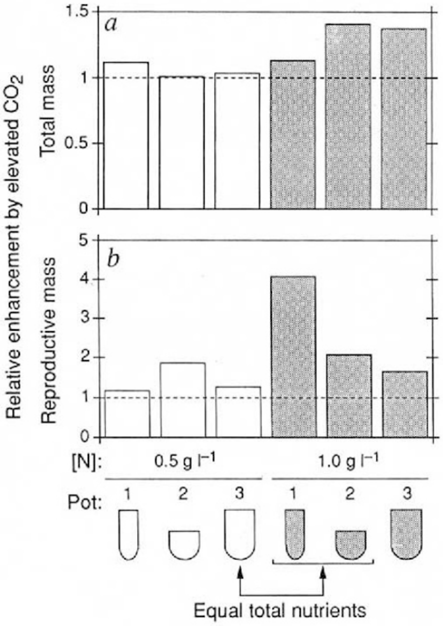
Plant responses to carbon dioxide

SIR — There have been several reports suggesting that non-field-based studies of plant responses to elevated atmospheric CO_2 may be compromised because small rooting volumes limit a plant's ability to respond to elevated CO_2 (refs 1–3). This hypothesis calls into question most of our present knowledge of vegetation responses to elevated CO_2, and is not supported by new evidence (K. D. M. McC., G. M. B. and F. A. B., manuscript submitted).



CO_2-induced growth enhancement of *Abutilon theophrasti* Medic. (elevated/ambient dry mass) as a function of pot size, shape and nutrient concentration. *a*, Total dry mass enhancement before fruit maturation; *b*, reproductive dry mass enhancement immediately after fruit maturation. Pots were 0.65 l (tall and narrow & short and wide pots) or 1.30 l in volume; nutrient concentrations were 0.5 g l^{-1} or 1.0 g l^{-1} of a balanced N–P–K fertilizer added to each pot every 3 days in sufficient amount to displace the soil solution present. Large pots of low nutrient concentration and small pots of high nutrient concentration received equal total nutrients (K. D. M. McC., G. M. B. and F. A. B., manuscript submitted).

Elevated CO_2 atmospheres stimulate photosynthesis (and growth) when photosynthetic products (sugars and starches) are used at a sufficient rate[4]. Plants grown in small pots have restricted root growth and thus reduced photosynthate demand[1,3]. However, a reduction in photosynthesis is not a necessary outcome of root restriction; photosynthetic rates may increase or not change.

Arp[1] reviewed published values of CO_2-induced photosynthetic enhancement, concluding that non-field-based studies suffer from root restriction and are thus unreliable tests of vegetation responses in the field. However, he did not examine correlations between the photosynthetic rates and aspects of nutrient supply, which can decrease with pot size.

In one of only two studies that directly examined the effects of pot size on CO_2 responsiveness, cotton (*Gossypium hirsutum*) grown in small pots had less CO_2-induced photosynthetic enhancement[3]. CO_2-induced growth enhancement was greatest in small pots, however. Leaf starch and sucrose contents were unaffected by pot size but were greater for high CO_2-grown plants in both small and large pots. The authors did not examine whether reduced nutrient supply, a function of soil volume, may have caused or contributed to the reduced photosynthesis.

We have examined the influence of both physical rooting space and soil nutrients (K. D. M. McC., G. M. B. and F. A. B., manuscript submitted). CO_2-induced growth and reproductive output enhancement are greatest in pots with greater nutrient concentrations, regardless of pot volume or total nutrient content (see figure). Enhancement of reproductive output is greater in plants growing in smaller volumes, particularly when the nutrient concentration within the pot was high. Remarkably, pot shape *per se* also influences growth and reproductive enhancements.

These results bear on the potential limitations to CO_2 enhancement in pot studies in two ways. First, small pots do not necessarily limit CO_2 responsiveness; they may not affect it or they may increase it. Second, CO_2 responsiveness is dependent on many aspects of growth conditions within pots, especially nutrient concentration and the physical dimensions of the pot.

The suggestion that small pots limit the CO_2 responsiveness of plants is compelling, but not supported, and it is premature to abandon decades of non-field-based research. Furthermore, plants in the field do not have unlimited below-ground resources with which to maximize growth in a CO_2-rich world. It would be risky to devise policies based on the presumption that the CO_2 fertilization effect will be sustained indefinitely in natural systems.

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A palatal rete in the right whale?

SIR — It has recently been suggested by Ford and Kraus[1] that the palate of the right whale (*Eubalaena glacialis*) possesses a previously undescribed vascular rete that has a thermoregulatory function. A rete is a specialized complex network of fine arteries and/or veins. Ford and Kraus suggest that right whales (Balaenidae) can dump heat by opening the mouth and allowing a flow of cold water over the hard palate. We find several potential flaws with this interpretation.

The right whale is not unique in having a highly vascularized palate. The palate of most mammals has a rich blood supply including arterial anastomoses and a venous plexus[2–4]. In all baleen whales the palate contains numerous small blood vessels and nerves associated with the formation of baleen that these whales use for filter feeding. This observation in rorqual whales (Balaenopteridae) previously led to the speculation that the palate may function in thermoregulation[5]. Our gross observations of the right whale suggested only a typical baleen whale vascular palate, not a unique rete system. We find no morphological evidence in Ford and Kraus's report that right whales possess a true specialized rete. It is also not clear how mechanoreceptors function directly in thermoregulation as proposed by these authors. Mechanoreceptors are probably involved in detecting water flow through the mouth and over the baleen as these whales feed.

Several additional aspects of the morphology and behaviour of right whales do not support the hypothesis that the palate functions to dump body heat. The palate of right whale is long, but extremely narrow. Therefore, the surface area is relatively small, especially when compared to other baleen whales. In addition, the palatal surface would be exposed to a flow of water only when the mouth is open. This occurs as right whales engage in skim feeding, but this species primarily feeds in higher lati-

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