

Why were dinosaurs so large? A food quality hypothesis

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ABSTRACT

Some dinosaurs, notably the sauropods, were the largest of all land animals, present or past. There is no generally agreed reason for this gigantism. We question the recent suggestion that this was due to high productivity, from high CO₂ concentrations, at the time of the dinosaurs. Instead, we suggest the reason for this large size was because typical Jurassic/Triassic plants, such as cycads and conifers, were of inherently low food quality (low nitrogen concentration). High CO₂ at the time of the dinosaurs would have resulted in an even lower food quality. Present-day megaherbivores are associated with relatively low-quality food-plants and we suggest this applied to sauropods.

Keywords: carbon dioxide, nutrients, sauropods.

INTRODUCTION

The biggest land animals of all time were the sauropods, such as *Argentinosaurus* and *Brachiosaurus*, which existed from the late Triassic and into the Cretaceous (Bakker, 1988; Burness *et al.*, 2002). The reasons for why they were so large, and so much larger than the largest terrestrial mammals, now or in the past, are still unresolved. Although Burness *et al.* (2002) reported a positive correlation between animal size (existing over the last 65,000 years) and available land area (e.g. island size), they noted that a greater extent of continuous land surface area would not explain the massive size of sauropods. Burness *et al.* (2002) and Maurer (2002) have recently argued that high CO₂ concentrations at the time of the dinosaurs would have increased plant productivity and this would have facilitated large size. We suggest this hypothesis ignores the critical issue of food quality, and also that the assumption of greatly enhanced primary productivity due to higher CO₂ concentrations may be flawed.

HERBIVORE DISTRIBUTION AND PLANT BIOMASS

It is widely accepted that the world is green (i.e. most plants are not cropped down to ground level by herbivores) because plant tissue quality is generally too low for consumption by contemporary animals (Jones and Hartley, 1986; White, 1993). Biomass

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tends to accumulate when the quality of food is low so that, presently, large mammalian herbivores tend to occur in areas of intermediate productivity (Olf *et al.*, 2002). Such areas have both sufficient quantity and quality of primary production to sustain megaherbivores (Olf *et al.*, 2002). The point is that high standing biomass is not directly correlated with large herbivore size. Food quality is an important factor and one which largely explains the absence of large herbivores in forests despite an abundance of apparent herbivore food.

Secondly, high concentrations of CO₂ pre-Tertiary would not necessarily have increased the productivity of herbivore food (e.g. foliage). The CO₂ fertilization effect is strongest in natural systems where light and nutrients are not limiting, particularly in open early successional stages with a low leaf area index. Thus, global primary productivity is likely to saturate at CO₂ concentrations far below those encountered pre-Tertiary (Scholes *et al.*, 1999), because other factors such as water and nutrients are limiting. Presumably, large sauropods had long necks to facilitate access to browse several metres off the ground. This suggests that a reasonable leaf area index existed during the time and thus that foliage production may not have been strongly influenced by high concentrations of CO₂.

MEGAHERBIVORES AND FOOD QUALITY

During the late Triassic and the Jurassic, a variety of conifers, as well as some ginkgoes, cycads, ferns and horsetails, would have constituted the main food plants of giant dinosaurs (Stewart, 1983; Bakker, 1993). Judged against present angiosperms and based on the nutrient content of contemporary non-angiosperms, dinosaur food plants would have had a low nitrogen concentration and high carbon:nitrogen ratios. Conifers (Becker, 2000), cycads (Marler and Willis, 1999) and ferns (e.g. Hietz and Briones, 2001) all have photosynthetic rates that are among the lowest in the contemporary world flora. Photosynthetic rates are strongly correlated with nitrogen concentration (Reich *et al.*, 1999) and thus food-value (Olf *et al.*, 2002). We suspect that Jurassic/Triassic food plants would thus have had a far lower average nitrogen concentration than the contemporary world flora. Among extant vertebrates, larger size is correlated with lower food quality (Owen-Smith, 1988; Olf *et al.*, 2002). We suggest that the even lower nutrient levels in the pre-angiosperm food plants of the late Triassic/Jurassic would have required the evolution of even larger size. We invoke this nutrient-quality hypothesis to explain the massive size of sauropods; they were large because they ate low-quality food.

Furthermore, not only were sauropod food plants, such as conifers and cycads, inherently low in nitrogen, but high CO₂ concentrations at the time would have effectively lowered their nitrogen content. It is well known that high CO₂ increases the carbon:nitrogen ratio in a wide range of plant types (e.g. Curtis, 1996). Also, high CO₂ may also have increased secondary compounds, effectively lowering food quality even further (e.g. Koricheva *et al.*, 1998).

Our nutrient concentration hypothesis allows a perspective on the still disputed topic of whether dinosaurs were endotherms (their gigantism presumably conferred warm-bloodedness). We find it unlikely that they were endotherms. The African elephant (3.9 tonnes), despite being largely a grazer (i.e. accessing relatively high-quality food) rather than a browser, spends about 80% of its waking day foraging (Owen-Smith, 1988). The largest terrestrial mammal, *Indricotherium* (an extinct 11 tonne Tertiary rhino; Burness *et al.*, 2002) must, therefore, by extrapolation, have been perpetually browsing. Thus it is unlikely that a significantly larger sauropod endotherm would have been able to have sufficient time to feed itself on a diet of significantly lower quality than is available today. We also suggest that the

low nutrient content of Triassic/Jurassic food must also have had an enormous impact on the nutrient budgets of juvenile sauropods, at least until they achieved the metabolic advantages of large size. Unlike the juveniles of most modern large herbivores, dinosaur young would not have had the crucial benefits of lactation. Were young brachiosaur hatchlings, after they emerged from eggs only 25 cm long, 'fed' regurgitated modified food ('milk') by parents, such as occurs in some herbivorous birds (White, 1993)? Did the juveniles partly have a carnivorous and or coprophagous diet? Marine iguanas currently begin life with this diet and only become fully herbivorous ectotherms when relatively large adults (White, 1993).

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