on the forests, wildlife, and indigenous people of this area, WWF warns. It is not necessary to use this area as there is already a total of 2.3 million hectares of idle or derelict land available for palm oil plantations in Kalimantan, an area greater than the proposed plantation, WWF points out.

In addition, oil palm is not recommended for planting in areas more than 200 metres above sea level, because of low productivity at these levels. The plantations are also recommended to be restricted to areas with an incline of less than 30 per cent. But most of the heart of Borneo border area is between 1,000 and 2,000 metres high, with infertile, shallow soils and steep slopes. Such rugged terrain means that the risk of erosion is high.

WWF explains that "although it makes little economic sense to plant palm oil in the uplands, the plantation companies would have access to timber, which they would fell and sell as part of the plantation preparation process. This could be extremely lucrative and there is evidence that some companies have applied for palm oil plantation licences in the past with this in mind."

Malaysia's oil palm plantations cover 40 per cent of its cultivated land and it is the world's largest producer and exporter of palm oil and Indonesia has also embarked on a major plantation programme. Despite the Indonesian government's assurance that the project would not harm the environment, WWF insists that development of palm oil plantations should follow strict sustainable and environmental principles which exclude the destruction of forests of high social and biological importance.

Quick guide

Spliced leader trans-splicing

Nicholas A. Stover[1], Michelle S. Kaye[2] and Andre R.O. Cavalcanti[2]

What is spliced leader (SL) trans-splicing? It is an mRNA maturation process, similar to intron splicing, which has been shown to occur in a limited number of eukaryotes. In SL *trans*-splicing, the cell replaces nucleotides at the 5′ end of some pre-mRNAs with those of a special class of small nuclear RNAs, called SL RNAs. These are short molecules with two functionally distinct halves: the 5′ half consists of the leader sequence that is transferred to a pre-mRNA, along with the SL RNA's methylguanosine cap; the 3′ half contains a binding site for the Sm protein complex, which binds many of the RNAs involved in intron splicing. These two halves are separated by a splice donor site, a GT dinucleotide. Nuclear machinery *trans*-splices the leader sequence to splice acceptor sites (AG dinucleotides) in the 5′ region of target pre-mRNAs. As a result, many mRNAs in SL *trans*-splicing species have a common sequence at the 5′ end.

How is SL trans-splicing related to intron splicing? The mechanism of SL *trans*-splicing is very similar to *cis*- (intron) splicing (Figure 1). In both cases, the 2′ hydroxyl group of a nucleotide (usually adenosine) severs the pre-mRNA backbone at the splice donor site, freeing the upstream exon to displace the intron sequence at the splice acceptor. In intron splicing, the splice donor and acceptor sites lie on the same strand of RNA, separated by the intron sequence, which contains the branch point adenosine. For SL *trans*-splicing, the splice donor site of the SL RNA is attacked by an adenosine between the 5′ end of the pre-mRNA and its SL addition site. The region of the pre-mRNA upstream of the SL addition site, which is removed when the leader sequence is attached, is known as the 'outron' — it is 'outside' the gene, whereas introns are 'inside'.

Strikingly, experiments in the nematode *Caenorhabditis elegans* demonstrated that the relative location of the donor and acceptor sites is sufficient to determine whether a splice

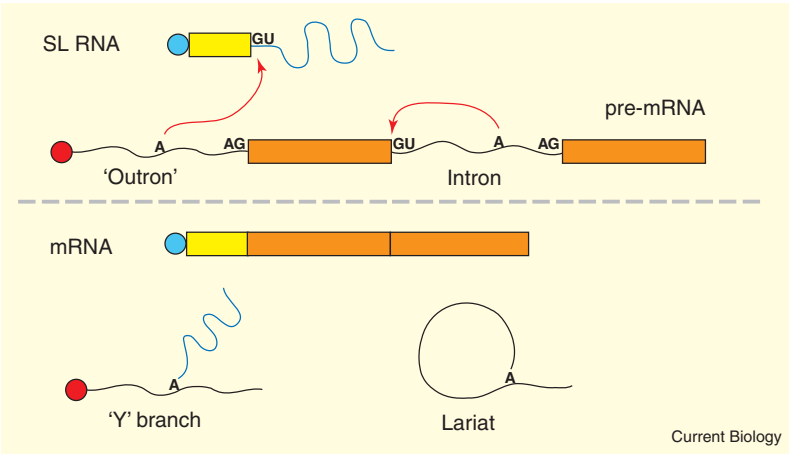

Figure 1. The leader sequence (yellow box) of an SL RNA is attached to the first exon (orange box) of a pre-mRNA by a *trans*-splicing reaction.

The outron of the pre-mRNA and the intron-like portion of the SL RNA form a 'Y' branched byproduct, similar to the lariat structure formed during intron splicing. The 2,2,7-trimethylguanosine cap structure (or 'Cap 4' in trypanosomes) found on SL RNAs and *trans*-spliced mRNAs (blue circles) differs from the 7-methylguanosine caps typically found on mRNAs (red circles). These caps impart novel properties to *trans*-spliced messages.

acceptor is cis- or *trans*-spliced. Cis-spliced acceptors can be converted to *trans*-splicing acceptors if the donor site upstream is mutated, and similarly an SL addition site will be cis-spliced if a donor site is inserted upstream.

What is the function of SL trans-splicing? SL addition provides the cell with an alternative way of capping mRNAs, a modification required for mRNA stability, transport and translation. The standard capping machinery is typically recruited by RNA polymerase II at the beginning of transcription to cap the growing RNA. In trypanosomes, SL addition is used to cap a subset of pre-mRNAs transcribed by RNA polymerase I, which does not recruit the capping machinery. In a wider range of eukaryotes, SL addition allows the formation of operons — adjacent genes that are transcribed as a single primary transcript. The cleavage reaction that precedes polyadenylation of each gene effectively chops the transcript into smaller pieces. Since only the message from the 5′ end retains the transcript's original cap, SL *trans*-splicing is needed to cap the remaining fragments.

Addition of an SL has also been shown to affect the translation rate of some genes, add missing start codons and trim off outron sequences. But while the role of SL addition in these processes is well established, the benefit of transcription by polymerase I, inclusion in an operon, translational regulation, substitution of a start codon and outron removal is not immediately obvious for most *trans*-spliced genes.

How is it phylogenetically distributed? The complete phylogenetic distribution of SL *trans*-splicing is not currently known. To date, SL *trans*-splicing has been found in six diverse groups of eukaryotes: nematodes, flatworms, cnidarians, ascidians, rotifers and euglenozoans. But it has not been detected in other well-studied eukaryotic taxa, such as fungi, plants, vertebrates and arthropods.

How did it evolve? There are two competing hypotheses describing the origin of SL *trans*-splicing. The 'SL *trans*-splicing early' hypothesis proposes that SL *trans*-splicing was present in the ancestral eukaryote and subsequently lost in most phyla. This hypothesis is supported in part by the continuing discovery of SL *trans*-splicing in an expanding range of eukaryotes. The 'SL *trans*-splicing late' hypothesis proposes that the process has emerged several times independently, and that features unique to SL addition — the SL RNA, *trans*-spliceosome-specific proteins, SL-specific translation enhancer proteins, operons, and so on — are also independently derived in these lineages. This hypothesis is supported by the observation that the few unique components shown to be involved in SL addition are not obviously conserved across different *trans*-splicing phyla. Further studies into the mechanism and effects of SL *trans*-splicing in different phyla will help to clarify its origin.

Why should I care? Many of the organisms that perform SL *trans*-splicing, such as trypanosomes, flatworms and nematodes are pathogenic to humans. Drugs that target components of the *trans*-spliceosome or disrupt the downstream effects of SL *trans*-splicing may be highly effective against these parasitic species, while causing little harm to patients.

Where can I find out more?

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[1]Department of Genetics, Stanford University School of Medicine, Stanford University, Stanford, California 94305, USA. [2]Department of Biology, Pomona College, Claremont, California 91711, USA.

Media review

Aliens — as we know them

Florian Maderspacher

Alien Worlds —
Big Wave productions.
(Catalogue: C4DVD10020;
Barcode: 6867441002093)

Utopias feature in art and literature of all ages — from Plato's Atlantis and Swift's lilliput down to modern science fiction writers like Stanislaw Lem or Isaac Asimov. Utopias have always been employed as a setting in which to explore what is possible and how things could be better — or worse. The recent TV programme, *Alien Worlds* — broadcast on Channel 4 in the UK and available internationally on DVD — attempts at creating an utopian setting to address one central question about the evolution of life on Earth: is life and the shapes it comes in a product of mere coincidence or did it have to come like this? Was the evolution of life forms and ultimately of intelligence chance or necessity?

Many an academic debate has been fought over this and *Alien Worlds* tackles the issue by envisioning two planets, a mere 50 light years away, that have evolved life. Planet Aurelia orbits a red dwarf star and has ceased rotating, so that one side experiences never-ending daylight while the other is in constant night; where the two sides meet the ice cap offers a truly spectacular view from space. The other world is a marvellous Blue Moon, which orbits a Saturn-like gas giant planet that in turn orbits a double star system.

These worlds differ from places conjured up by the average science fiction programme, because they are scientifically thought through. The programme's producers have gathered together a team of astronomers, climatologists and biologists to put the features of the planets and their inhabitants