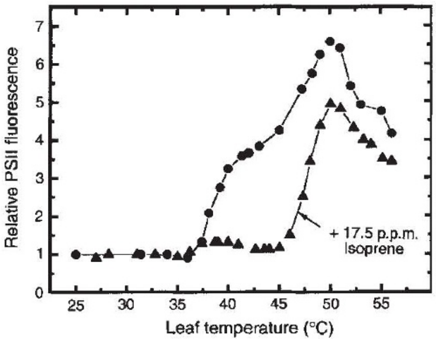
Why plants emit isoprene

SIR — Global emission of isoprene (2-methyl-1, 3-butadiene) from vegetation is estimated at 3×10^{14} g yr^{-1}, similar to methane[1]. Because isoprene reacts very rapidly with hydroxyl radicals, it plays an important role in atmospheric chemistry[2–4]. Why plants emit isoprene has been a mystery since Sanadze[5] first discovered the phenomenon in the 1950s.

Isoprene is emitted from many but not all plants. It is dependent upon photosynthesis and typically accounts for 2% of photosynthesized carbon at 30 °C in aspen and oak trees[6,7]. Darkness, inhibitors of photosynthesis, or an atmosphere of pure N_2 will stop isoprene emission. Isoprene emission is much more sensitive to temperature than is photosynthesis. Over short periods of time, isoprene emission can increase as much as tenfold with a 10 °C increase in leaf temperature[8]. Plants grown at 20 °C or less do not emit isoprene until induced by treatment at 30 °C for 4 to 6 h. Water stress, which is often accompanied by high temperature stress, also induces plants to make isoprene[8]. These observations led us to consider whether isoprene synthesis helps plants cope with high temperature.

Isoprene provided thermal protection in a range of conditions, including darkness. We found the greatest degree of thermal protection when leaves were exposed to 1,000 μmol m^{-2} s^{-1} photons (half of sunlight) and a nitrogen airstream (to suppress isoprene emission). The increase in chlorophyll fluorescence which indicates irreversible leaf damage[9] occurred at 37.5 °C in a leaf without isoprene but it occurred at 45 °C in a leaf given 17.5 p.p.m. isoprene in the airstream (see figure). In normal air, we estimate that the concentration of isoprene inside leaves at 40 °C is typically between 1 and 20 p.p.m. and is much higher during water stress. We have demonstrated thermal protection in experiments where photosynthesis was measured as CO_2 uptake and we have been able to demonstrate dose dependence. We speculate that isoprene could dissolve into membranes and alter their properties or alter membrane–protein interactions to increase thermal tolerance. Other isoprenoid compounds are also important in membrane physiology[10].



Effect of exogenous isoprene on chlorophyll fluorescence from a kudzu (*Pueraria lobata* (Willd.) Ohwi.) leaf grown at 28 °C. Chlorophyll fluorescence yield was measured with a pulse-modulated fluorometer (PAM, Heinz Walz; Eiffeltrich). White light was provided by a xenon-arc lamp and was 1,000 μmol m^{-2} s^{-1}. Endogenous isoprene production was suppressed by conducting the experiment in N_2. Isoprene was added to the airstream by passing it through a short piece of polyvinyl chloride tubing inside an Erlenmeyer flask containing a high concentration of isoprene. Isoprene diffused through the tubing into the air stream at a constant rate. Isoprene in the air stream was measured by injecting a 10-ml sample of air into a cryogenic trap held in liquid N_2 which was then warmed to release the isoprene into a Shimadzu gas chromatograph fitted with a photoionization detector. The gas chromatograph was calibrated by mixing liquid isoprene in two stages down to 256 p.p.b. in N_2. Thermal protection has been seen in measurements made with more than 20 pairs of leaves under various conditions, including darkness.

Because isoprene is made rapidly and also lost rapidly from the leaf, its concentration will be well correlated with leaf temperature through the day. The high rate of synthesis, coupled with the volatility, provides a mechanism for rapidly increasing the isoprene concentration inside leaves when they heat up and decreasing the concentration upon leaf cooling. This could be advantageous in environments with fluctuating temperature. It also means that the greatest rates of isoprene emission from vegetation are likely to occur on hot, still days when there is a potential for high levels of tropospheric ozone in polluted air. Ozone abatement has been based primarily on reduction of anthropogenic hydrocarbons, but given the large amount of biogenic isoprene released on hot days, control of anthropogenic NO_x may be more effective.

Thermal tolerance resulting from isoprene can be substantial and the concentration of isoprene required is within the range expected in plants. The temperature-sensitivity of isoprene synthesis and the inducibility by high temperature and water stress support our hypothesis that thermal tolerance explains why many plants emit isoprene. We believe that thermal tolerance may be the primary explanation for why plants emit isoprene.

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Exotic pests and parasites

SIR — Orr *et al.* in Scientific Correspondence[1] describe the competitive dominance of the red imported fire ant *Solenopsis invicta* at food resources in Brazil, which is diminished when under attack by phorid flies, and suggest that this parasite could be used to control the ant in the southern United States. We can add an interesting note to the American story of *S. invicta*, and comment on the role of parasitism in structuring natural communities.

S. invicta might have escaped regulation by its coevolved parasitic organism in an alien ecosystem when it was introduced into the southern United States in the 1940s, but at some time after this it acquired another exotic parasite species, the strepsipteran *Caenocholax fenyesi*[2], first described in Brazil in 1904. This parasite is common in South America, but its host in endemic areas is still unknown. We speculate that the strepsipteran was introduced into the southern United States with another host ant species, but now commonly occurs in the red imported fire ant. This is a good example of an introduced species (the red imported fire ant) which has become aggressive and abundant in an alien ecosystem where its natural parasites (including the phorid fly) are absent. Now the niche left by the natural parasite seems to have been taken over by a new parasite (the strepsipteran). It is to be hoped that this parasite may be followed by others (for example, microbial, introduced phorids) and a balance will begin to be restored.

C. fenyesi belongs to the curious strepsipteran family Myrmecolacidae, the males of which parasitize hosts belonging to a different order from the hosts of females. In the New World the male and female and their hosts of only one species are known[3]; of the 87 species of Myrmecolacidae described worldwide, five have been females and only two of these have been associated with their males. Myrmecolacidae are more numerous and speciose in the New World than the Old. The only species of Myrmecolacidae found in the southern United