



Why are there no C₄ forests?☆

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ABSTRACT

C₄ photosynthesis is absent from the arborescent life form, with the exception of seven Hawaiian *Euphorbia* species and a few desert shrubs that become arborescent with age. As a consequence, wherever C₄ trees can establish, their height advantage enables them to outcompete low stature C₄ vegetation. Had C₄ photosynthesis been able to evolve in an arborescent life form, forest cover (by C₄ trees) could have been much more extensive than today, with significant consequences for the biosphere. Here, we address why there are so few C₄ trees. Physiological explanations associated with low light performance of C₄ photosynthesis are not supported, because C₄ shade-tolerant species exhibit similar performance as shade-tolerant C₃ species in terms of quantum yield, steady-state photosynthetic and use of sunflecks. Hence, hypothetical C₄ trees could occur in the regeneration niche of forests. Constraints associated with the evolutionary history of the C₄ lineages are more plausible. Most C₄ species are grasses and sedges, which lack meristems needed for arborescence, while most C₄ eudicots are highly specialized for harsh (arid, saline, hot) or disturbed habitats where arborescence may be maladapted. Most C₄ eudicot clades are also young, and have not had sufficient time to radiate beyond the extreme environments where C₄ evolution is favored. In the case of the Hawaiian *Euphorbia* species, they belong to one of the oldest and most diverse C₄ lineages, which primed this group to evolve arborescence in a low-competition environment that appeared on the remote Hawaiian Islands.

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1. Introduction

The inspiration for this review arose from a serendipitous mistake by the lead author. As a new faculty member at the University of Georgia in 1988, R. Sage had the opportunity to meet Professor James Ehleringer who was visiting the Savannah River Ecology lab to deliver a seminar. Professor Ehleringer was already a lead-

ing figure in physiological ecology, so it was quite an honor to be asked by him during the meeting to co-author a paper on C₄ plants for *TREE (Trends in Ecology and Evolution)*. Sage misinterpreted Ehleringer's request to instead prepare a paper on "C₄ trees". Since the paradigm had it that there were no C₄ trees, save for one from Hawaii, Sage responded that it seemed like a rather limiting topic and proceeded to tell Professor Ehleringer about an interesting hypothesis that low atmospheric CO₂ in recent geological time promoted the evolutionary origin of C₄ photosynthesis. Ehleringer found the low CO₂ hypothesis intriguing and mentioned that new isotopic work out of Thure Cerling's group indicated C₄ plants spread over the landscape of Pakistan 8–10 million years

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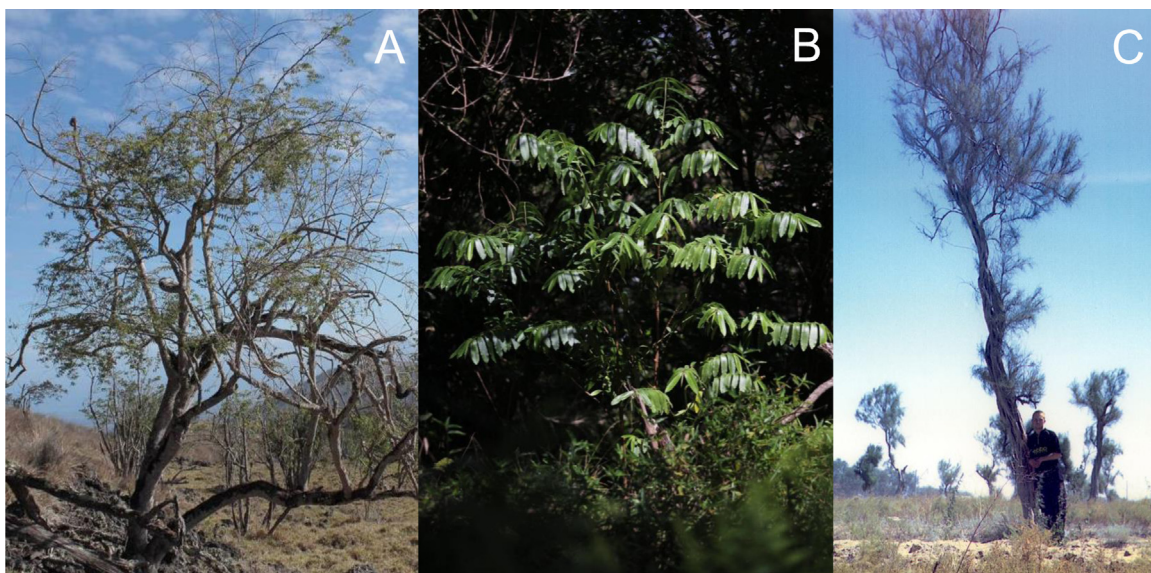


Fig. 1. Photographs of three C_4 “trees”. (A) A 6 m *Euphorbia olowaluana* tree from the island of Hawaii, USA. (Photo courtesy of Karl Magnacca); (B) A 3 m *Euphorbia herbstii* from the Island of Oahu, Hawaii U.S.A. (Photo courtesy of Matt Garma). (C) *Haloxylon aphyllum* from arid regions of Kazakhstan (photo courtesy of Ferit Kocacinar and reprinted with permission from Sage, 2001).

ago (Quade et al., 1989). With the Quade et al. results, the low CO_2 idea had support, and together with Bob Pearcy and Larry Flanagan, Ehleringer and Sage published the hypothesis in an influential paper in *TREE* (Ehleringer et al., 1991). This paper inspired substantial research that supports the hypothesis, such that by now it is generally accepted that CO_2 decline in the past 30 million years facilitated, in part, most origins of the C_4 pathway (Cerling et al., 1997; Christin et al., 2014, 2011, 2008; Ehleringer et al., 1997; Vicentini et al., 2008; Zhang et al., 2013).

While the question of low CO_2 and C_4 evolution gained momentum following that conversation, the issue of C_4 trees, or more precisely, the lack of C_4 trees, has not. This is somewhat surprising because it had been discussed among physiological ecologists over the previous 20 years (Ehleringer, 1978; Osmond et al., 1982). Thus, when Sage misinterpreted Ehleringer’s invitation to write an article on C_4 trees, it left a strong impression, and a desire to resolve the question. This desire grew over the years, inspiring brief discussions in numerous review papers, although none with a clear resolution (Sage et al., 1999; Sage and Kubien, 2003; Sage and McKown, 2006; Sage and Pearcy, 2000; Sage and Stata, 2015; Sage, 2013). While initially an issue for physiological ecologists, the importance of this question has increased as subsequent research clarified the role of C_4 photosynthesis in the origin and function of the modern biosphere (Bobe and Behrensmeyer, 2004; Bond et al., 2005; Edwards et al., 2010; Osborne, 2011; Sage and Stata, 2015). In this paper, it is our objective to specifically focus on the question of why C_4 photosynthesis is generally absent in arborescent species, particularly those that form forest canopies. We begin with an overview of the distribution of the C_4 pathway in the world’s flora and ecosystems, and discuss its significance for biotic evolution and the modern biosphere. Next, we address possible explanations for why the C_4 pathway is rare in the tree life form. There are a few exceptions to the paradigm of no C_4 trees that are relevant to the discussion, and they are discussed in some length. We conclude that while physiological limitations may constrain C_4 performance within woodlands, they do not readily explain why the C_4 pathway is largely absent from the arborescent life form. Instead, limited evolutionary time, and a range of constraints associated with phylogenetic ancestry reduced opportunities for arborescence to evolve in the C_4 flora.

2. The distribution of C_4 photosynthesis in the biosphere

A recent accounting of the C_4 flora documents about 8100 C_4 species distributed in 19 families of angiosperms (Sage, 2016). Most (6368) of the tabulated C_4 species are monocots, mainly grasses and sedges. Grasses and sedges (graminoids) do not form trees since they lack secondary meristems that produce woody trunks (Esau, 1965). While numerous graminoid species form lignified stalks and exceed 6 m in height, none of the C_4 grasses and sedges approach arborescence, defined as having the size, form and character of a tree, that is, a perennial woody plant with a dominant central trunk and crown, typically over 2 m in height (Merriam-Webster, 2016). Bamboos are grasses that form tall, woody stalks that rival traditional forest trees in height (the world’s tallest bamboo is *Dendrocalamus giganteus* which can reach 25 m); however, they occur in the C_3 Bambusoideae tribe of grasses, which is phylogenetically distant from the PACMAD clade where all C_4 grasses occur (Kellogg, 2002). As such, the question of why C_4 trees are lacking must be addressed in the eudicots.

Eudicots account for nearly 1800 C_4 species in 16 families. These species are scattered in at least 34 distinct evolutionary lineages (Table 1). Most of these occur in the order Caryophyllales, which includes the Chenopodiaceae (560 C_4 species in 10–13 distinct C_4 lineages), Amaranthaceae (250 C_4 species in 5 lineages), and Euphorbiaceae (350 C_4 species in *Euphorbia*) (Sage, 2016). The large majority of C_4 eudicots are herbaceous forbs or low-stature woody perennials (subshrubs). About 400 C_4 eudicots are shrubs, and a handful of these approach arborescence with advanced age (Sage, 2016). Most of the C_4 shrubs occur in the Chenopodiaceae, notably in the genera *Atriplex* and *Haloxylon*, which form the largest C_4 shrubs (eFloras, 2008a; Osmond et al., 1980). In the Polygonaceae, the genus *Calligonum* is comprised of 80 species of shrubs or subshrubs, all of which are C_4 (eFloras, 2008a; Sage, 2016). Over a half-dozen C_4 *Euphorbia* species also form shrubs, the best studied of which occur in Hawaii (Pearcy et al., 1982; Yang, 2012). Two Hawaiian species – *Euphorbia olowaluana* and *E. herbstii* (formerly *E. forbesii*) stand out as they exhibit true arborescence (growing to 6–10 m, with a dominant trunk), and thus are the clear exception to the paradigm of no C_4 trees (Fig. 1A, B); five other Hawaiian *Euphorbia* species (*E. atrococca*, *E. halemanui*, *E. celastroides*, *E. remyi*,

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