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Original Paper

Stress-activated retrotransposon sequences in *Pinus sylvestris* gene regions

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Abstract

Scots pine (*Pinus sylvestris* L.) faces increasing threats from climate change related stresses such as heat and fungal pathogens like *Heterobasidion annosum*. Retrotransposons, mobile genetic elements that are widely distributed in the Scots pine genome, may contribute to stress adaptation. This study analysed 16 retrotransposon families activated under heat stress, comparing them with genomic regions flanking genes that were differentially expressed after fungal inoculation. Results showed that some of the heat-stress activated retrotransposons are also differentially expressed after fungal inoculation and share sequence similarities with genomic regions flanking stress-responsive genes. These findings suggest a potential role of retrotransposons in Scots pine adaptation to a wide range of stress conditions, highlighting the need for further research on their functional significance. This information can be used to understand how long-lived organisms such as Scots pine adapt to changing environmental conditions, providing possible options for the long-term management of forests in the context of climate change.

Key words: abiotic stress, biotic interactions, epigenetic regulation, genomic plasticity, transposable elements.
Abbreviations: HSP, high-scoring segment pair; LTR, long terminal repeat.

Introduction

Climate change is posing a great challenge to many forest tree species, and mitigating its impacts requires coordination of a diverse range of management and adaptation strategies (Vacek et al. 2023). Climate change effects, particularly hotter temperatures, are expected to significantly impact European forest tree species (Buras, Menzel 2019). An increase in Scots pine (*Pinus sylvestris* L.) mortality over the last 20 years has been reported throughout the distribution area in Europe, both at the distribution margins, as well as in climatic optimum regions, and in a review of studies of Scots pine mortality, drought and/or heat was reported as the primary cause of mortality (Bose et al. 2024). Additionally, climatic changes can facilitate the spread and growth rate of *Heterobasidion annosum*, a highly significant fungal pathogen of Scots pine, causing additional losses. *H. annosum* initially infects stands via airborne spores, often by growth on freshly cut stumps. Subsequently, the fungus can spread between individual trees via root contacts. Increased air temperatures and relative humidity increase sporulation of *H. annosum* (Lione et al. 2025), and therefore the spread of this fungus can be expected to increase as a result of climate change, particularly in managed forest settings.

Adaptation to stress conditions is a prerequisite for the survival of organisms and populations, particularly for long-lived, immobile species such as conifers. Scots pine has the widest distribution range within the *Pinus* genus, ranging throughout Eurasia, from western Europe to the far east, and from southern Spain (37°N) to northern Scandinavia (70°N) (Houston Durrant et al. 2016). The species is highly adaptable to a wide range of growing conditions and has high genetic diversity, probably as a result of post glacial recolonization from multiple refugia (Houston Durrant et al. 2016). High genetic diversity can ensure the long-term adaptability of populations and species, in conjunction with phenotypic plasticity (Leites, Benito Garzón 2023).

It is increasingly recognised that nucleotide variation in protein coding genes is only a small proportion of the total genetic variation in plant genomes (Lei et al. 2021). Retrotransposons are genetic elements capable of moving within the genome by first being transcribed into RNA and then converted back into DNA through reverse transcription. These elements are widespread in plants and significantly contribute to the evolution of plant genes and genomes. In numerous instances, retrotransposons make up more than half of the nuclear DNA content (Kumar, Bennetzen 1999). The activation and transposition of retrotransposons within plant genomes can be a source of novel genetic diversity that can rapidly prompt adaptive responses to a wide range of stress conditions (Baduel, Quadrana 2021), and retrotransposons play a crucial role in plant genome plasticity (Emmerson, Catoni 2025).

Retrotransposons have been reported to be activated in a range of stress conditions, including heat, cold and drought (Ito 2022), providing an opportunity for plants to rapidly respond to changing environmental and climatic conditions. Retrotransposons in plant genomes play a significant role in heat stress responses, and retrotransposon insertions near protein coding genes can influence their expression via a range of mechanisms, including the regulation of small RNAs and DNA methylation pathways (Papolu et al. 2022).

However, most studies of the activation of retrotransposons have focussed on one particular stress condition, and studies about activation of the same retrotransposons or retrotransposon families under different stress conditions are scarce. In this study, we identified retrotransposons reported to be activated in heat stress conditions from previously published studies, and retrieved sample sequences of the identified retrotransposon families from publicly available databases. These retrotransposon sequences were used to search for similar sequences in the Scots pine transcriptome as well as in 5' genomic regions flanking protein-coding genes differentially expressed after inoculation with *H. annosum.* This provides an initial insight into the role of particular retrotransposon families in responses to diverse stress conditions in Scots pine, and indicates further research directions to facilitate understanding of the adaptation of Scots pine to climate change.

Materials and methods

Retrotransposon family sequences

A number of retrotransposon-like sequences were previously reported to be expressed in response to heat stress in Scots pine (Voronova et al. 2011). The sequences of these sixteen retrotransposon families were obtained from the NCBI database (Table 1).

*Scots pine transcriptome data (*H. annosum *inoculation/wounding)*

The retrotransposon sequences were compared to a previously published Scots pine transcriptome data set, where differential gene expression was investigated in individuals inoculated with *H. annosum* compared to wounded and untreated controls (Šķipars, Ruņģis 2021). The RNA-seq analysis was done with the CLC Genomics Workbench 12.0.3 using the default parameters (mismatch cost = 2, insertion cost = 3, deletion cost = 3). A p-value of $<$ 0.05 was used to identify differentially expressed sequences between inoculated, wounded and control treatments.

Genome sequence of regions flanking genes differentially expressed after H. annosum inoculation/wounding

In addition, the retrotransposon sequences were used to perform a BLAST search of the genomic regions adjacent to genes differentially expressed after inoculation with

Table 1. NCBI accession numbers, sequence length, position and source species for the sixteen retrotransposon families

Retrotransposon family	NCBI accession number	Sequence length (nucleotides)	Position (if not full-length sequence)	Coverage of element	Source species
Bare1	AJ582612.1	1891		Long terminal repeat (LTR)	*Hordeum pusillum*
Carmilla	JN544193.1	14382	13453-27834	Complete element	*Triticum aestivum*
Conan	HE774676.1	360	143903-144262	3' fragment	*Triticum aestivum*
Diaspora	U96295.1	544	3647-4190	Integrase; disrupted by SIRE-1	*Glycine max*
Erika	DQ537335.1	13132	28801-41932	Complete element	*Triticum aestivum*
Geneva	KR813335.1	3654	520259-523912	Complete element	*Hordeum vulgare*
Horpia2	HM124452.1	321	31749-32069	LTR	*Hordeum vulgare*
Ifis	FN564426.1	13333	357005-363718, 364224-370842	Complete element	*Triticum aestivum*
Karin	FJ447462.1	6472	46070-51698, 60080-60922	Non-LTR retrotransposon	*Triticum aestivum*
Laura	MG582649.1	14074	75905-89978	Complete element	*Triticum monococcum*
Maximus	AH014393.2	13765	159448-160510, 180160-182637, 184461-194162, 219277-219439, 227633-227991	Complete element	*Hordeum vulgare*
Oryco1-1	AL928755.5	4927	12146-17072	Complete element	*Oryza sativa*
Persephone	FJ896242.1	4265	10837-15101	Complete element	*Hordeum vulgare*
Sabrina	HE774676.1	6890	18316-25205	Complete element	*Triticum aestivum*
Tnt 1-94	X13777.1	5334		Complete element	*Nicotiana tabacum*
Wham	FN564434.1	9517	910667-911396, 918940-927726	Complete element	*Triticum aestivum*

H. annosum (Šķipars, unpublished results). Briefly, low coverage whole genome sequencing data was used to identify 5’ flanking regions of differentially expressed genes from the previously described Scots pine transcriptome data set (Šķipars, Ruņģis 2021). Sequencing of the Scots pine genome using an Oxford Nanopore PromethION flow cell provided a 5x genome coverage, which enabled identification of approximately 3000 nucleotides of 5’ genomic sequence flanking 62 genes that were differentially expressed after inoculation with *H. annosum* or wounding. The sixteen heat-stress activated retrotransposon sequences were used for BLAST analysis against these 62 genomic regions flanking stress-related genes using the CLC Genomics Workbench 12.0.3 using the default parameters (mismatch cost = 2, insertion cost = 3, deletion cost = 3). An *e*-value of < 0.05 was used to identify similar sequences in the gene regions.

The workflow and obtained results are shown in Fig. 1.

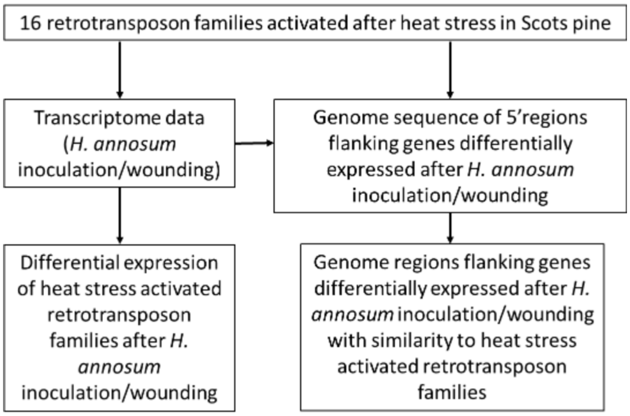

Fig. 1. Study workflow and obtained results.

Results

Differential expression of heat-stress activated retrotransposon families after H. annosum *inoculation/wounding*

Reads with similarity to all 16 retrotransposon family sequences were found in the transcriptome data (Table 2). At least one read with similarity to the retrotransposon sequences was found in all treatment transcriptome sequencing libraries, with the exception of the Horpia2 family, where no matching reads were found in the wounded libraries. Over all treatment libraries, the number of reads similar to the retrotransposon sequences ranged from four (for the Conan family) to 997 (for the Karin family). Only two of the retrotransposon sequences were differentially expressed between the *H. annosum* inoculated, wounded and control transcript libraries. These were Geneva, which was more highly expressed in inoculated versus control treatments (fold change: 3.26, *p*-value: 0.03), and Bare1, which was more highly expressed in control versus wounding treatments (fold change: 7.46, *p*-value: 0.04).

Genome regions flanking genes differentially expressed after H. annosum *inoculation/wounding with similarity to heat-stress activated retrotransposon families*

The sixteen retrotransposon family sequences were compared to the genomic sequences in the 5’ region of previously identified differentially expressed genes, and eight had BLAST hits with e-values < 0.05 (Table 3). The number of High-scoring Segment Pairs (HSPs) ranged from 36 for the Tnt 1-94 sequence to one for the Carmilla

Table 2. Number of reads matching the retrotransposon family sequences in the transcriptome libraries. *, sequences that were differentially expressed between treatment libraries

Retrotransposon family	Total matching reads – inoculated	Total matching reads – wounded	Total matching reads – control	Total matching reads – all treatments
Karin	426	266	305	997
Ifis	109	67	72	248
Maximus	112	62	58	232
Carmilla	76	36	54	166
Wham	58	45	36	139
Laura	74	31	33	138
Erika	61	45	31	137
Sabrina	63	25	40	128
Tnt 1-94	35	22	17	74
Persephone	30	20	19	69
Oryco1-1	19	19	14	52
Geneva	23*↑	9	4*↓	36
Bare1	8	1*↓	9*↑	18
Diaspora	7	1	1	9
Horpia2	2	0	4	6
Conan	1	2	1	4

Table 3. Retrotransposon family sequences with similarity to genomic regions flanking stress-related genes in the Scots pine genome

Retrotransposon family	Number of HSPs	Lowest E-value	Longest HSP length (nucleotides)	No. of unique gene regions	No. of unique gene regions in which other retrotransposon sequences were found
Tnt 1-94	36	8.17e–28	849	15	11
Sabrina	37	3.69e–08	65	18	9
Maximus	15	4.09e–11	255	13	10
Oryco1-1	9	1.90e–35	465	8	3
Laura	5	7.07e–21	383	4	3
Conan	2	1.70e–03	39	2	2
Erika	4	4.54e–04	188	2	1
Carmilla	1	2.00e–02	27	1	0

sequence. The length of HSPs ranged from 849 nucleotides (Tnt 1-94 sequence) to only 27 nucleotides (Carmilla sequence). The number of unique gene regions with similarity to the analysed retrotransposon families ranged from 18 (Sabrina) to one (Carmilla).

Twenty-four of the identified 5’ gene regions had similarity to only one of the retrotransposon families, while 17 had similarity to two or three retrotransposon families. As expected, the retrotransposon families with the highest number of hits to the gene regions also had similarity to the highest number of gene regions with similarity to multiple retrotransposon families (Table 4). The annotations of the genes in the 17 gene regions with similarity to multiple retrotransposon families indicate that the genes are involved in a range of functions. All the genes were previously identified as being differentially expressed in response to fungal (*H. annosum*) infection or wounding (Šķipars, Ruņģis 2021). Two of the genes were annotated as transcription factors (WRKY and VQ motif-containing protein), while others were catalases and other protein-coding genes. Six of the genes were not annotated.

Discussion

Retrotransposons are ubiquitous in plant genomes, and have been shown to be much more than ‘junk DNA’, and play

Table 4. Gene regions with similarity to more than one retrotransposon family

P. sylvestris gene region sequence ID	*P. sylvestris* gene annotation	Tnt 1-94	Sabrina	Maximus	Oryco1-1	Laura	Conan	Erika
0655a3ed	Anti-microbial protein	x	x					
2ce51680	No annotation		x	x			x	
404f38fa	Abscisic acid water deficit stress and ripening inducible-like protein	x	x					x
45e55033	No annotation		x			x		
4a4ff114	No annotation	x		x				
4e7a97b6	CASP-like protein 5A1	x	x					
793cd0b7	No annotation		x	x				
813ed920	Probable WRKY transcription factor 31	x		x				
86fd76fe	Peroxidase 40	x	x					
8c93da45	Dehydrin 7 protein			x	x	x		
9a9c0f96	No annotation	x	x					
b452e5c0	No annotation		x	x				
bd106f5c	VQ motif-containing protein 22-like (transcription factor)	x		x			x	
d842e64f	Abscisic acid and water-stress induced protein	x		x				
d8d7c9c2	Alpha carbonic anhydrase 7			x	x			
db8947e2	Hemoglobin 1	x		x	x			
e4397adf	Class V chitinase	x				x		

a role in influencing evolutionary and adaptive processes in plants (Ariel, Manavella 2021). In particular, transposable sequences can be associated with genes, and can act as functional enhancers of plant responses to environmental stresses (Klein, Anderson 2022). Stress response pathways and gene expression networks are relatively well studied in plants, both for abiotic and biotic stress responses (Zhang et al. 2022; Du et al. 2024). Furthermore, there is increasing evidence that highlights the role of transposable elements in the formation of these networks and pathways and the mechanisms of how they are modulated (Negi et al. 2016).

This study investigated sixteen retrotransposon families that were previously shown to be activated in Scots pine after an abiotic stress (heat) treatment (Voronova et al. 2011). The potential involvement of these retrotransposon families in responses to biotic stressors in Scots pine was explored by determining the expression of these retrotransposon families after inoculation with the fungal pathogen *H. annosum* or wounding. In addition, DNA sequence similarity between these retrotransposon families and genomic regions containing genes that were differentially expressed after inoculation with *H. annosum* or wounding (Šķipars, Ruņģis 2021) was determined.

The results obtained in this study indicated that transcripts with sequence similarity to all sixteen retrotransposon families were found in *H. annosum* inoculated, wounded and control transcriptome libraries with the exception of the Horpia2 family after wounding. However, the expression of this family was also low in the inoculated and control transcriptome libraries (2 and 4 transcripts identified, respectively). Therefore this transcript might have also been identified in the wounded libraries with increased sequencing depth. Two of the transcripts with similarity to the retrotransposon families were differentially expressed between treatments, with the Geneva-like transcript being more highly expressed in inoculated samples compared to controls, and the Bare1-like transcript having lower expression in wounded samples compared to controls. This suggests that the retrotransposon families with changes in transcription levels after heat stress at least partially overlap with those with transcriptional changes after fungal infection and/or wounding. There is some evidence of the overlap of plant responses to biotic and abiotic stresses (Nejat, Mantri 2017), however, more research is required to determine the extent of shared responses to different stresses.

Transposons can influence gene expression at a transcriptional level, but also at post-transcriptional and translational levels (Kan, Li 2023). Therefore, 5' genomic regions of genes differentially expressed in biotic stress conditions were searched for DNA sequence similarity with the retrotransposon families activated in response to abiotic stress. Sequence similarity with eight of the sixteen retrotransposon families was found. Interestingly, retrotransposon sequences similar to the two differentially expressed transcripts were not identified in the gene regions. Sequences similar to three retrotransposon families (Sabrina, Conan and Carmilla) were less than 100 nucleotides in length, however some gene regions had extensive similarity with the retrotransposon families. The longest stretch of DNA sequence similarity was with the Tnt 1-94 family (849 nucleotides), but extensive similarity was also found with the Oryco1-1 family (465 nucleotides) and the Laura family (383 nucleotides). Further investigation of the gene regions with similarity with the retrotransposon families is needed to investigate potential functional or structural roles that these sequences may have, as well as further targeted sequencing to potentially identify full-length and functional retrotransposons in these gene regions. It will be possible to make a better assessment of this once a high-quality reference genome sequence of Scots pine is available.

Over 40% (17 of 41) of the gene regions had DNA sequence similarity to multiple (two or three) retrotransposon families. It has been known for a long time that the transcription of retrotransposons is activated in stress conditions (Grandbastien 1998), and that this can enhance their insertion in to genomic regions containing transcriptionally activated genes (Alzohairy et al. 2014). As described in the current study, transcripts with similarity to all sixteen retrotransposon families were identified in the Scots pine transcriptome. Of the 17 gene regions with similarity to multiple retrotransposon families, six of the genes in these regions were not annotated, which reflects the relatively sparse information that is available about the Scots pine genome. The genes with annotations were transcription factors as well as enzyme-coding genes. Two of the genes were annotated as abscisic acid and water-stress induced proteins, and one as a dehydrin. These genes were differentially expressed in response to fungal inoculation, but drought and water stress can also be a consequence of heat stress. Further investigation of these pathogen induced genes under different stress conditions is needed to identify commonalties between stress responses in Scots pine. Another alternative explanation for the sequence similarity with multiple retrotransposon families is that these Scots pine sequences represent novel retrotransposons. Further analysis of these gene regions can identify functional retrotransposon structures (i.e. inverted terminal repeats, transposase genes etc.), but these will probably require addition targeted sequencing, as retrotransposons can be several kilobases long (Finnegan 2012). These 5' genomic regions flanking stress-related genes with similarity to multiple retrotransposon families may represent hotspots of retrotransposon insertions, indicating that these genes could be hubs of gene networks that are activated under a range of stress conditions.

Any form of stress can make plants more susceptible to other stressors (Zandalinas, Mittler 2022), and this study provides an initial insight into the role of retrotransposons in the response of Scots pine to two different stress conditions, biotic (fungal infection) and abiotic (heat stress). Climate change will result in a complex array of stresses that will impact ecosystems, interacting and reinforcing each other (Nawaz et al. 2023). Scots pine is a keystone species in the hemi-boreal region in Europe, as well as being an economically significant species for forestry in this area. Therefore, forest management and breeding approaches need to be developed that can be used to facilitate the adaptation of Scots pine to climate change to ensure the stability of ecosystems and the forestry sector. This study suggests that Scots pine responses to different stress conditions may have common elements, and indicates further research directions to better understand the role of retrotransposons in stress responses in Scots pine.

Conclusions

This study investigated the presence of previously identified heat-stress activated retrotransposon family sequences in transcribed sequences after *H. annosum* inoculation and wounding stress, as well as in genomic sequences in the 5' region of stress-related genes. The results indicated that two of the 16 investigated heat-stress activated retrotransposon family sequences were differentially expressed in the Scots pine transcriptome after *H. annosum* inoculation and wounding stress. Eight of the 16 heat-stress activated retrotransposon family sequences had sequence similarity with the 5' genomic regions near stress-related genes, and 17 of the 5' genomic regions had sequence similarities with multiple retrotransposon families. These gene regions could be retrotransposon insertion hotspots, and further investigation of these genes is needed to determine if they are hubs of gene expression networks that are activated in response to a range of stress conditions in Scots pine. This information will provide additional information about molecular adaptation mechanisms in Scots pine and assist in the development of forest management practices to facilitate the adaptation to climate change.

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