

is known, at least in platelets, to activate protein kinase C¹². The synergistic effects of increase in free intracellular calcium and the calcium-independent activation of protein kinase C have been clearly demonstrated in the platelet^{13,14} and it is this kinase, of course, that is activated by and appears to be a receptor for tumour promoters such as tetradecanophorbol acetate (TPA)¹⁶. It is an attractive notion that synergism between calcium-dependent and calcium-independent events may be a general feature of cellular control.

The critical question still remains: does the breakdown of phospholipid *in vivo* precede and control the elevation of intracellular calcium or are the responses essentially independent? The extreme rapidity of the ITP increase in blow-fly salivary gland, which clearly precedes an increase in ⁴⁵Ca²⁺ flux across the cell, is consistent with the former, but in this tissue only PI-4,5-bisphosphate is hydrolysed by a PI phosphodiesterase and hydrolysis of the other phosphoinositides is contingent upon their previous conversion to the bisphosphate. In other cells, for example, 2H3 basophils¹¹, however, each of the phosphoinositides appear to act as substrates for one or more PI phosphodiesterases. In these cells a large increase in intracellular calcium, measured by the fluorescent indicator quin 2, is maximal within three minutes of stimulation, by which time there is only a small increase in the level of ITP. The levels of all of the inositol phosphates continue to rise thereafter, even though the free calcium concentration actually falls. In 2H3 cells therefore, the evidence that ITP regulates calcium looks much less convincing than in the salivary gland. The fact remains that although the calcium signal can be inhibited in 2H3 cells without affecting PI stimulation, the converse requirement, necessary to confirm independent

mechanisms, has not been demonstrated. Comparison of the kinetics of calcium and PI responses in different cell systems has not revealed any consistent patterns, perhaps simply reflecting phenotypic variation in the extent to which calcium-independent or calcium-dependent events predominate during stimulation. The final resolution of the relationship between PI and intracellular calcium levels will

probably need to wait for the production of specific inhibitors of the PI cycle.

If ITP does eventually turn out to be the 'missing link' between PI stimulation and calcium, as Streb and his colleagues suggest, the relief will be great, not only from those who have stuck to PI through thick and thin but also from those of us who simply want to know how calcium signals are generated. □

Ecology

Ecological diversity and stress

from Peter D. Moore

EVIDENCE for the notion that ecological systems are most diverse when they are subjected to a certain degree of stress is now being accumulated from a wide range of habitats. Stress can take the form of a physical limitation to overall productivity or of a degree of disturbance which prevents the assumption of dominance by certain aggressive or highly productive species. The principle has been stated in various ways¹⁻⁴ and has been illustrated in habitats as diverse as terrestrial grasslands and intertidal zones. In two recent studies, sites were artificially manipulated to introduce various forms of stress and the effect monitored. The results ably illustrate the complexity of competitive interactions in plant communities.

One of the studies was conducted in sub-alpine meadows on the high slopes of the Olympic Mountains in the western United States⁵. In these grasslands, overall productivity is related to such factors as soil nutrients, moisture and temperature. Diversity (measured by the Shannon-Wiener index *H'*) shows maximum values where there is moderate stress and thus where total productivity is sub-optimal.

Transplant experiments were used to reveal the role of competition in the reduction of diversity in the most mesic conditions. It was found that species transplanted from high-diversity sites to highly productive sites generally survived well if surrounding plots were cleared of competitors, but succumbed rapidly if the plots were uncleared. Seedlings were particularly sensitive to competition.

Certain species were then selectively removed by clipping and the reaction of the remaining plants monitored. The effects of removal of the dominant species were most marked in the more productive (less stressful) habitats. Occasionally the removal of one dominant, such as the sedge *Carex spectabilis*, simply permitted another plant to assume dominance, such as the grass *Festuca idahoensis*, often with a higher resultant productivity. Nutrient additions simply served to enhance the dominance of the most competitive species, where such a species was forthcoming, and hence reduce diversity further. These findings are in keeping with the ideas of Grime⁴ and of

Tilman⁶ who proposed that decreasing nutrient supply leads to increasing species richness until the point is reached where nutrients become limiting to the survival of coexisting species.

A comparable situation exists when the stress upon the plant community is due to grazing pressures. Paine⁷ proposed a concept of 'keystone species' in which the keystone is a predatory species which controls the population density of its prey and may thus prevent it from dominating a community through appropriating an undue share of resources. Hixon and Brostoff⁸ have now described a more complex situation in which a predatory damselfish which inhabits Hawaiian coral reefs controls the populations of herbivorous fish which in turn influence the algal components of the reef ecosystem. The relationships were examined by placing artificial settling surfaces in three types of site: within damselfish territories, outside territories and in fish-exclusion cages. After a year, the greatest algal diversity (*H'*) was found inside the damselfish territories and the lowest outside; caged samples were intermediate in diversity. Thus a high grazing intensity and an absence of grazing both resulted in lower algal diversities than intermediate grazing levels where damselfish controlled the population of grazing fish.

In effect, the grazing stress here is equivalent to the nutrient stress in the montane grasslands: increasing stress restricts the tendency for resources to be channelled into certain potentially dominant species and thus increases community diversity up to the point where tolerance limits of the more sensitive species are reached and extinctions commence. As far as diversity is concerned, a little stress can go a long way. □

Peter D. Moore is Senior Lecturer in Plant Sciences at King's College, 68 Half Moon Lane, London SE24 9JF.

Robin Hesketh is a lecturer in the Department of Biochemistry, University of Cambridge, Tennis Court Road, Cambridge, CB2 1QW.

1. Michell, R.H. *Biochim. biophys. Acta* **415**, 81 (1975).
2. Hokin, M.R. & Hokin, L.E. *J. Biol. Chem.* **203**, 967 (1953).
3. Michell, R.H., Kirk, C.J., Jones, L.M., Downes, D.P. & Creba, J.A. *Phil. Trans. R. Soc. B* **296**, 123 (1981).
4. Kirk, C.J., Creba, J.A., Downes, C.P. & Michell, R.H. *Biochem. Soc. Trans.* **9**, 377 (1981).
5. Creba, J.A., Downes, C.P., Hawkins, P.T., Brewster, G., Michell, R.H. & Kirk, C.J. *Biochem. Soc. Trans.* **9**, 377 (1981).
6. Weiss, S.J., McKinney, J.S. & Putney, J.W. *Biochem. J.* **206**, 555 (1982).
7. Siess, W. & Lapetina, E.G. *Biochim. biophys. Acta* **752**, 329 (1983).
8. Serhan, C.H., Broekman, M.J., Korchak, H.M., Smolen, J.E., Marcus, A.J. & Weissmann, G. *Biochim. biophys. Acta* **762**, 420 (1983).
9. Berridge, M.J. *Biochem. J.* **212**, 849 (1983).
10. Berridge, M.J., Dawson, R.M.C., Downes, C.P., Heslop, J.P. & Irvine, R.F. *Biochem. J.* **212**, 473 (1983).
11. Beaven, M.A., Moore, J.P., Smith, G.A., Hesketh, T.R. & Metcalfe, J.C. (in preparation).
12. Nishizuka, Y. *Trends in Biochem. Sci.* **8**, 13 (1983).
13. Michell, R.H. *Trends in Biochem. Sci.* **8**, 263 (1983).
14. Castagna, M., Takai, Y., Kaibuchi, K., Sano, K., Kikkawa, V. & Nishizuka, Y. *J. Biol. Chem.* **257**, 7847 (1982).
15. Rink, T.J., Sanchez, A. & Hallam, T.J. *Nature* **305**, 317 (1983).
16. Yamanishi, J., Takai, Y., Kaibuchi, K., Sano, K., Castagna, M. & Nishizuka, Y. *Biochem. biophys. Res. Commun.* **112**, 778 (1983).

1. Connell, J.H. *Science* **199**, 1302 (1978).
2. Grime, J.P. *Plant Strategies and Vegetation Processes* (Wiley, 1979).
3. Grime, J.P. *Am. Nat.* **111**, 1169 (1977).
4. Grime, J.P. *Plant Strategies and Vegetation Processes* (Wiley, Chichester, 1979).
5. del Moral, R. *Am. J. Bot.* **70**, 232 (1983).
6. Tilman, D. *Am. Nat.* **116**, 362 (1980).
7. Paine, R.T. *Am. Nat.* **100**, 65 (1966).
8. Hixon, M.A. & Brostoff, W.N. *Science* **220**, 511 (1983).