

Homage to L. M. Coutinho: fire adaptations in cerrado plants

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Charles Darwin never considered fire as a possible evolutionary force. We have learned a lot since then, and currently there is overwhelming evidence that many plants have adapted to historic fire regimes (Keeley *et al.* 2011, 2012). However, evolutionary fire ecology is a young discipline that has only recently taken root – especially in Mediterranean ecosystems (He *et al.* 2012; Keeley *et al.* 2012; Pausas and Schwilk 2012; Pausas 2015a). An important exception was the work of Professor Coutinho (1934–2016) from the University of Sao Paulo, Brazil, who was discussing fire adaptations in South American savannas (cerrado) during the 1970s (e.g. Coutinho 1976, 1977). At that time, fire was thought to be mostly introduced by humans – in the cerrado and in many ecosystems worldwide. Fire was considered an important factor in determining the structure of vegetation, and it was accepted that many cerrado species resist fire (Eiten 1972); however, few researchers were discussing specific fire adaptations in plants. The few researchers studying fire adaptations were focused on Mediterranean ecosystems (Wells 1969; Mutch 1970) and their work was scarcely recognised during the 1970s. For instance, Axelrod (1973, 1989) and Raven and Axelrod (1978) wrote extensively on the origin of Californian flora and assigned no role to fire in the evolution of this fire-adapted flora (Keeley *et al.* 2012). Meanwhile, Coutinho had a clearly dynamic view of cerrado vegetation at both ecological and evolutionary scales. He understood that lightning-generated natural fire regimes could select for adaptive response in plants (Coutinho 1976); and he considered that human fires replaced lightning fires. He also understood the dynamic nature of cerrado mosaics where forest expanded in wet periods and retracted in dry periods with greater fire activity (Coutinho 1976), and thus considered forest and savanna as alternative states in the cerrado (Dantas *et al.* 2016).

In his PhD (Coutinho 1976), Coutinho performed experimental burns in different seasons in the ‘Cerrado de Emas’ (Pirassununga, Sao Paulo) and provided relevant and novel information on fire behaviour (Coutinho 1978) and nutrient cycling (Coutinho 1979) for the cerrado. In the latter study, he proposed that despite fires generating a loss of nutrients, a fire interval of three years would maintain an equilibrium between input and output; in fact, he suggested that fire would encourage primary productivity by accelerating nutrient cycling (Coutinho 1976; Pivello and Coutinho 1992). A very important contribution of his PhD was the study of fire-stimulated flowering in the

cerrado – a fire-adaptive trait that is still little studied (Lamont and Downes 2011). He documented that the flowering of most herbaceous and suffruticose (geoxyle) species of cerrado depends quantitatively or qualitatively on fire (Fig. 1). This suggests that cerrado could be the ecosystem where this trait is most prominent; however, this finding is unknown in the international literature (Lamont and Downes 2011). He performed laboratory experiments that involved burning, cutting, fumigating with smoke and imposing drought and different photoperiods on plants growing in pots (four species). He thus showed that flowering is stimulated by the elimination of the aboveground parts, and not by changes in light, heat or chemical cues. He further demonstrated – in an anatomical study – the transformation of vegetative buds into floral buds a few days after a fire (he termed this process pyromorphogenesis; Coutinho 1976; Coutinho *et al.* 1982). After his PhD, he described serotiny in some cerrado plants (Coutinho 1977); that is, plants that keep the fruit or infrutescens closed during fire to protect the seeds, and then open them to disperse and recruit post-fire. Serotiny is another fire-adaptive trait that has generally been well studied – mostly in pines in the northern hemisphere (He *et al.* 2012; Pausas 2015a) and in Proteaceae in the southern hemisphere (Lamont *et al.* 1991) – but not in

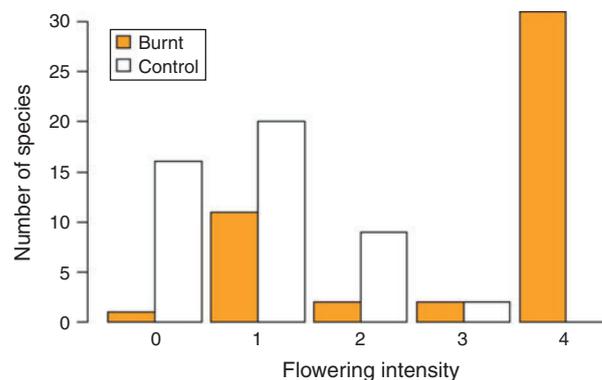


Fig. 1. Frequency distribution of the flowering intensity index (from 0 to 4) after fire (shaded; 90 days post-fire) and in control conditions (white) in 47 species (belonging to 20 families) of a cerrado ecosystem (prepared from data in Coutinho 1976). The 31 species with the highest post-fire flowering belong to 17 different families.

savannas. His pioneering research remains to be examined in more detail and framed with current knowledge; and it should also be evaluated in other savannas worldwide. Coutinho also demonstrated the existence of fire-stimulated germination in *Mimosa* species from cerrado (Coutinho and Jurkevics 1978); recent studies suggest that there are few other species with fire-stimulated germination, despite the general response of cerrado plants having seeds tolerant to fire (Ribeiro *et al.* 2013; Ramos *et al.* 2016). A few years later, he showed that fire was an old and major factor in the cerrado, by providing evidence of charcoal from cerrado soils dated at 8600 years (Coutinho 1981). Currently, and thanks to phylogenetic techniques, we know that fire may have been an important evolutionary factor in cerrado some 10 million years ago (Simon *et al.* 2009). Another prominent adaptation of cerrado plants is the very thick and suberised bark for fire protection and epicormic resprouting (Pausas 2015b). Although he did not make a formal study of this trait, Coutinho specifically noted that the bark was thick in the trunk (as is well known in pines), as well as in lateral branches located 2–3 m above ground level (i.e., at the top of the flame where fire temperatures can be very high) (Coutinho 1990). This detail has only recently been recognised as a trait differentiating Brazilian cerrado from African savannas (Pausas 2015b, 2017). Similarly, he also suggested that xylopodia could be a response to fire, but that more research was needed (Coutinho 1976); this research has only recently been published (Maurin *et al.* 2014).

Coutinho was a pioneer of evolutionary fire ecology. He is known among Brazilian researchers for his contributions to cerrado ecology, and because he was professor at one of the major Brazilian universities (University of Sao Paulo). His legacy will remain for future generations, especially thanks to his recent book on Brazilian biomes (Coutinho 2016; published just after his death). However, he is little known elsewhere, perhaps because he was not part of the dominant Anglo-Saxon culture (Amano *et al.* 2016), but also because he was ahead of his time, when fire and evolution were still distant concepts. Only recently has the evolutionary role of fire in the cerrado been fully recognised (Simon *et al.* 2009; Dantas and Pausas 2013), supporting his modern view of this emblematic ecosystem that surprised the founders of ecology (Warming 1893).

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