ARTICLE IN PRESS
PALAEO-07607; No of Pages 14
Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2015) xxx–xxx
Contents lists available at ScienceDirect
Palaeogeography, Palaeoclimatology, Palaeoecology
journal homepage: www.elsevier.com/locate/palaeo

Can atmospheric composition influence plant fossil preservation potential via changes in leaf mass per area? A new hypothesis based on simulated palaeoatmosphere experiments.

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ARTICLE INFO

Article history:
Received 17 July 2015
Received in revised form 13 November 2015
Accepted 2 December 2015
Available online xxxx

Keywords:
Plant preservation
Leaf taphonomy
Atmospheric composition
LMA
Fossil plants

ABSTRACT

Atmospheric composition, particularly levels of CO_2 and O_2, impacts all aspects of life but its role in relation to plant preservation in the fossil record is largely unconsidered. Plants, angiosperms in particular, have been widely shown to increase leaf mass per area (LMA) under high CO_2 conditions and decrease LMA in low CO_2 conditions. Leaf thickness has long been known to be a contributory factor in preservation potential in the plant fossil record, with thicker leaves considered to have a greater recalcitrance than thinner ones. Therefore, any change in leaf density/thickness, through changes to LMA, could lead to an increased or decreased preservation potential of fossil leaves at times of elevated or decreased CO_2, respectively. Additionally, the impact of changes to atmospheric O_2 and to the atmospheric CO_2:O_2 ratio on LMA has not been previously considered in detail. This investigation examines the effect of simulated Mesozoic atmospheres, times of high CO_2 and low O_2, on LMA in a suite of gymnosperms that act as nearest living equivalents for common elements of Mesozoic floras. Exposure to high CO_2 (~1500 ppm) led to a statistically significant ($p < 0.001$) increase in LMA in four out of 6 species, and exposure to combined high CO_2 and low O_2 (~13%) induced a statistically significant ($p < 0.001$) increase in LMA in all six species. The investigation also examined the effects of atmospheric composition on %N, a key plant trait known to co-vary with LMA under modern atmospheric compositions that provides information on plant function and relates to photosynthetic efficiency. Most species showed decreased %N in treatments with increased LMA in agreement with modern ecological studies and supporting the co-varying nature of LMA and %N regardless of CO_2:O_2 ratio. These findings suggest that atmospheric composition has a pronounced impact on LMA. Based on these results, we propose the hypothesis that atmospheric composition is an important taphonomic filter of the fossil leaf record. Further research is now required to test the significance of atmospheric composition versus other well-known taphonomic filters.

1. Introduction

There are numerous factors, biological, physical and chemical, that influence whether or not a once living plant or animal enters the fossil record (Kidwell, 2001; Briggs, 2003; Benton and Harper, 2009; McNamara et al., 2012; Butler et al., 2015; Redelstorff and Orr, 2015). For plants, the majority of macrofossil assemblages are leaf litter (Greenwood, 1991), making leaves among the most common plant organs preserved in the fossil record. Therefore, a detailed understanding of how leaves are preserved and the taphonomic filters that act on leaf preservation in the fossil record is extremely important and has been the subject of much work over the last several decades. After climate and source vegetation, which both control the leaf litter available for preservation (Spicer, 1989; Greenwood, 1991; Burnham et al., 1992, 2005; Gastaldo and Staub, 1999), depositional environment is most likely the primary control that determines preservation potential of leaf macrofossils (Gastaldo et al., 1987a, 1987b, 1996; Gastaldo, 1989; Spicer, 1989; Greenwood, 1991; Ferguson, 2005; Gee, 2005; Gastaldo and Demko, 2011). Other factors that are known to impact on preservation potential include the chemical composition of plant organs (Collinson et al., 1998; Briggs, 1999; Retallack, 2011; Witkowski et al., 2012); premineralisation (Briggs, 1999; Channing and Edwards, 2003; Scott and Collinson, 2003a, 2003b; Labe et al., 2012) and the thickness of leaves (Spicer, 1989; Gastaldo, 2001). There are numerous other factors that can impact on the preservation potential of leaves in the plant fossil record and a summary of some of the key taphonomic filters is provided in Table 1. One factor that has not, to the best of our knowledge, been investigated for its effect on preservation potential of plant

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http://dx.doi.org/10.1016/j.palaeo.2015.12.006
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Please cite this article as: Bacon, K.L., et al., Can atmospheric composition influence plant fossil preservation potential via changes in leaf mass per area? A new hypothesis base..., Palaeogeogr. Palaeoclimatol. Palaeoecol. (2015), http://dx.doi.org/10.1016/j.palaeo.2015.12.006

Table 1
Summary of controls on plant fossil leaf preservation with selected references. This list is not meant to be exhaustive, but rather to provide a summary of some key references for some of the key taphonomic filters that are known to act on the plant fossil record.

Control	Comment	Selected references
Major controls — determines whether or not fossils may be preserved at a given time, in a given location		
Climate	Climate acts as the primary control on both plants (which types of plants grow in which climates), rates of decay, and sedimentation (rates and bedforms)	Bailey and Sinnott (1916) Gastaldo and Staub (1999) Gastaldo et al. (2005) Spicer (1989) Spicer et al. (2009)
Type of flora	Source flora will control the potential leaf rain to the local and regional area.	Burnham et al. (1992) Burnham et al. (2005) Greenwood (1991) Spicer (1989)
Environment of deposition	Potentially the most important filter on the leaf fossil record. Fine grained sediments more likely to preserve fossil leaves than thicker grained sediments, crevasse splay or catastrophic flooding events preserve more of the regional flora, well aerated sediments preserve fewer fossils due to bacterial decomposition.	Ferguson (2005) Gastaldo et al. (1987a, 1987b) Gastaldo and Demko (2011) Gastaldo (1989) Gastaldo et al. (1996) Gee (2005) Greenwood (1991) Spicer (1989)
Sedimentation rate at time of deposition	Greater sedimentation rates increase preservation potential.	Spicer (1989)
Minor controls (geological) — help to determine if a particular location is likely to preserve fossil leaves at a given time		
Bedform type	Deposition in more braided or fluvial bedform types decreases preservation potential. Deposition in flooded or crevasse splay beds increases preservation potential.	Ferguson (2005) Gastaldo (1989) Gastaldo et al. (2005) Spicer (1989)
Water table at time of deposition	High and stable water table increases likelihood of preservation.	Gastaldo (2001) Gastaldo and Demko (2011) Gastaldo (1994)
Pore-water chemistry	Controls rates of premineralisation and other geochemical effects.	Gastaldo and Demko (2011) Gastaldo (1994)
Charcoalification	Charcoalification by wildfires or volcanic activity increases preservation potential.	Scott (2001) Scott (2010) Spicer (1989)
Chemical alteration	Alteration by minerals (e.g. pyritisation, silicification, calcification etc) increases preservation potential.	Briggs (1999) Channing and Edwards (2003) Labe et al. (2012) Scott and Collinson (2003)
Development of microbial film	Development of a microbial film before or during fossilisation increases preservation potential.	Dunn et al. (1997) O'Brien et al. (2002)
Minor controls (biological) — helps to determine the likelihood of leaves of given taxa being preserved within a particular location at a particular time		
+Time of abscission of leaf	Abscission during the rainy season increases preservation potential due to higher water table and greater sedimentation rates.	Spicer (1989)
Distance travelled post abscission	Increasing distance travelled, particularly as part of river bedload, decreases preservation potential due to damage to leaf in transit.	Burnham et al. (1992) Ferguson (2005) Spicer (1989)
Size of leaf	Larger leaves are less likely to be preserved.	Greenwood (1991) Gastaldo (2001)
Thickness of leaf	Thicker leaves are more likely to be preserved. Sun leaves tend to be over-represented.	Gastaldo (2001) Spicer (1989)
Plant type	Plants that produce many small, thick leaves are more likely to have some leaves preserved than plants that produce thinner, larger leaves. Plants that do not abcise leaves have far less likelihood of being preserved in the fossil record. Leads to over- and under-representation of certain groups of plants in the fossil record.	Ferguson (1985) Ferguson (2005) Mander et al. (2010) Steart et al. (2005)
Chemical composition of the leaf	Leaves with greater lignin or other strength-enhancing components have a greater chance of preservation due to decreased rates of decomposition. Leaves with greater N content are likely to decompose faster.	Collinson et al. (1998) Briggs (1999) Ferguson (1985) Greenwood (1991) Retallack (2011) Spicer (1989) Van Bergen (2001) Witkowski et al. (2012)
Atmospheric composition	Leaves increase LMA/leaf thickness in higher CO_2 and lower O_2 atmospheres. This potentially acts as a second order taphonomic filter and increases (high CO_2 and or low O_2) or decreases (low CO_2) leaf preservation potential.	The current study

material in the fossil record is atmospheric composition at the time of leaf growth and deposition. Atmospheric composition has shifted dynamically throughout Earth history, and plants in turn have responded via morphological (Niklas, 1986; McElwain et al., 1999; Beerling et al., 2001; Beerling, 2005; Haworth et al., 2011; Bacon et al., 2013), ecophysiological (Boyce, 2009; Franks and Beerling, 2009; Steinthorsdottir et al., 2012; Haworth et al., 2014, 2015) and anatomical (Thomasson et al., 1986; Field et al., 2011; de Boer et al., 2012) adaptation. Here we ask, could functional adaptation to atmospheric composition in the past have influenced fossil leaf preservation potential?

Leaf mass per area (LMA) is an important functional trait of plants that expresses leaf dry-mass invested per unit of light-intercepting