brief communications

tures have so far been adequately demonstrated in *T. weissflogii*.

Considering first the nature and location of the carboxylase and decarboxylase, Reinfelder et al. suggest¹ that the significance of PEP carboxylase in diatoms may have been missed because of lack of carbon limitation during cell culture. In many studies, however, the dissolved CO₂ concentration was probably the least well controlled growth condition⁴, particularly for enzyme assays in which the requirement for algal biomass outweighed other considerations. Earlier reports of PEP carboxylase activity in diatoms were probably due in fact to PEP carboxykinase activity^{5,6}. The PEP carboxylase activity found by Reinfelder et al. in the chloroplast (53% of total) in the Percoll-purified chloroplast fraction of T. weissflogii¹, and the finding of 22% Rubisco activity in the soluble fraction, suggest considerable cross-contamination of the preparations, which would cast doubt on the localization of PEP carboxykinase.

Reinfelder *et al.* also base their conclusions on ¹⁴C-tracer kinetics. The shortest labelling time they observed using ¹⁴C is 5 s, with much higher labelling of malate than has previously been found in diatoms⁵. However, even the 65% labelling by ¹⁴C they report in the C₄ (β-carboxyl) position of malate is not sufficient to justify designation as C₄ biochemistry because secondary carboxylation of labelled PEP, arising from labelled phosphoglycerate generated by Rubisco, can occur.

One crucial diagnostic test for C4 biochemistry is whether the label on malate extrapolates back to 100% at time zero. However, the two points provided in the data of Reinfelder *et al.*¹ are insufficient to establish a time course. The brown seaweed Ascophyllum nodosum (Phaeophyceae) is closely related to diatoms: it has a similar C₄-like photosynthetic physiology⁷ and shows significant ¹⁴C-labelling of C₄ compounds⁸. But under conditions of inorganic-carbon saturation (sea water), the initial ¹⁴C-incorporation product after 1-2 s of photosynthesis is phosphoglycerate⁷. Also, C4 plants that use PEP carboxykinase as their decarboxylating enzyme use aspartate⁹ rather than malate¹ as a substrate.

The finding that phosphoglycerate is the first product of carbon fixation in photosynthesis by *Ascophyllum*⁷ and by various diatoms⁶ suggests that heterokont algae photosynthesize using a C₃ pathway and that synthesis of C₄ compounds using β -carboxylases (mainly, if not exclusively, PEP carboxykinase) has a ubiquitous anaplerotic role in these organisms. The increased labelling of C₄ compounds relative to phosphoglycerate under conditions of low inorganic carbon is also seen when growth rate is limited by (non-carbon) nutrients or by light⁶. Invoking a role for C_4 photosynthesis to explain the physiological properties and ¹³C-discrimination values of diatoms seems unnecessary, given the capacity of such cells to accumulate inorganic carbon and hence CO_2 by means of the biophysical CO_2 concentrating mechanism — a process for which there is a large amount of evidence^{6,7,10}. Until these issues are unequivocally resolved and the other features of C_4 photosynthesis are demonstrated, we believe that it is premature to designate marine diatoms as C_4 photosynthesizers in the traditional sense.

Andrew M. Johnston*, John A. Raven†, John Beardall‡, Richard C. Leegood§

*Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, UK

e-mail: ajohns@scri.sari.ac.uk

Biological Sciences Institute, University of Dundee,
Millers Wynd, Dundee DD1 4HN, UK
Department of Biological Sciences, Monash
University, Clayton, Victoria 3800, Australia
Spepartment of Animal and Plant Sciences,
University of Sheffield, Sheffield S10 2TN, UK
Reinfelder, J. R., Kraepiel, A. M. L. & Morel, F. M. M. Nature

- Reinfelder, J. R., Kraepiel, A. M. L. & Morel, F. M. M. Nature 407, 996–999 (2000).
- 2. Riebesell, U. Nature 407, 959-960 (2000).
- Badger, M. R. & Spalding, M. H. in *Photosynthesis: Physiology* and *Metabolism* (eds Leegood, R. C., Sharkey, T. D. & von Caemmerer, S.) 369 (Kluwer Academic, Dordrecht, 2000).
- Johnston, A. M. & Raven, J. A. Marine Ecol. Prog. Ser. 87, 517–521 (1992).
- Beardall, J., Mukerji, D., Glover, H. E. & Morris, I. J. Phycol. 12, 409–417 (1976).
- 6. Beardall, J. Aquat. Bot. 34, 105–130 (1989).
- 7. Johnston, A. M. Can. J. Bot. 69, 1123-1132 (1991).
- Johnston, A. M. & Raven, J. A. *Phycologia* 26, 159–166 (1987).
 Sage, R. F. & Monson, R. K. (eds) C₄ Plant Biology 596 (Academic, San Diego, 1999).

10. Raven, I. A. Adv. Bot. Res. 27, 85–209 (1997)

Reinfelder et al. *reply* — Johnston *et al.* are not convinced that a C_4 photosynthetic pathway exists in microalgae. The essential feature of C_4 photosynthesis is the fixation of inorganic carbon as a C_4 compound that is subsequently decarboxylated to provide CO_2 as a substrate for Rubisco in the Calvin cycle. It is known that many microalgae incorporate at least some inorganic carbon directly into C_4 compounds such as malate, but the controversy hinges on whether this carbon is released and fixed by Rubisco.

The extrapolation of ¹⁴C incorporated into the C4 position of malate to 100% at time zero, which is proposed as a crucial diagnostic test by Johnston et al., is thus not a direct verification of C4 photosynthesis. It would be experimentally difficult to determine and is not mathematically well defined — for example, this approach yields an intercept of only 89% in maize, a well-known C₄ plant¹. A better demonstration is provided by the transfer of ¹⁴C from the C₄ compound malate to the C₃ compound phosphoglycerate, the first product of Rubisco, as we have shown. Also, we have recently found (unpublished results) that addition of the C4 compound oxaloacetate to compensated cultures of *T. weissflogii* triggers immediate production of O_2 in the light, but no O_2 consumption in the dark, which further supports our proposal that this diatom uses C_4 photosynthesis.

Johnston *et al.* also comment on the substrate of PEP carboxykinase and the localization of enzymes. However, oxalo-acetate, which is the substrate for PEP carboxykinase, can be produced by oxidation of aspartate or malate. We agree that cellular-fractionation techniques cannot definitively establish how the enzymes of a photosynthetic C_4 pathway are compartmentalized — so far, fractionation results have been confirmed by other techniques in the case of carbonic anhydrase, which has been shown to be located in the cytoplasm of *T. weissflogii* using antibodies.

There is strong evidence that marine diatoms can concentrate inorganic carbon for photosynthesis^{2,3}, but little to indicate how such a mechanism might work. C_4 pathways are used to accomplish this in multicellular C_4 plants and so may serve the same function in marine diatoms.

John R. Reinfelder

Department of Environmental Sciences, Rutgers University, 14 College Farm Road, New Brunswick, New Jersey 08901-8551, USA

e-mail: reinfelder@envsci.rutgers.edu

- Hatch, M. D. & Osmond, C. B. in *Encyclopedia of Plant* Physiology Vol. 3 (eds Stocking, C. R. & Heber, U.) 144–184 (Springer, Berlin, 1976).
- 2. Raven, J. A. Adv. Bot. Res. 27, 85-209 (1997).
- Tortell, P. D., Rau, G. H. & Morel, F. M. M. Limnol. Oceanogr. 45, 1485–1500 (2000).

Aerodynamics

Insects can halve wind-turbine power

For no apparent reason, the power of wind turbines operating in high winds may drop, causing production losses of up to 25 per cent¹. Here we use a new flowvisualization technique to analyse airflow separation over the blades and find that insects caught on the leading edges in earlier low-wind periods are to blame. These potentially catastrophic power glitches can be prevented simply by cleaning the blades.

Unpredictable changes in power levels have been noted on wind farms in California, with power sometimes falling to half the output predicted from the turbine design and generating two or more different power levels at the same wind speed (Fig. 1a). Although this phenomenon (termed 'double' or 'multiple' stalling) has been investigated^{2–4}, the cause has remained unknown.

One study⁵ commissioned by a turbine manufacturer (NEG Micon) used a new invention called a stall flag⁶ (patent, Energy Centre of The Netherlands) as a flow-

brief communications

separation detector (Fig. 1b) to try and solve the problem. This device works on the principle of a hinged flap that opens up in a separated airflow to uncover an individual reflector (Fig. 1c) which allows the flow to be visualized. Operation of a stall flag on a turbine with a rotor diameter of 44 metres is illustrated in Fig. 1d, in which the light tracks are from exposed reflectors and indicate where the blades stall.

We found that the stalling behaviour of the blades depends on the degree of contamination of the leading edges. However, the reduction in power should be continuous (as debris on the blades would be expected to accumulate gradually) rather than stepped in distinct levels as shown in Fig. 1a.

We considered the possibility that flying insects caught on the turbine blades could explain this effect. Insects prefer to fly in conditions of high air humidity, low wind and temperatures above about 10 °C. Under these circumstances, they will increasingly foul the leading edges of the blades. In low winds, the incident angle between the flow and the blades is small, which corresponds to low air velocity around the leading edges, so the blade is not susceptible to contamination of the leading edge and the power output is unaffected. Insects rarely fly in high winds, so turbines operating in steady high-wind conditions do not become contaminated and power levels remain constant.

In high winds, however, the angle between the flow and the blades increases and the aerodynamic suction peak (the area of minimum pressure and maximum air velocity) shifts to the leading edge. If this happens to be already spattered with dead insects, power output will fall: the greater the contamination at the suction peak, the sooner the blades will stall and the more lift will be lost (Fig. 1e). Thus after each period of low wind, the amount of insect contamination may change, causing a different power level to be produced in high wind.

We verified this hypothesis experimentally by using stall flagging to compare airflow over smooth blades with that over blades that had been artificially roughened on their leading edges (by installing a zigzag tape of maximum thickness 1.15 mm). The two turbines used were within 50 metres of each other to ensure equal inflow (Fig. 1f). A 25-Hz digital video camera recorded the stall-flag signals, providing thousands of computer-processed images which indicated that flow separation on the roughened blades was significantly increased at wind speeds of $11-25 \text{ m s}^{-1}$. This effect extended over the entire blade span, which explains the previously observed power losses (Fig. 1a). Moreover, power output from roughand smooth-bladed turbines was equal at low wind speeds, but higher from the 'clean' blades at high wind speeds (Fig. 1g), neatly reproducing the effect shown in Fig. 1a.



Figure 1 Insects cause multiple levels of power output from wind turbines. **a**, Example of production of two or more power levels at the same wind speed on different dates. **b**, The stall flag, consisting of a hinged flap and a reflector. **c**, Stall flags, showing the separated-flow area on an aerofoil. **d**, Recording of stall-flag signals from the NEG Micon turbine in California. The light tracks are produced by reflected light from open stall flags. **e**, Illustration of the insect hypothesis proposed to explain multiple power levels. **f**, The two turbines used for validation of the insect hypothesis; these were only 50 m apart to ensure equal air inflow. **g**, Power curves for the two turbines with 'rough' or 'clean' blades, which are similar to those in **a**.

We also studied a time series for the power output from four different turbines and found that the power at high wind speeds decreased markedly after every period of low wind speed, rising again after the blades were cleaned either manually or by rain, as expected. It is likely that accumulation of ice or dirt on the blades could create distinct power levels in high winds in the same way as insect contamination.

Gustave P. Corten*, Herman F. Veldkamp†

*Unit of Wind Energy, Energy Centre of The Netherlands, PO Box 1, 1755 ZG Petten, The Netherlands e-mail: corten@ecn.nl †NEG Micon A/S, Alsvej 21, 8900 Randers, Denmark

 Madsen, H. A. Aerodynamics of a Horizontal Axis Wind Turbine in Natural Conditions (Risø-M, Denmark, 1991).

- Dyrmose, S. Z. & Hansen, P. The Double Stall Phenomenon and How to Avoid It (IEA Joint Action Aerodynamics of Wind Turbines, Lyngby, 1998).
- Snel, H. et al. Progress in the Joule Project: Multiple Stall Levels (EUWEC Proc., Nice, 1999).
- 4. Bak, C. et al. Wind Energ. 2, 195–210 (1999).
- Corten, G. P. Insects Cause Double Stall (13th IEA Expert Meeting on the Aerodynamics of Wind Turbines, Stockholm, 1999).
- Corten, G. P. Flow Separation on Wind Turbine Blades. Thesis, Univ. Utrecht (2001).

correction

Thin solid films roll up into nanotubes O. G. Schmidt, K. Eberl

Nature 410, 168 (2001)

Citation of additional earlier work by Prinz *et al.* (for example, see ref. 1) relating to these results was inadvertently omitted.

 Prinz, V. Ya. et al. Inst. Phys. Conf. Ser. 166 Ch. 4, 199–202; 203–206 (2000).