

**Table 1 Copulatory and siring success of Soay sheep rams**

Term	d.f.	Effect	s.e.	Wald statistic ( $\chi^2$ )	P
<b>Male copulatory success*</b>					
Watch duration (logged)	1	1.454	0.483	9.07	0.003
No. of females in oestrus	1	0.506	0.117	18.71	<0.001
No. of females in oestrus <sup>2</sup>	1	-0.0167	0.00562	8.82	0.003
Week of rut	1	-10.31	3.991	6.68	0.010
Hindleg length	1	-0.0844	0.0650	1.68	0.194
Horn length	1	0.00611	0.00228	7.18	0.007
Hindleg length: week of rut	1	0.0559	0.0207	7.29	0.007
<b>Male siring success†</b>					
No. of females lambing	1	0.0556	0.00810	47.01	<0.001
No. of females lambing <sup>2</sup>	1	-0.000293	0.0000725	16.32	<0.001
Week of lambing	1	5.137	1.667	9.49	0.002
Hindleg length	1	0.119	0.0331	12.83	<0.001
Horn length	1	0.00767	0.00168	20.85	<0.001
Hindleg length: week of lambing	1	-0.0258	0.00865	8.85	0.003

We analysed temporal behavioural and paternity data using generalized linear mixed models with a logit link function. These control for repeated measures of behaviour and paternity by fitting male identity and year as random effects<sup>12</sup>. A colon between terms denotes two-way interactions.

\*Minimal model of male copulatory success. The response is binary, indicating whether a mounting attempt occurred during a focal watch performed in 1996–98;  $n = 371$ . Median watch duration was 1 h.

†Minimal model of male siring success. The response variable takes the form of binomial proportions, being the number of days in a given week on which a male gains a paternity,  $n = 897$ . Includes analysis of 170 paternities assigned between 1988 and 1999<sup>1</sup>. Temporal behavioural and paternity analyses can be compared owing to the correspondence between conception and lambing distributions, gestation being  $151.2 \pm 1.3$  days (mean  $\pm$  s.d.)<sup>13</sup>. Hindleg length is a linear indicator of skeletal size. Age, weight and basal-horn circumference were tested in each model but were excluded (all  $P > 0.1$ ). For further details, see <http://www.ecology.net.stir.ac.uk/kilda/depletion>.

determining sperm production rate<sup>7</sup>, yet we find a negative correlation between testicular circumference and number of sperm ejaculated (Fig. 1d). This suggests that males producing smaller ejaculates towards the end of the rut had greater capacity for ejaculate production at the start of it. To our knowledge, this is the first demonstration that limitations on ejaculate production may constrain male reproductive success in a wild vertebrate population.

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Biotechnology

**Transgenic crops in natural habitats**

Although improved crop yields can be engineered by genetically modifying plants, there is ecological concern over whether these plants are likely to persist in the wild in the event of dispersal from their cultivated habitat. Here we present the results of a long-term study of the performance of transgenic crops in natural habitats. Four different crops (oilseed rape, potato, maize and sugar beet) were grown in 12

different habitats and monitored over a period of 10 years. In no case were the genetically modified plants found to be more invasive or more persistent than their conventional counterparts.

In the late 1980s, there were three conjectural risks associated with genetically modified (GM) crops: that they would become weeds of agriculture or invasive of natural habitats; that the introduced genes would be transferred by pollen to wild relatives, whose hybrid offspring would then become more weedy or invasive; or that GM plants would be a direct hazard to humans, domestic livestock or beneficial

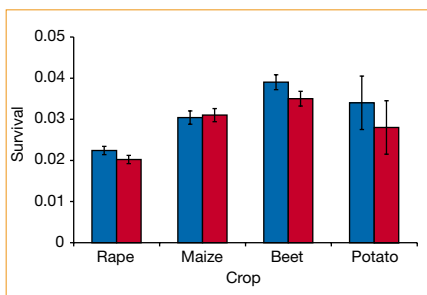
wild organisms, for example by being toxic or allergenic. Our study assesses the grounds for the first two of these fears.

We have shown previously that GM oilseed-rape plants did not perform better or persist for longer than conventional plants over a 3-year period<sup>1</sup>. We now compare the results of monitoring conventional and GM lines of four crop species over 10 years<sup>2,3</sup> in a field experiment conducted in 12 different habitats (four in each of Cornwall, Sutherland and Berkshire in the United Kingdom) and repeated in the years 1990, 1991 and 1992 in order to determine whether GM crops would be more invasive or more persistent in natural habitats than non-GM crops. We tested all the crop species and GM constructs that were available in 1990: oilseed-rape and maize plants expressing tolerance of the herbicide glufosinate, sugar beet tolerant of glyphosate ('Roundup'), and two types of GM potato expressing either the insecticidal *Bt* toxin or pea lectin.

The sites were monitored each year to follow the fate of sown individuals, to measure recruitment onto unsown areas nearby, and to determine whether there was any resurgence following natural disturbance in later years. Figure 1 shows the fraction of seeds sown (or tubers planted) that produced mature plants at the end of the first growing season. We found that there were no significant differences in average recruitment between conventional and GM plants for any of the four crops (full details and significance tests are provided in Supplementary Information). None of the crops, GM or conventional, increased in abundance at any of the sites.

Population sizes of all crops declined after the first year as a result of increased competition from native perennial plants. In no case did the GM lines persist for significantly longer than their conventional counterparts. For oilseed rape, seedling establishment was significantly lower for GM plants compared with conventional lines in six out of 12 cases, and were not significantly greater in any case. Subsequent survival was significantly lower for GM lines in three out of 12 cases and significantly higher in two cases. For maize, seedling establishment was significantly lower for the GM line in two out of 12 cases, and significantly greater in no case. Subsequent survival was significantly higher for the GM line in one case, but all lines were extinct by the beginning of the second year.

For potato, survival of planted tubers to the end of the first growing season was significantly lower for GM lines in one case out of eight, and significantly higher in one instance. The few cases of increased GM-plant survival that were significant in the short term did not translate into long-term differences in persistence (see Supplementary Information). Survival of perennating



**Figure 1** The performance of conventional (blue) and transgenic (red) crops in natural habitats. Survival is the fraction of seeds sown (or tubers planted in the case of potato) that produce mature plants at the end of the first growing season. Error bars, 1 s.e. Data are averaged over habitats and replicates within habitat. In no case did populations of either conventional or transgenic plants increase, and transgenic plants never persisted significantly longer than conventional plants. All populations of maize, rape and sugar beet were extinct at all sites within 4 years of sowing. Potato still survives at one site, 10 years after planting, but the survivors are all conventional.

potatoes was significantly lower for GM lines in one case out of eight, and never significantly higher.

For sugar beet, the genetic background (inbred or outbred) was much more important than whether the plants were genetically modified; outbred lines outperformed inbred lines in three cases out of four. GM lines showed significantly lower recruitment from seed in two cases out of four, and significantly higher recruitment in no case. Survival of GM sugar-beet seedlings was significantly lower for one transition at one site, but all sugar-beet lines were extinct within two years at all four sites. Survival of sea beet was significantly higher than sugar beet at all four sites, but it too was extinct at all sites by the end of the third year. The survival of sea beet on open ground elsewhere in Silwood Park, where potted plants had stood in 1992, sounds the cautionary note that perennial plants can persist for extended periods in extremely odd places.

These experiments involved GM traits (resistance to herbicides or insects) that were not expected to increase plant fitness in natural habitats. Our results do not mean that other genetic modifications could not increase weediness or invasiveness of crop plants, but they do indicate that arable crops are unlikely to survive for long outside cultivation. The ecological impact of plants with GM traits such as drought tolerance or pest resistance that might be expected to enhance performance under field conditions will need to be assessed experimentally when such plants are developed.

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Supplementary information is available at <http://www.nature.com> or as paper copy from the London editorial office of *Nature*.

Materials science

Nanoscale control of chain polymerization

Polymer industries depend on the spontaneous polymerization of molecules into chains in response to an appropriate trigger. We have succeeded in inducing and guiding chain polymerization over tiny distances, initiating and terminating linear propagation at any chosen point to a spatial precision of about 1 nm by using the probe tip of a scanning tunnelling microscope. Being able to exert such fine control over nanoscale fabrication and interconnection should help to take molecular nanoelectronics beyond the present silicon-based-device technology.

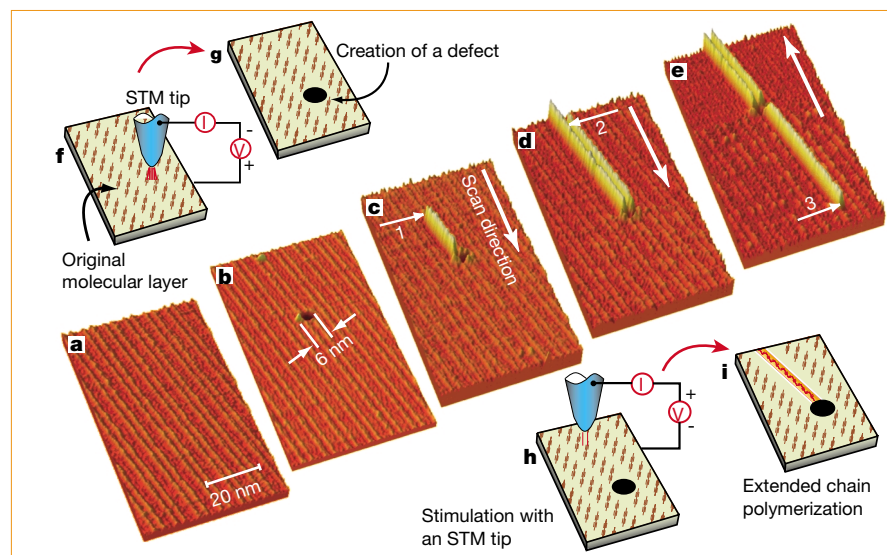
We chose a self-ordered monomolecular layer of a diacetylene compound (10,12-nonacosadiynoic acid) adsorbed on a graphite surface because this molecular species polymerizes in a three-dimensional solid state<sup>1–3</sup> (although this does not guarantee that polymerization can occur in a two-dimensional monomolecular layer). Also, polymerization results in polydiacetylene compounds that behave as conjugated linear polymers and should function as electrically conductive ‘nanowires’ upon

transfer of charge from the surroundings<sup>4,5</sup>.

Figure 1a shows a typical scanning tunnelling microscope (STM) image of the monomolecular layer. Each bright line running from top to bottom corresponds to a linear array of diacetylene moieties of the self-ordered molecules (the two different alternating spacings between the bright lines are due to the antiphase arrangement of the molecules). We were able to induce chain polymerization in the monomolecular layer by local stimulation with the STM tip (Y.O. and M.A., manuscript in preparation) and to control it efficiently at the nanoscale level (Fig. 1b–e).

First, we created an artificial defect in the form of a 6-nm-wide hole at a predetermined position in the monomolecular layer<sup>6</sup> (Fig. 1b) by placing the STM tip at this position and applying a positively pulsed sample bias (+5 V in height, 10 μs in width; see also Fig. 1f, g). We again imaged the area shown in Fig. 1b, this time scanning from top to bottom (Fig. 1c) with a negatively pulsed sample bias (–4 V, 5 μs) applied when the scanning tip passed the point indicated by arrow (1), which caused a bright line to appear between the point and the artificial defect. This line represents a polymerized polydiacetylene nanowire, as confirmed by structural analysis, starting at the point indicated by arrow (1) and ending at the defect (Fig. 1h, i).

We imaged the same area once more (Fig. 1d), applying another negatively pulsed sample bias when the tip passed the point indicated by arrow (2): chain polymerization started at this point as well and also terminated at the hole (compare Fig.



**Figure 1** Scanning tunnelling microscope (STM) images and diagrams showing the process of controlling the initiation and termination of linear chain polymerization with an STM tip. STM images were obtained in air at room temperature in constant-current mode. **a**, STM image of the original monomolecular layer of 10,12-nonacosadiynoic acid. **b**, Creation of an artificial defect in advance in the monomolecular layer using an STM tip. **c**, First chain polymerization, initiated at the point indicated by arrow (1) using an STM tip, and terminated at the artificial defect. **d**, Second chain polymerization, initiated at arrow (2). **e**, Third chain polymerization, initiated at arrow (3). **f**, **g**, Creation of an artificial defect in advance with an STM tip. **h**, **i**, Initiation of chain polymerization with an STM tip, and termination of the polymerization at the artificial defect.

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