAM photosynthesis, they reduce water loss and maintain photosynthetic integrity under limited water supply, ultimately ensuring the plants' reproductive success (Cushman, 2001). Moreover, such transitions from C_3 to CAM photosynthesis can relate to daily temperature fluctuations, shortened day length, and increased soil salinity (Makrushin et al., 2006).

Representatives of the genus *Euphorbia* L. also exhibit photosynthetic mosaicism by combining different photosynthetic pathways (C_3 in *E. hirta* L. and C_4 combined with CAM in *E. heterophylla* L.) within individual species and even among different organs of the same plant. Photosynthetic mosaicism can be facultatively activated in response to environmental conditions, enabling spurge plants to adapt to arid conditions and providing them with an evolutionary advantage. This phenomenon

in Euphorbiaceae is enhanced by anatomical heterogeneity, functional variability, and ecological flexibility, and is accompanied by evolutionary 'bursts' in the development of new photosynthetic strategies in response to climate change and aridification (Horn et al. 2014). Thus, photosynthetic mosaicism in Euphorbiaceae is an evolutionary survival strategy that has enabled the genus *Euphorbia* to become one of the most diverse and ecologically successful among angiosperms. It demonstrates how plants can 'experiment' with different carbon fixation pathways, creating a complex ecological picture.

The C_2 photosynthesis, a component of the mosaic type of photosynthesis, is considered an evolutionarily important intermediate stage between the classic C_3 and the more efficient C_4 photosynthesis pathways within the same leaf. It creates a 'mosaic' of cells with different photosynthetic functions. Its key feature is the reuse of CO_2 produced during photorespiration in vascular bundle lining cells, thereby reducing carbon losses and increasing productivity under stressful conditions.

This type of photosynthesis is found in the *Euphorbia* subg. *Chamaesyce* (Gray) Caes. ex Rchb. sect. *Anisophyllum* Roesler in J.É.Duby subsect. *Acutae* Boiss., in particular *E. acuta* Engelm., *E. angusta* Engelm., and *E. johnstonii* Mayfield, exhibiting evolutionarily intermediate anatomical and physiological features of a transitional state between the C_3 and C_4 photosynthetic systems. For example, the carbon isotope ratios of *E. angusta* and *E. acuta* were similar to C_3 . In contrast, the activities of key enzymes in the C_4 metabolic cycle in these species were similar to, and significantly lower than, those typically observed in C_4 plants (Sage et al., 2011b).

C_2 photosynthesis in these species suggests evolutionary mechanisms underlying the gradual emergence of C_4 photosynthesis and highlights the importance of Euphorbiaceae as a model for studying plant adaptation strategies. Abundant observations indicate that C_2 photosynthesis is a mandatory step for the evolution of C_4 carbon fixation. However, numerous C_2 species are not related to C_4 phylogenetic groups, demonstrating that C_2 photosynthesis does not automatically lead to C_4 photosynthesis (Sage et al., 2011b; Riina et al., 2012).

Table 1. General properties, basic metabolic parameters, and conditions affecting the photosynthesis of plants with CAM, C₃, and C₄ metabolism (Zaimenko, 1987).

CAM	C ₃	C ₄
Species grow in an arid climate	Species grow in a temperate climate	Species grow in tropical and subtropical climates
Low productivity	Average productivity (20–30 t/ha)	High productivity (80 t/ha)
Peripheral reticulum absent, one type of chloroplast present	Peripheral reticulum is generally absent; one type of chloroplast is present	Kranz-type anatomy, with a peripheral reticulum and two types of chloroplasts that differ in structure
Carbon dioxide acceptors: phosphoenolpyruvate carboxylase in the dark, ribulose diphosphate carboxylase in the light	Primary CO ₂ acceptor – ribulose diphosphate carboxylase	Primary CO ₂ acceptor – phosphoenolpyruvate carboxylase
Primary product: oxalate acetate in the dark, phosphoglycerate in the light	Primary product: glyceric acid	Primary product: oxaloacetate
Two pathways of CO ₂ fixation	One pathway of CO ₂ fixation	Two pathways of CO ₂ fixation
Low glycolate synthesis. Photorespiration is absent in terms of gas exchange	High glycolate synthesis. Photorespiration	Low glycolate synthesis. Photorespiration is absent in terms of gas exchange
High water use efficiency. Low salinity	Low water use efficiency. Medium salinity	High water use efficiency. High salinity
In bright light, photosynthesis saturation does not occur	Photosynthesis saturation occurs at a light intensity of 1/5 of full sunlight	In bright light, photosynthesis saturation does not occur
High affinity for carbon dioxide at night	High CO ₂ compensation point	Low CO ₂ compensation point
Stomata open at night	Stomata open during the day	Stomata open during the day

The results of biochemical, anatomical, and physiological studies of plants with different mechanisms of CO₂ assimilation allow for their comparison as presented in Table 1.

Today, crop production faces a number of environmental issues, such as soil salinization, pollution by mineral fertilizers, and depletion of water resources. Human economic activities and active military operations in Ukraine increase the areas of land unsuitable for agricultural use. Furthermore, energy sources are rapidly depleting. One promising way to solve these problems is to search for plants that can successfully grow on marginal lands, resist drought and salinization, accumulate biologically active compounds suitable for phytochemical, pharmaceutical, and nutraceutical use, and serve as raw materials for industry and biofuel production.

Representatives of the genus *Euphorbia*, in particular *E. tirucalli*, *E. umbellata* (Pax) Bruyns,

and *E. milii* Des Moul., can serve as such plants. These and numerous other Euphorbiaceae species are already widely used for their ornamental value and high aesthetic appeal, as well as for their active use in medicine and the pharmaceutical industry. They can also be an efficient and cost-effective source of biofuels (Schmelzer & Gurib-Fakim, 2008; Wei et al., 2021).

Euphorbia tirucalli (Fig. 1) is a dicotyledonous succulent shrub or small tree of the family Euphorbiaceae. The natural distribution of the species covers the paleotropical region of Madagascar, the Cape Province (South Africa), East Africa, and Indochina. Moreover, it is widely grown as an ornamental plant in many tropical countries and America (Webster, 1994; Van Damme, 2001; Bruyns et al., 2006; Janssens et al., 2009; Levchyk et al., 2024). It is a drought- and salt-tolerant plant that can grow in a wide range of environmental conditions but is not

frost-tolerant. Due to its rapid growth and biomass accumulation regardless of weather and climatic conditions, it can be a significant source of biofuel (Schmelzer & Gurib-Fakim, 2008; Hastilestari et al., 2013). The unique properties of *E. tirucalli*, like those of other so-called heat-resistant plants, stem from its ability to increase the thermal denaturation resistance of its protein molecules, which leads to very high metabolic intensity and increased levels of specialized proteins and RNA (Grodzinsky, 2013).

Stress resistance and tolerance to difficult living conditions are also partly explained by the plant's photosynthetic system. The succulent stems of *E. tirucalli* lack Kranz anatomy and have a CAM photosynthetic system, whereas the non-succulent leaves follow C_3 photosynthesis (Bender, 1971; Smith, 1982; Hastilestari et al., 2013). Hence, this species is highly stress-tolerant and can serve as a pioneer plant in arid and semi-arid environments (Van Damme, 1989).

The combination of a CAM stem and C_3 leaves ensures *E. tirucalli* a unique place in the plant world. *E. tirucalli* is a tree with a woody stem, whereas most species where this combination is already known and described are short-lived subshrubs or lianas (Van Damme, 1989). Many morphological, anatomical, and physiological adaptations make plants of the *E. tirucalli* species resistant to drought and salt stress. Due to CAM photosynthesis, the succulent stems of these plants use water rather efficiently. Herewith, stomata located in the longitudinal grooves of the stem and a ring-shaped wax coating around the stomata provide additional protection against drought (Van Damme, 1989).

Furthermore, the malic acid cycle associated with CAM photosynthesis continues even during drought. This enables the plant to maintain a low internal water potential, allowing it to use external water as soon as it becomes available. Sodium and chloride ions are retained in roots and old stems and do not reach the photosynthetically active tissues, which is an important defense mechanism for salt tolerance in *E. tirucalli* (Van Damme, 1989).

It is the combination of the C_3 and CAM pathways of photosynthesis in *E. tirucalli* that may help ensure its survival under harsh weather and climatic conditions. The CAM pathway of photosynthesis leads to



Figure 1. General habit of *Euphorbia tirucalli*.

greater accumulation of carboxylic acids at night than in C_3 plants, thereby increasing osmotic potential and, in turn, enhancing salt tolerance. Moreover, *E. tirucalli*, like other succulents, stores additional water in parenchyma and vacuoles to dilute incoming salt ions. This serves as both a reserve and an important mechanism for the plant to survive under limited water supply (Van Damme, 2001; Mwine et al., 2013).

In case of drought, non-succulent C_3 leaves of *E. tirucalli* die, while the plant's metabolism is maintained by CAM photosynthesis in the stems. This phenomenal switch explains the species' ability to accumulate biomass rapidly under adverse environmental conditions. The presence of two photosynthetic pathways, spatially distributed across different organs, is a biologically appropriate adaptation reflecting differences in tissue anatomy. Thus, *E. tirucalli* demonstrates flexibility in switching between C_3 and CAM metabolism, which ensures its ecological resilience and adaptability (Hastilestari et al., 2013).

Euphorbia tirucalli plants, like all species of the family Euphorbiaceae, produce latex in secretory cells (laticifers), which is an aqueous



Figure 2. *Euphorbia milii* in the collection of the O.V. Fomin Botanical Garden of Taras Shevchenko National University of Kyiv.

emulsion of 30 terpenes. Consequently, these plants have great economic value because their latex contains terpenoids, sterols, and hydrocarbons similar to those in petroleum. Mixing latex with other substances can produce biodiesel. Triterpenoids are organic compounds that can be found as components of plant latex, which can be split like petroleum to obtain high-octane gasoline (Ramawat, 2010; Zhang et al., 2019). Moreover, latex contains phenolic compounds, mucus, lipophilic components, and nitrogen compounds (Luza et al., 2015).

Since *E. tirucalli* plants possess numerous pharmacological properties, their raw materials are widely used in both folk and evidence-based medicine worldwide to treat a range of serious diseases, including oncological conditions. Meanwhile, latex is not only a source of biofuel but also a pesticide against mosquitoes, bacteria, nematodes, and mollusks, and is used as a glue or adhesive (Schmelzer & Gurib-Fakim, 2008; Hastilestari et al., 2013; Levchyk et al., 2024).

Thus, *E. tirucalli* is a classic example of photosynthetic mosaicism, in which the spatial distribution of C_3 and CAM pathways

ensures the species' ecological resilience and high productivity.

The next bright representative of the family Euphorbiaceae is *Euphorbia milii*. It is a perennial shrub up to 1 m tall, with a fleshy stem, succulent leaves, and ornamental inflorescences, endemic to Madagascar. Due to its ornamental value, the species has a worldwide distribution and is widely cultivated (Fig. 2).

The species prefers arid and semi-arid areas with high insolation and seasonal drought. Such conditions are conducive to the development of CAM photosynthesis in succulent *Euphorbia* species. Though not as pronounced as in classic CAM species (e.g., *E. tirucalli* or *E. trigona* Mill.), the morphological features of *E. milii*, namely succulent stems and relatively thick leaves, point to the plant's adaptability to drought. At dawn and dusk, the leaves of these plants retain significant amounts of malate and citrate, and their levels increase over time during drought. The peculiarity of the anatomy of an *E. milii* leaf points to possible C_2 photosynthesis. It consists of columnar and spongy parenchyma, which together form a

photosynthetic mosaic of the mesophyll that combines light absorption and gas exchange, and a bundle sheath with chloroplasts.

Therefore, *E. milii* is not a regular CAM species, as CAM is low and operates in a cyclic mode. The photosynthetic strategy of this species combines C_3 and CAM cycling, implying partial use of CAM mechanisms without nocturnal CO_2 fixation. This intermediate strategy between the C_3 and CAM types of carbon fixation helps plants reduce water loss (rather than accumulate carbon) and exemplifies an evolutionary transition state between C_3 and CAM photosynthesis in the genus *Euphorbia* (Herrera, 2013).

Euphorbia umbellata (Fig. 3) is a semi-succulent evergreen shrub or small tree with large fleshy leaves, native to dry tropical regions of Africa. It mainly grows in seasonally dry tropical biomes, where it prefers slopes, rocky outcrops, and forest edges. The species has been introduced and naturalized in many tropical and subtropical countries, including India and Bangladesh (Sahu et al., 2019; POWO, 2026; LLIFLE, 2026; Extension Gardener, 2026; Useful Tropical Plants, 2026).

Morphologically, the plant is characterized by branched shoots, succulent leaves with well-developed mesophyll typical of C_3 plants, and the presence of latex. Unlike some other *Euphorbia* species (e.g., *E. tirucalli* or *E. milii*) that can use CAM photosynthesis, *E. umbellata* uses daytime photosynthesis and the C_3 pathway, as confirmed by its leaf anatomy and ecological features.

This makes it a typical example of a tropical C_3 plant that adapts to seasonal drought through morphological rather than biochemical mechanisms, compensating for water loss with fleshy leaves and latex rather than CAM metabolism (Schmelzer & Gurib-Fakim, 2008; Luza et al., 2015).

The leaves of *E. umbellata* are used in nanotechnology to synthesize silver nanoparticles with antibacterial activity (Sahu et al., 2019). In this regard, further research into the photosynthesis and properties of *E. umbellata* plants remains relevant and scientifically justified.

Euphorbia tithymaloides (Fig. 4) is an evergreen succulent or semi-succulent erect shrub up to 2.4 m tall, with simple green smooth fleshy leaves arranged alternately on characteristic zigzag green stems capable of



Figure 3. General habit of *Euphorbia umbellata* (Photo credits: Forest & Kim Star, CC BY).

accumulating water (World of Succulents, 2026). The species originates from tropical and subtropical North and Central America, where it naturally remains widespread from Florida and the Caribbean to Central America and the Amazon. It grows on dry slopes, forest edges, and lighted places with periodic water shortages.

Euphorbia tithymaloides is a CAM species. However, environmental influences such as drought and heat cause its photosynthetic flexibility. This is confirmed by experimental studies of diurnal fluctuations in CO_2 fixation, titratable acidity, and malic acid content in leaves. Photosynthetic flexibility is an evolutionary adaptation of the species for long-term survival in adverse soil and microclimatic conditions (Reddy et al., 2003).

As of now, the type of photosynthesis has already been identified in some representatives of the family Euphorbiaceae. In particular, the geophyte common in pastures, *Euphorbia fischeriana* Steud., has C_3 photosynthesis, while the therophyte common on disturbed and cultivated lands, *E. humifusa* Willd., uses C_4 photosynthesis

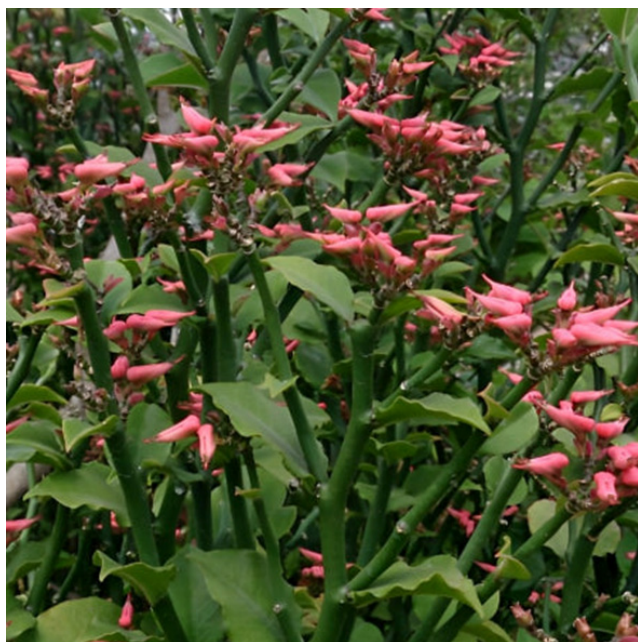


Figure 4. General habit of *Euphorbia tithymaloides* (Photo credits: planetdesert.com).

(Wang, 2005). Based on indicators of carbon isotopic composition, gas exchange in leaves, and enzyme activity, it was determined that *Euphorbia* species, such as *E. aphylla* Brouss. ex Willd., *E. bubalina* Boiss., *E. stenoclada* Baill., *E. polygona* Haw., *E. caput-medusae* L., *E. innocua* L.C.Wheeler, *E. didiereoides* Denis ex Leandri, and *E. platyclada* Rauh. (syn. *E. bosseri* Leandri), function according to the CAM type of photosynthesis (Herrera, 2013; Horn et al., 2014).

In general, plants with C_3 , C_4 , and CAM metabolism constitute the main functional types and are widely used to study the relationship between plants' physiological features and their respective life strategies. The following parameters help identify C_3 and C_4 plants: Kranz anatomy in leaves, low CO_2 compensation point, and the ratio of photosynthetic enzymes (Wang, 2005).

The evolution of kranz anatomy remains one of the greatest mysteries of plant biology, with its solution becoming increasingly important in light of attempts to introduce C_4 -type carbon metabolism into C_3 crops. Taking into account the type of photosynthesis in cultivated plants is a key factor in crop production, as it is directly related to soil and climatic conditions, land use systems, and human activities (Wang, 2005). Meanwhile, the recognition of the evolution of C_4 photosynthesis as one of the key events in the

formation of the modern biosphere highlights the strategic importance of this research for the future of crop production and global food security (Sage et al., 2014).

Plants with different life forms and photosynthetic pathways exhibit distinct physiological and ecological responses to climatic conditions, geographical factors, land-use systems, and anthropogenic impacts. Herewith, many therophytes represent C_4 forms, including both woody species and promising crops. Due to the role of pioneer species in succession restoration and their high resistance to environmental stressors, their agricultural potential is significant. Herewith, identifying the type of photosynthesis is key for effective land management and adaptation to global climate change (Wang, 2005).

Further scientific research should focus on genetic improvement of plants, improvements in photosynthetic efficiency, improvements in cultivation techniques to intensify production, improvements in product quality, and the development of effective technologies for biofuel extraction and use (Schmelzer & Gurib-Fakim, 2008).

Currently, the European Union is implementing a large-scale international research project, "3to4" (CORDIS, 2024), which has provided fundamental knowledge and tools for transferring the characteristics of C_4 photosynthesis to crops with C_3 photosynthesis. Its practical implementation is expected to become possible within 15–20 years, allowing yields to increase by 50% by the mid-21st century. The model species involved in the project include *Arabidopsis thaliana* (L.) Heynh., *Brassica napus* L., *Amaranthus edulis* Speg. (syn. *A. caudatus* L.), *Atriplex prostrata* Boucher ex DC., *A. rosea* L., and *Oryza sativa* L. In this regard, representatives of the family Euphorbiaceae are also studied in detail, in particular *Euphorbia angusta* (C_3), *E. acuta* (C_3 – C_4), *E. lata* Engelm. (C_3 – C_4), and *E. mesembryanthemifolia* Jacq. (C_4) (Williams et al., 2013).

The fact that the C_4 pathway of photosynthesis evolved independently and in parallel in numerous species of C_3 plants suggests a possibility of its emergence under certain conditions and the real prospect of artificial reproduction, as evidenced by modern biotechnological research capable of significantly accelerating natural evolutionary

processes and increasing the yield of key food, industrial, and energy crops (Karki et al., 2013). This is particularly relevant for Ukraine, where the effective use of plant resources is strategically important to ensuring food and energy security.

Conclusions

- The Calvin cycle, characteristic of the C_3 type of photosynthesis, is the oldest and most universal mechanism of carbon fixation, as evidenced by its wide distribution among plants. C_4 and CAM photosyntheses are considered evolutionary modifications of this cycle, formed as adaptive strategies to high temperatures and limited water availability.
- In the context of global climate change, the family Euphorbiaceae is of significant scientific interest as a model system due to its high resilience and ecological flexibility. Its representatives boast a cosmopolitan distribution (except Antarctica), rich species diversity, and the ability to use different types of photosynthesis (C_2 , C_3 , C_4 , and CAM) or to change the method of carbon fixation depending on environmental conditions.
- The C_4 photosynthesis is a convergent evolutionary system that involves anatomical and biochemical modifications of the C_3 pathway. It provides increased plant productivity under hot, arid conditions, tolerance to high insolation, and metabolic intensity. The C_4 photosynthesis has independently evolved more than 62 times and serves as a key model for studying the mechanisms of plant evolutionary adaptation.
- The C_4 metabolism evolved gradually through a series of successive evolutionary changes: from preadaptations and proto-Kranz anatomy, through the C_2 stage, to full-fledged C_4 photosynthesis with spatial distribution of processes and suppression of the C_3 pathway in the mesophyll.
- The CAM type of photosynthesis provides nocturnal CO_2 fixation and its daytime reuse in the Calvin cycle under closed stomata, occurring within the same cell with temporally separated processes. Such metabolism is an adaptation that allows

plants to survive in drought and other extreme environments.

- The C_2 type of photosynthesis is an evolutionary intermediate stage between the classic C_3 and the more efficient C_4 pathways. It is used within the same leaf, thanks to the 'mosaic' of cells with different photosynthetic functions, and is a necessary stage in the formation of C_4 carbon fixation.
- Photosynthetic mosaicism in representatives of the genus *Euphorbia* is manifested as a combination of different carbon fixation pathways (C_3 , C_4 , and CAM), which can be facultatively activated depending on environmental conditions. Such anatomical and functional variability confers high ecological flexibility and is an evolutionary advantage in arid conditions.
- Different photosynthetic strategies among representatives of the genus *Euphorbia* – from the combination of C_3 and CAM in *E. tirucalli* and *E. milii* to the morphological adaptation to C_3 in *E. umbellata* – reflect a wide range of evolutionary solutions and ensure their stability and potential for use in extreme conditions.
- The use of biotechnological approaches allows for a significant acceleration of the transition of C_3 plants to C_4 photosynthesis compared to the natural evolutionary process. The development of crops with improved photosynthetic apparatus will increase yields of food, industrial, and energy crops and contribute to the effective and sustainable use of plant resources in Ukraine.

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Особливості фотосинтезу у представників родини Euphorbiaceae Juss.

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У статті здійснено літературний аналіз особливостей та переваг C_4 - і САМ-фотосинтезу у представників родини Euphorbiaceae Juss. порівняно з класичним C_3 -метаболізмом. Визначено передумови та можливі етапи переходу рослин від C_3 до C_4 і САМ типів фотосинтезу. C_4 -фотосинтез є конвергентною еволюційною системою, що виникла незалежно понад 62 рази, передбачає анатомічні та біохімічні модифікації C_3 -шляху, забезпечує високу продуктивність у спекотних і посушливих умовах, толерантність до інсоляції та інтенсивність метаболізму, слугуючи ключовою моделлю адаптаційної еволюції. Етапи його становлення включають накопичення преадаптацій, формування протокранц анатомії, появу C_2 -фотосинтезу, налаштування фотосинтетичних компонентів та розвиток повноцінного C_4 -шляху із одночасним пригніченням C_3 -метаболізму.

У САМ-рослин фіксація CO_2 відбувається вночі через карбоксилювання фосфоенолпірувату з утворенням C_4 -кислот, тоді як удень, при закритих продихах, використовується внутрішній запас CO_2 після їх декарбоксилювання, що забезпечує часову сегрегацію процесів. C_2 -тип фотосинтезу розглядається як проміжний еволюційно важливий етап між класичним C_3 та ефективним C_4 шляхами, виявлений у підроді *Chamaesyce* роду *Euphorbia* (*Euphorbia acuta* Engelm., *E. angusta* Engelm. та *E. johnstonii* Mayfield).

У родині Euphorbiaceae описано феномен “фотосинтетичної мозаїчності”, що поєднує різні шляхи фіксації вуглецю, викликає наукове зацікавлення й потребує поглибленого дослідження. Поєднання C_3 - та САМ-шляхів у *E. tirucalli* L. забезпечує стійкість і швидке накопичення біомаси, тоді як проміжна стратегія *E. milii* Des Moul. (C_3 з частковою САМ-циклізацією) зменшує втрати води та ілюструє перехідний стан між C_3 і САМ. *Euphorbia umbellata* (Pax) Bruyns є типовою тропічною C_3 -рослиною, що адаптується до сезонної посухи за допомогою морфологічних механізмів (м'ясисті листки, латекс) без залучення САМ. Удосконалення культур із покращеним C_4 -фотосинтезом здатне підвищити врожайність харчових, технічних та енергетичних рослин і забезпечити ефективне використання рослинних ресурсів України.

Ключові слова: Euphorbiaceae, типи фотосинтезу, кранц-анатомія, стійкість, преадаптації, мозаїчність