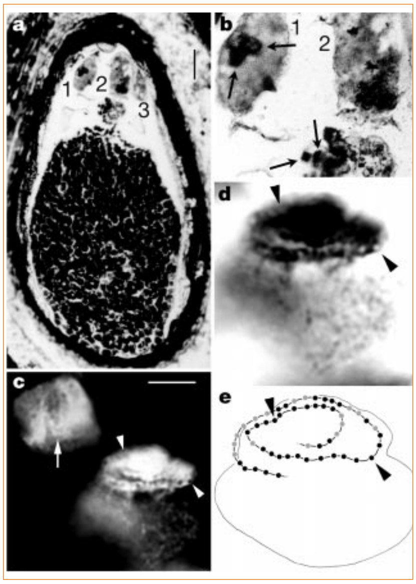

Figure 1 Fossil motile sperm in a Late Permian *Glossopteris* ovule. Specimens are housed at Chuo University, Tokyo. **a–d,** Light micrographs of specimen H397018 E_2lat., slide 5. **a,** Longitudinal section of the ovule, showing the megagametophyte (below) and three pollen tubes (numbered 1–3) in the pollen chamber (top). **b,** Enlarged view of pollen tubes 1 and 2. Top-left arrows indicate immature sperm in tube 1. Tube 2 (right) is ruptured basally and two motile sperm have been released (lower-right arrows; also evident are the contents of tube 2 and megagametophyte tissue). **c,** The two released sperm at higher magnification; image has been reversed to enhance detail. Arrow, multilayered helical structure represented by alignment of circular bodies; arrowheads, line of basal bodies. **d,** Detail of sperm on the right in **c**, showing the basal-body alignment (arrowheads). **e,** Schematic diagram of the same sperm, showing the positioning of the basal bodies (arrowheads). Scale bars, 100 μm (**a**, **b**) and 5 μm (**c**, **d**).

them each contain a pair of young sperm of immature morphology, and the fifth has been ruptured basally, evidently in the process of dispersing two mature sperm (Fig. 1b–d). No prothallial or sterile cells are evident.

One entire sperm is about 13.9 μm across, with a helical configuration that represents the multilayered structure upon which numerous basal bodies are inserted[4,5]. This structure is strikingly similar to the flagellate band of many living pteridophytes[6,7], *Ginkgo*[8] and cycads[9]. Part of a second sperm also has a spiral structure (Fig. 1c, left arrow). A single line of small dots occurs at roughly regular intervals (Fig. 1c, d, arrowheads), which are inferred to be basal bodies or the basal plate that connects the basal bodies to the flagella (Fig. 1e).

A mature *Glossopteris* sperm has 37 basal bodies, as determined by optical sectioning. A complete multilayered structure is estimated to be about 45 μm long with more than 50 basal bodies, each at a mean interval of 0.57 μm, which form two anticlockwise gyres (Fig. 1e). By contrast, *Ginkgo*'s multilayered structure reaches 300 μm in length, with 1,000 flagella on three gyres[4], whereas that of the cycad *Zamia*, one of the largest known plant sperm, is a helical band of 1,600 μm in length, with six gyres bearing several tens of thousands of flagella arranged in 8–12 rows at short intervals (0.1 μm; ref. 5).

Glossopteris sperm is therefore more similar in size to that of most other vascular plants, including pteridophytes (*Botrychium*, 10 μm, ref. 6; *Lycopodium*, 8–10 μm, ref. 7; *Equisetum*, 19.7 μm, ref. 7), conifers (*Torreya*, 13–19.5 μm; *Pinus*, 24 μm; *Thuja*, 35 μm; ref. 10), gnetophytes (*Ephedra*, 16 μm; ref. 10) and angiosperms (*Hordeum*, 11.7 μm; ref. 11). Only the putative sperm found in fossil medullosans are comparable in size to those of cycads, to which they are often allied, and whose sperm are unusually large[9,12].

The pollen tube of *Glossopteris* differs from the highly branched, haustorial pollen tubes of both *Ginkgo* and cycads, as well as from the longer, sparsely branched or unbranched siphonogamous pollen tubes of *Callistophyton*, conifers, bennettitaleans[13] and angiosperms. *Glossopteris* pollen tubes are the simplest known among vascular plants. They are slightly elongated, unlike in the fossil medullosan ovule *Pachytesta*, where mature sperm inside the pollen protoplast apparently did not elongate to form a pollen tube[12] — a type of structure that has been interpreted as an early stage in the evolution of pollen tubes[12]. Together, our findings indicate that *Glossopteris* had a very simple mode of reproduction that was more similar to that of cycads and *Ginkgo* than to those of other extant seed plants.

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COMMUNICATIONS ARISING

Ecology

Is fertilization efficiency misleading?

Given the need to increase crop production in the future while minimizing any associated impact on the environment, it is important to understand the relationship between global crop production and fertilization. Tilman *et al.*[1] argue that fertilization beyond current levels is unlikely to increase crop yields (production per unit area) as effectively as in the past, due to diminishing returns. However, their evidence is misleading and does not support their conclusions. Diminishing returns are not readily apparent on a global scale.

Figure 2 of Tilman *et al.*[1] shows trends in global cereal yield and 'nitrogen-fertilization efficiency' (defined as production per unit mass of nitrogen-fertilizer consumption) from 1961 to 1996. In the figure, nitrogen-fertilization efficiency plummets over time while yield climbs relatively linearly, presumably as fertilization increased over this period (verified here using data from the United Nations Food and Agriculture Organization). The figure seemingly supports the authors' statements, such as "further increases in nitrogen and phosphorus application are unlikely to be as effective at increasing yields (Fig. 2a) because of diminishing returns (Fig. 2b)". However, the response depicted in their Fig. 2b is a mathematical artefact of the relationship between crop yield and fertilizer-application rate (mass per unit area), and so does not support the authors' conclusions.

In fertilizing crops, the ideal response would be one in which a given increase in fertilizer-application rate leads to a constant increase in crop yield or, identically, a given increase in total fertilizer application leads to a constant increase in production. This ideal system, in which the effectiveness of fertilization does not decline as fertilizer use increases, is mathematically represented by $p = af + b$ (where p is the crop production, f is the amount of fertilizer applied, a is the slope of the response and b is the production in the absence of fertilizer).

With this linear response, the nitrogen-fertilization efficiency is represented by $p/f = a + b/f$, and so is inversely proportional to f. As f approaches zero, this efficiency approaches infinity, and declines as f increases, tending towards the value of a. This behaviour is quantified by the derivative of fertilization efficiency, namely $-b/f^2$. Thus, even when a crop shows an ideal response to fertilization, fertilization efficiency declines (Fig. 1).

It seems that global cereal production has followed the linear relationship described above, and has not shown dimin-

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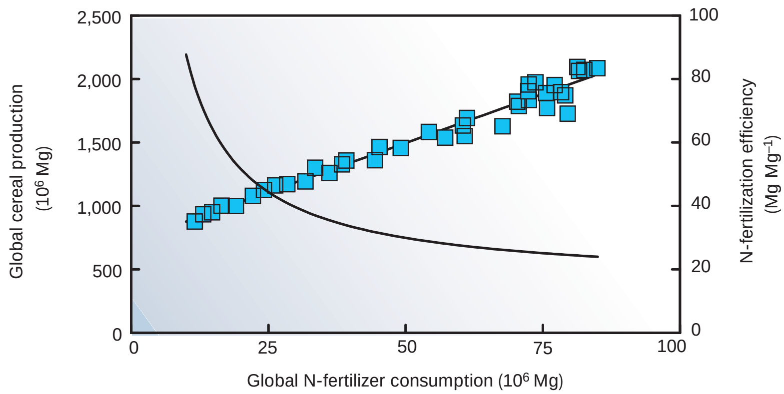

Figure 1 Regression between global cereal production and nitrogen-fertilizer consumption, showing a relatively constant increase in production per unit increase in fertilizer use, and no evidence of diminishing returns. Boxed points are actual data (from the United Nations Food and Agriculture Organization 2002; http://apps.fao.org); the thin line ($P = 15.47f + 722.3$) is the result of a regression of production on fertilizer consumption. Even within this linear relationship, nitrogen-fertilization efficiency (calculated by dividing the regression line by fertilizer consumption; thick line) declines as fertilizer consumption increases.

ishing returns from fertilization (Fig. 1; data from the United Nations Food and Agriculture Organization). The term 'diminishing returns', which was first used in relation to agricultural productivity[2,3], describes a decline in the marginal output, or the increase in output per unit change in input, when the level of a variable input is increased[4], rather than a decline in the ratio of output to input. 'Nitrogen-fertilization efficiency', as calculated by Tilman *et al.*[1], is not a useful way to represent the effectiveness of fertilization.

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Tilman et al. *reply* — An important question that arises from Hafner's comment is why global crop production[1] should appear to be a linear function of global nitrogen fertilization, even though crop production has consistently shown diminishing returns from increased fertilization in field trials[2–4]. Although we concur that our Fig. 2b does not unambiguously demonstrate diminishing returns, evidence based on data from the United Nations Food and Agriculture Organization indicate that global crop production and yield[5] do indeed show diminishing returns for increased fertilization.

Crop responses to nitrogen fertilizer are expected to exhibit diminishing returns because yields may be limited simultaneously by the availability of light, water, nitrogen and the other essential nutrients. As nitrogen fertilizer is added to alleviate nitrogen deficiency, other resources will then become limiting, causing the crop's response to nitrogen to diminish[6]. Moreover, nitrogen losses increase with increased nitrogen application because surplus inorganic nitrogen (NO_3^- and NH_4^+) in the root zone is leached into the groundwater or lost to the atmosphere in gaseous form.

Hafner's univariate analysis ignores other agricultural inputs, particularly irrigation, that change simultaneously with increasing nitrogen fertilization. It is more appropriate to determine the dependence of global crop production (cereals, coarse grains and root crops) and global crop yield (production divided by global land dedicated to these crops) on global nitrogen fertilization while controlling for global irrigation.

In tests for a nonlinear (saturating) effect of nitrogen fertilization (J. Fargione *et al.*, unpublished results), one using global rates of production, fertilization and irrigation per hectare, and the other using production, fertilization and irrigation per hectare, we found a significantly saturating effect of nitrogen fertilization. Multiple regression of yearly global crop production on irrigation and nitrogen fertilization revealed a significant positive linear effect of irrigation ($F_{1,36} = 56.9$, $P < 0.0001$) and a simultaneous saturating (quadratic) effect of nitrogen fertilization. The nitrogen effect had a significantly positive linear ($F_{1,36} = 13.8$, $P = 0.0007$) and a significantly negative quadratic ($F_{1,36} = 7.23$, $P < 0.018$) term for 1961–2000. The negative quadratic term in the fitted model gave a curve for the dependence of global crop production on nitrogen fertilization that approached its peak at current global rates of nitrogen fertilization.

A multiple regression of global crop yield (production per hectare) on global irrigation per hectare and on global nitrogen fertilization per hectare also indicated diminishing returns (J. Fargione *et al.*, unpublished results). Global crop yield increased with irrigation per hectare ($F_{1,36} = 64.2$, $P < 0.0001$) but was a saturating function of fertilization per hectare, with a positive linear term ($F_{1,36} = 13.4$, $P = 0.0008$) and a negative quadratic term ($F_{1,36} = 4.36$, $P = 0.044$) for this 40-year period. The fitted curve for yield approached its peak at current global rates of nitrogen fertilization. Twenty-two similar analyses for each of 11 periods from 1961 through to each year from 1990 to 2000 also revealed significantly diminishing returns.

Although multiple regressions that use collinear variables cannot demonstrate causal relationships unambiguously, and although we did not control for improved crop varieties, it is likely that there have been diminishing returns of increased global nitrogen fertilization at least since 1990. If this is the case, other technologies (see ref. 7, for example) may help to increase global crop yields; indeed, the United States' maize yield increased by almost 40% from 1980–2000 without any increase in nitrogen fertilization[6]. Plant breeding, biotechnology and advances in crop and soil management will probably account for most of the future increases in global crop production, without the negative environmental effects that are attributed to nitrogen fertilizers.

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