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Visualization of Bloch waves and domain walls

The theory of wave propagation in periodic structures[1] and its major concept, Bloch's theorem, have typically been assigned to the realm of solid-state physics[2], but they are now becoming useful in optics[3], acoustics[4] and hydrodynamics[5]. Bloch's theorem is constructive and aesthetic, starting from the idea of perfect order and dealing with infinite extended states. But Bloch's solution is unstable against a small amount of disorder.

This is particularly true of one-dimensional systems, in which Denardo *et al.*[6] found robust localized transition regions between two extended standing-wave domains; they suggested searching for these phenomena in higher dimensions. We used liquid surface waves in which both seemingly extended Bloch states and localized domain walls can be seen alternately in two-dimensional systems.

We have taken advantage of the phenomenon that occurs when the boundary meniscus of a liquid vessel undergoing vertical vibration gives rise to a parasitic surface wave at the excitation angular frequency ω, which propagates inwards for a large distance[7]. To ensure that we worked only with such meniscus waves, the vibration amplitude of the vessel, A, is maintained below the Faraday threshold value A_c, which prevents the growth of the subharmonic Faraday instability[7,8].

We used a square methacrylate box with inner sides of 7 cm attached to the vibration exciter by an aluminium rod at one corner of the box. To modulate the liquid depth, the bottom of the box is drilled in a regular square arrangement of cylindrical holes with a radius of 1.75 mm and a depth d of 2 mm. The unit cell side is 7.5 mm. The bottom of the box is then covered with a thin liquid layer of depth h_1 (up to 0.5 mm). The liquid depth over the cylindrical holes is then $h_2 = h_1 + d$, so h_2 is between 2.0 and 2.5 mm.

To enhance the coalescence of this thin layer so that the formation of drops can be prevented, the capillary length a of the chosen liquid[8] must be very low, 0.93 mm. The kinematic viscosity of the liquid, ν, is also very low, 0.8×10^{-2} cm^2 s^{-1}, so the dispersion relation for inviscid liquids[7,8] can be applied on an unperturbed homogeneous bottom: $\omega^2 = gk(1 + a^2k^2)\tanh(kh)$, where k is the wavenumber, g is the acceleration due to gravity, and h is the uniform liquid depth.

Although each wall generates a meniscus wave, when the vibrating rod excites from one corner, the predominant wave goes along the [110] direction. The spatial wave equation for an unperturbed homogeneous isotropic continuum is $\nabla^2\psi + (\omega^2/V^2)\psi = 0$, where $V = \omega/k$ is the phase velocity. A solution of this equation is the plane wave $\psi = C\exp(i\mathbf{k}\cdot\mathbf{r})$, where C is a constant, $\mathbf{k}$ is the wavevector and $\mathbf{r}$ is the position vector on the liquid surface.

We have used a periodic field with two slightly different velocities: V_1 on the host background and V_2 on the cylindrical holes, where $V_1 < V_2$. According to Bloch's theorem[1,2], the solution of the perturbed wave equation is $\psi = u(\mathbf{r})\exp(i\mathbf{k}\cdot\mathbf{r})$, where $u(\mathbf{r})$ is a modulation function exhibiting the same periodicity as the underlying Bravais lattice. We show several snapshots of seemingly extended states aesthetically modulating the free liquid surface with the symmetry of the underlying square lattice (Fig. 1). The vibration amplitude is forced just to the limit below the appearance threshold of the Faraday instability. Such oscillatory motions could have their origin in Bloch's theorem, so that both the propagative plane wave, $\exp(i\mathbf{k}\cdot\mathbf{r})$, and the underlying modulation function, $u(\mathbf{r})$, can be clearly distinguished (Fig. 1, top). The stability of such extended Bloch states against the inevitable infinitesimal disorder of any realistic experiment might be due to the nonlinearity of our parametrically driven two-dimensional system; this is able to restore the lightly broken translational invariance, which in turn prevents Anderson localization[6].

Then we intentionally introduce some disorder: ~4% in dimple locations and 10% in h_2/h_1 depth ratios. In this case, highly

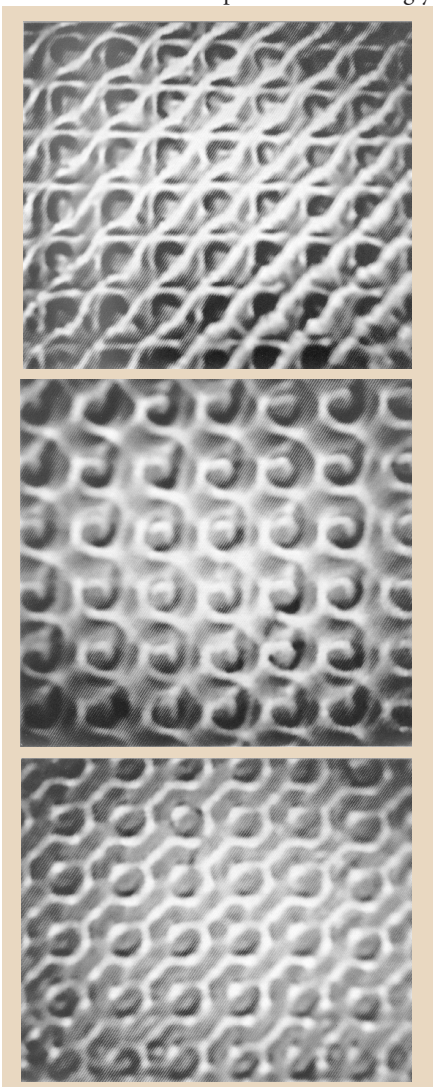

Figure 1 Extended Bloch states at excitation frequencies of 22, 30 and 35 Hz (from top to bottom). The propagative plane wave is running along the [−1,1,0] direction.

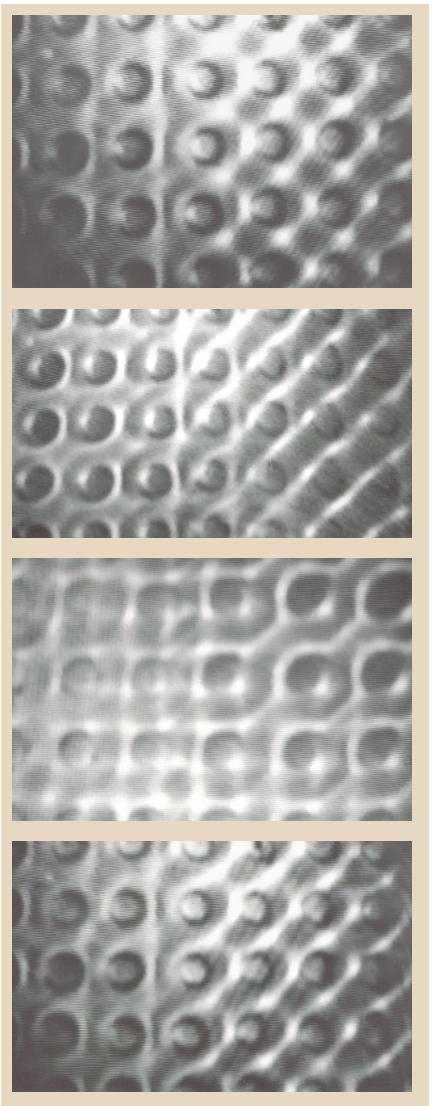

Figure 2 Localized domain walls between robust standing-wave domains. Wavevectors run along the [1,0,0] and [−1,1,0] directions with wavelengths l and $2^{1/2}l$, respectively. A sequence of snapshots is shown from top to bottom. The [1,0,0] domain is always at the left. The excitation frequency is ~20 Hz.

localized domain walls separating standing-wave regions with different but well-defined wavevectors can also be observed (Fig. 2). Thus, localization phenomena found earlier in one-dimensional vibratory systems[6] can be generalized to higher dimensions.

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Genetic flexibility of plant chloroplasts

The chloroplast genome is thought to be monomorphic, or genetically uniform within individual plants[1]. But a single plant cell may contain several hundred chloroplasts, each containing up to 900 copies of DNA[2], so there is a huge potential for accumulating and maintaining mutations. I found that the chloroplast genome of common groundsel, *Senecio vulgaris*, is polymorphic for a point mutation that confers resistance to triazine herbicides. Moreover, this polymorphism can vary within and among different leaves of a single plant.

Common groundsel is an annual weed found almost all over the world. It is strongly self-fertilizing, and was the first species to develop resistance to triazine herbicides[3]. To assess the level of chloroplast DNA polymorphism within individual plants, I used six different portions of each of five leaves of seven plants of various origin to analyse the frequency and distribution of a point mutation in a chloroplast gene that confers resistance to triazine herbicides (Fig. 1). I used the polymerase chain reaction to amplify a 277-base-pair-long chloroplast DNA fragment of the *psbA* gene spanning the point mutation conferring triazine resistance[4].

Restriction analysis of the amplified sequence using *Mae*I resulted in two fragments of 123 and 154 base pairs in triazine-resistant individuals, and in three fragments of 35, 88 and 154 base pairs in susceptible individuals. The 123-base-pair restriction fragment is therefore diagnostic for triazine resistance and the 88-base-pair fragment indicates susceptibility; polymorphism of chloroplast DNA is observed if fragments of both 88 and 123 base pairs occur together within a leaf sample. Sequencing of the amplification product confirmed the restriction pattern (GeneBank accession number, AF061287; data not shown).

Abundant polymorphism was evident in all but the phenotypically resistant plants (Fig. 1). The pattern of polymorphism in the crosses (S × R, R × S) indicates maternal inheritance. Paternal leakage seems to be infrequent, as the R × S plants were sixth-generation backcrosses, indicating that there is stable transmission of polymorphic states to the progeny. The level of polymorphism in *S. vulgaris* is variable between plants ($P = 0.0001$ among all plants, as well as among the polymorphic plants only; nested analysis of variance on arcsin square-root-transformed proportions[5]). Variation between different leaves is observed in some plants (NL2, $P = 0.0001$; S × R, $P = 0.0005$; UK3, $P = 0.0164$) but not others (the monomorphic R and R × S; S, $P = 0.2991$; CH, $P = 0.0705$). Large values for residual mean squares in polymorphic plants show that considerable variation also occurs within single leaves (data not shown; see Fig. 1). Many samples showed variable amounts of additional fragments, such as a 186-base-pair fragment typically found in triazine-susceptible genotypes of other weeds[4], indicating several other polymorphisms. Because the samples originated from different countries, chloroplast DNA polymorphism seems to be a widespread characteristic of this plant.

Heteroplasmy (the existence of more than one type of chloroplast within an individual) may be attributed to somatic mutation or biparental inheritance, and is believed to sort out within one or very few generations[6]. Together with the fact that the point mutation that confers triazine resistance is associated with considerable fitness costs[7], this should lead to a rapid loss of heteroplasmic states from plants. However, the resistant genotype is not rapidly eliminated from populations, even after periods without any triazine treatment, as can be seen from the genotype of the 'susceptible' laboratory-reared S line, which, since its collection in the field in 1973 and after several cycles of reproduction, still carries a considerable degree of polymorphism (Fig. 1). Assuming that paternal inheritance is infrequent in this strongly selfing weed, this indicates that transmission of the polymorphic chloroplast DNA state to the progeny can be maintained over many generations. The fitness costs of the point mutation that confers triazine resistance may therefore only be important if the level of polymorphism exceeds a certain carrying capacity.

In *Drosophila*, the evolution of heteroplasmic states of mitochondrial DNA types is affected by their fitness with respect to selective forces[8]. Within-plant polymorphism of chloroplast DNA has the potential for environmentally imposed selective

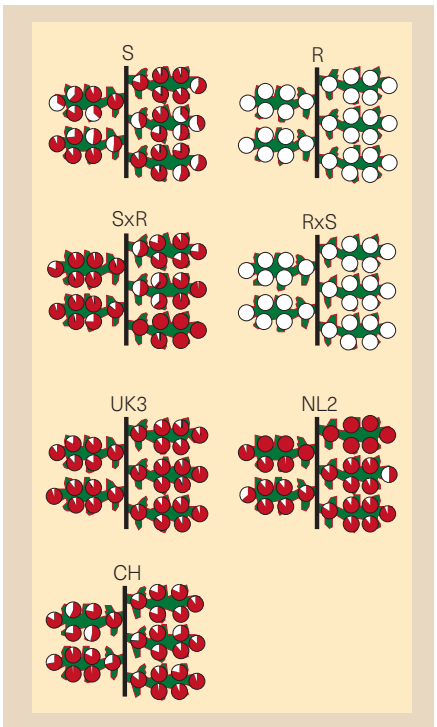

Figure 1 Analysis of chloroplast DNA polymorphism. Samples of *Senecio vulgaris* (ssp. *vulgaris* var. *vulgaris*) originated from Switzerland (CH), the Netherlands (NL2), Britain (UK3)[10] and from four inbred lines from the western United States: R (triazine-resistant parental biotype), S (triazine susceptible parental biotype), R × S (triazine-resistant sixth-generation backcrossed biotype with R cytoplasm and S nuclear genome) and S × R (triazine-resistant sixth-generation backcrossed biotype with S cytoplasm and R nuclear genome)[11]. Each leaf sample consisted of a small leaf disc (~2.4 mm^2) punched out of six leaf positions of each of the first five leaves using the tip of a disposable Pasteur pipette, homogenized in 100 μl lysis buffer (20 mM Tris, pH 7.4, 20 mM EDTA, 2 M NaCl), heated three times for 5 min at 85 °C, vortexed and centrifuged. Then 3 μl extraction solution was used with fluorescently labelled primers to amplify part of the *psb A* gene, and 4 μl amplification product was digested with *Mae*I as described for several weeds[4]. Two to four restriction analyses were performed on each amplification product, and 2 μl digested DNA was analysed. Possible effects of star activity of the restriction enzyme were tested by digesting different concentrations of purified amplification products. Levels of chloroplast DNA polymorphism for individual leaf samples are shown as the median of the restriction analyses of the amplification products of the ratio between the quantity of the 88-base-pair fragment (red) and the quantity of the 123-base-pair fragment (white), based on fragment peak amplitudes. Because the undigested 277-base-pair fragment found in many analyses may be due to either incomplete digestion or a resistant genotype lacking the 154-base-pair restriction site, the index probably underestimates the relative frequency of resistant genotypes.