Title:	Splicing of branchpoint-distant exons is promoted by Cactin Tls1 and the ubiquitin- fold-activated Sde2.
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Abstract:	Intron diversity facilitates regulated gene expression and alternative splicing. Spliceosomes excise introns after recognizing their splicing signals: the 5′-splice site (5′ss), branchpoint (BP) and 3′-splice site (3′ss). The latter two signals are recognized by U2 small nuclear ribonucleoprotein (snRNP) and its accessory factors (U2AFs), but longer spacings between them result in weaker splicing. Here, we show that excision of introns with a BP-distant 3′ss (e.g. rap1 intron 2) requires the ubiquitin-fold-activated splicing regulator Sde2 in Schizosaccharomyces pombe. By monitoring splicing-specific ura4 reporters in a collection of S. pombe mutants, Cay1 and Tls1 were identified as additional regulators of this process. The role of Sde2, Cay1 and Tls1 was further confirmed by increasing BP–3′ss spacings in a canonical tho5 intron. We also examined BP-distant exons spliced independently of these factors and observed that RNA secondary structures possibly bridged the gap between the two signals. These proteins may guide the 3′ss towards the spliceosome's catalytic centre by folding the RNA between the BP and 3′ss. Orthologues of Sde2, Cay1 and Tls1, although missing in the intron-poor Saccharomyces cerevisiae, are present in intron-rich eukaryotes, including humans. This type of intron-specific pre-mRNA splicing appears to have evolved for regulated gene expression and alternative splicing of key heterochromatin factors.
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