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Predicting sapstain and degrade in fallen trees following storm damage in a *Pinus radiata* forest

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ABSTRACT

Storm damage in production forests constitutes a major source of economic loss world wide, yet the retrieval of salvageable timber remains problematic. In particular, an inability to anticipate when sapstain and degrade will appear hampers the planning of log recovery operations. A study was conducted to monitor the deterioration of fallen trees following two winter storms causing wind and snow damage in a *Pinus radiata* plantation forest in the upper South Island of New Zealand. Percentage sapstain, incidence of basidiomycete decay fungi, and frequency of bark beetle infestation increased, while percentage sapwood moisture content decreased, over a period of 1 year. These changes proceeded more rapidly in fallen trees that were severed at stump height, to simulate breakage, than in those that were left partially rooted. There was little beetle activity at the time of the storms, but *Arhopalus ferus* (Coleoptera: Cerambycidae), and *Hylastes ater*, *Hylurgus ligniperda* and *Pachycotes peregrinus* (Coleoptera: Curculionidae: Scolytinae), were collected in flight traps during the following spring and summer. The predominant fungal species associated with sapstain was *Diplodia pinea*, while *Ophiostoma piceae* and *Grosmannia huntii* were isolated near the end of the period. The main decay fungi obtained were *Phlebiopsis gigantea*, *Stereum sanguinolentum*, and *Schizophyllum commune*. A generalized linear mixed model was constructed to predict the development of sapstain in fallen trees for conditions prevailing during the study after a storm at the same time of year. According to the model, a 10 m long butt log of 22 cm mid length diameter will have minimal stain (<10% of the cross sectional area affected) when cut from severed stems up to 4 months after the storm; if taken from still-rooted trees this period will extend to 1 year. However, because of large between-tree variation, economically productive log recovery will also depend on the proportion of trees that lie below an acceptable sapstain threshold. Further research is needed to determine regional and seasonal influences on the development of sapstain in fallen trees.

1. Introduction

Storms are a major cause of destruction in forests world wide (e.g. Gandhi et al., 2008; Grayson, 1989; Haymond and Harms, 1996; Nieuwenhuis and O'Connor, 2001; Strehlke, 1974). However, although much has been published describing the effects of individual storm events and how to manage stands to reduce potential damage, less information is available on the effective retrieval of large volumes of fallen wood after a storm (Childs, 1966; Gleason, 1982; Grayson, 1989). Options for reducing the cost of storm damage tend to be handicapped by a shortage of basic information necessary to plan log recovery operations. In particular there is uncertainty about the window of time available before logs become unsalvageable due to fungal staining or decay, and infestation by insects. Forest managers must often rely on personal experience and take an adaptive approach to management as circumstances change (Childs, 1966; Grayson, 1989; Strehlke, 1974). To overcome these constraints, and enhance wood recovery rates after storm damage, a program of systematic monitoring will be required (Butcher and Drysdale, 1991).

Some useful anecdotal information was recorded following two storms in 1964 and 1975, both in Canterbury, a drier part of the South Island of New Zealand. On both occasions, when fallen radiata pine (*Pinus radiata* D. Don) remained partially rooted trees were still salvageable after more than a year (Butcher and Drysdale, 1991; Childs, 1966; Wendelken, 1966). This result was independent of

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the timing of the storms, which took place at the end of winter and in early autumn, respectively. A similar outcome followed a major storm in the United Kingdom in autumn 1987, where the extent of timber degradation was dependent on whether trees were either broken or uprooted (Grayson, 1989). Sapstain remained low in stands of pine (*Pinus sylvestris* L. and *P. nigra* var. *maritima* (Ait.) Melville) during the first year after this storm because many of the windthrown trees were still partly rooted and foliage remained green throughout the summer (Dannatt and Garforth, 1989; Evans et al., 1989; cf. Eisenbarth, 1995). In New Zealand, Gleason (1982) and Littlejohn (1984) documented the industry experience following a storm in 1982 in a central North Island radiata pine forest. These reports did not clearly distinguish between snapped and intact uprooted trees. Very little degradation occurred until spring, 6 months after the storm when changes were made to the processing of both sawn timber and pulp wood following the appearance of a low incidence of sapstain (Gleason, 1982; Somerville et al., 1989). Infestation by bark- and wood-boring beetles was not an issue due to limited insect activity during the cooler autumn and winter periods.

On 30 July, 2008, a severe winter wind storm caused extensive uprooting and breakage in plantations of *P. radiata* in the Nelson region of the northern South Island of New Zealand. Heavy snow led to further damage elsewhere in the same region 2 weeks later, predominantly from uprooting, where trees fell with some roots still intact within the soil. About 2000 ha of plantation were affected by the storms over the whole region and a salvage operation was commenced to recover merchantable timber. Rapid development of sapstain was of particular concern with the approach of warm spring weather, which would favour the causal fungi and coincide with annual bark beetle (Scolytinae) flights (Hosking, 1977). These insects are significant as they are known vectors of sapstain fungi (e.g. Reay et al., 2006a,b; Romón et al., 2007). Although the event was unfortunate, the circumstances provided an opportunity to obtain quantitative information on the rate of sapstain development in the fallen trees. A study was therefore initiated in a forest on rolling hill country affected by the storm.

Priority was given to a number of variables. It was clear that a useful distinction should be made between snapped and partially rooted trees, which were likely to deteriorate at different rates. The degree of water saturation is well known as a regulatory factor within wood as moisture content values greater than 120% (dry weight basis) maintain low oxygen levels that prevent the growth of most (but not all) species of degrade fungi (Clifton, 1978; Hood and Ramsden, 1997; Hood et al., 1997; Liese, 1984; Metzler and Hecht, 2004; Peralta et al., 1993; Seifert, 1993). The objective of this study was therefore to monitor the rates of sapstain development and the associated biological agents of degrade in the fallen rooted and severed stems. A modelling approach was used to predict the period available for log retrieval under similar climatic conditions following a storm at the same time of year. In this paper we present our conclusions and suggest future research avenues for improving the management of timber salvage operations.

2. Materials and methods

2.1. Study sites

Five study sites, each approximately 200 m by 200 m, and ranging 6–18 km apart, were selected for monitoring. Stands varied in age (13–19 years), altitude (300–500 m a.s.l.), slope, and in type and date of storm damage. Site 3 experienced increased exposure to sunlight and wind prior to the completion of the study due to the salvaging of wind-damaged stands in the immediate vicinity. Climate data for the 15 months following the storms obtained from a permanent weather station situated within the forest are shown in Table S1.

A total of 20 fallen trees, 10 uprooted and 10 severed (snapped or cut), were arbitrarily selected and tagged at each site for a series of samplings during the 17 months period after the storms. Snapped stems were used during the first sampling, but because of a shortage of accessible naturally broken trees, the stems of 8 fallen trees per site were cut at stump height (ca. 0.5 m above original ground level) to simulate windsnap for subsequent samplings. This was done on 17–18 September 2008, at the time of the first sampling, 34 or 50 days after the severe wind and snowfall events, respectively. Sampling was undertaken on 6 occasions from 4 trees (2 severed and 2 rooted) at each site during each sampling time. However, on two occasions only 2 trees were sampled in order to spread sampling across the full period of sapstain development, which varied between severed and rooted stems. Sampling dates were therefore: 17–18 September 2008 (early spring), 10 November 2008 (late spring), 19 February 2009 (late summer), 28 April 2009 (autumn; severed trees, only); 8 July 2009 (winter); and 24 November 2009 (late spring; rooted trees, only).

2.2. Tree and disc processing

Sapstain development and bark beetle infestation was monitored by cutting discs from sample trees. Five 3 cm-thick discs were taken from each tree at intervals of 3 m (first sample time) or 2.5 m (remaining sample times) along the stem, offsetting slightly if this position coincided with a branch node. The initial disc was cut at stump height (0.5 m from the base) on rooted trees, or near the point of severance on severed trees. Discs were immediately labelled and sealed in plastic bags, and stored at 4 °C usually within 12 h, in order to minimise moisture loss and further fungal growth before measurement. Due to this destructive method of sampling, each tree was sampled only once.

Sapstain was recorded by photographing each disc using a specially constructed stage to compensate for image distortion, as follows. On each image, zones of stain and the position of the cambium were outlined manually as polygons using ESRI ArcGIS 9.3 (Redlands, California, USA) to estimate sapstain as a percentage of the whole disc (excluding bark). During the image analysis, no allowance was made for heartwood which, when present, occurred only in small amounts. Moisture content of the inner and outer sapwood was determined (dry weight basis) within 36 h of sampling. Two small blocks were cut from the sapwood at an arbitrary point around the circumference of each disc, one taken from the outer half and the other from the inner half along the same radius. Blocks were weighed at room temperature to constant mass before and after drying at 80 °C in a ventilated oven.

2.3. Insect sampling

A record was made of the occurrence of bark beetles and wood borers as potential carriers of sapstain fungi, as well as being direct agents of damage to salvageable wood in their own right. Beetle infestation of study trees was monitored from sampling time 3 (19 February 2009) onwards. During field sampling, 0.5 m lengths of stem were cut above but contiguous with the positions of discs 1 and 4, and a record made of any external evidence of beetle colonisation (entrance holes and frass) on these stem sections. In addition, all five sample discs were also assessed for beetle colonisation (i.e. presence of galleries with adults or larvae). Similarly, contact with the ground or another fallen stem was recorded as this is likely to influence the probability of beetle colonisation.

The phenologies of the bark beetles *Hylastes ater* (Paykull), *Hylurgus ligniperda* (F.), and *Pachycotes peregrinus* (Chapuis) (Coleoptera: Curculionidae: Scolytinae), and the longhorn beetle

Arhopalus ferus (Mulsant) (Coleoptera: Cerambycidae), were determined using eight-unit Lindgren funnel traps (PheroTech, Delta, BC, Canada). Two general attractants for pine-infesting wood borers and bark beetles, α-pinene and ethanol, were used as lures as described in Brockerhoff et al. (2006a). Two traps were installed at each site, and beetles were collected every 2 weeks during autumn, summer and spring, and monthly during winter. Additional beetle phenology data were obtained from long-term monitoring traps that had been installed previously at several locations in nearby plantations. Data from long-term monitoring traps were used to obtain regional estimates of beetle activity before trap data became available from the storm-affected sites.

As an additional indicator of seasonal beetle activity, eight small billet logs measuring 30–40 cm (length) × 8–15 cm (diameter) were placed at each site during the first sample time (17 September 2008). Bark was subsequently removed and a record made of the onset and duration of beetle colonisation (entrance holes, galleries and live insects). Infestations were differentiated between the upper and lower longitudinal segments of the undisturbed billet to assess the effect of ground contact.

2.4. Fungal isolation and identification

Isolations to identify and quantify decay fungi were undertaken systematically within 10 days of sampling from discs 1 and 4, only, on all study trees for each sampling time. An arbitrary sector was cut from each disc using a small axe. This was bisected aseptically along the radial longitudinal plane in the laboratory by using the axe to initiate a split and then separating each portion manually, avoiding any external contact with the newly created surfaces. Five small chips were incised with a sterile scalpel from along a radial line on one freshly exposed surface, the first three from depths of 1, 2 and 3 cm, respectively, below the cambium; the fifth chip from near the disc centre; and the fourth chip midway between the third and fifth sample points. Chips were plated onto a medium selective for basidiomycetes consisting of 2% malt agar supplemented with 100 ppm streptomycin sulphate and 10 ppm benomyl. In all, 969 isolation attempts for decay fungi were made during the study. After incubation for periods up to 10 weeks, emerging isolates were sub-cultured in tubes of 2% malt agar. Bacterial colonies were mostly recorded and not isolated. Culturally identical isolates were sorted into groups, and a record was kept of those recognised as basidiomycetes (those identified in previous work or unknown species with clamp connections; Hood and Gardner, 2005). Remaining fungi (except yeasts, sporulating hyphomycetes, and mucoraceous species) were examined with α-naphthol, and those testing laccase positive (indicative of white rot behaviour) were also treated as decay fungi. A culture code modified from Nobles (1965) as previously described (Hood and Gardner, 2005), was prepared for each basidiomycete species in order to record its key identification features when grown on 2% malt agar plates for more than 6 weeks.

Isolations to identify the fungi causing sapstain were also attempted on non-selective 2% malt agar plates. Five or more chips for plating were cut from a stained portion of wood on a freshly exposed surface after aseptically splitting along the radial longitudinal plane through a zone of sapstain. Isolations were only attempted if sapstain was present, and mostly from only one stained region per tree. Isolations were made from either disc 1 or 4, or occasionally from another disc if these were unstained. Emerging isolates were sorted into groups, and where possible identified macro- and microscopically from their vegetative morphology and fruiting structures. Fruiting was encouraged for a representative selection of isolates believed to be *Diplodia pinea* (Desm.) J. Kickx f. (syn. *Sphaeropsis sapinea* (Fr.) Dyko & B. Sutton) by growing on gamma irradiated *P. radiata* twigs and needle segments.

In addition to morphological identification, a selection of isolates were resolved using sequence analysis of the internal transcribed spacer (ITS) region. Isolates were sub-cultured on sterile GelAir cellophane (BIO-RAD Laboratories, Hercules CA, USA) that was placed on 1.5% malt agar plates. Mycelium was scraped directly off the cellophane and placed into a sterile 1.5 mL centrifuge tube for DNA extraction, which was undertaken using the REDExtract-N-Amp™ Plant PCR kit (Sigma, St. Louis, Missouri, USA), following the manufacturer's instructions. The internal transcribed spacer regions of the rDNA were amplified using the primer combination ITS1F (5′CTTGGTCATTTAGAGGAAGTAA3′) and ITS4 (5′TCCTCCGCTTATTGATATGC3′) (Bruns and Gardes, 1993). For basidiomycete species the basidiomycete specific primer combination of ITS1F and ITS4B (5′CAGGAGACTTGTACACGGTCCAG3′) was used (Gardes and Bruns, 1993). DNA was amplified using the PCR mix supplied with the REDExtract-N-Amp™ kit, including *Taq* enzyme, hot start *Taq*Start antibody and dNTPs, the primer concentration being 50 pmol/μL. The thermocycling programme was as follows: initial denaturation 95 °C for 6 min, followed by 35 cycles of 95 °C for 30 s, 60 °C for 40 s and 72 °C for 40 s, followed by a final extension step of 72 °C for 5 min on an Eppendorf Mastercycler Gradient Thermal Cycler. PCR products were visualised by electrophoresis and purified using the ExoSAP method (Exonuclease I, *Escherichia coli* and Shrimp Alkaline Phosphatase, SAP) according to the supplier's instructions (Fermentas Life Sciences, Lithuania). Sequence analysis was carried out at Macrogen Inc., Korea. DNA sequences were edited and aligned using Sequencher version 4.7 (GeneCodes Corp., Ann Arbor, Michigan, USA) and identities were determined by GenBank BLAST search (Altschul et al., 1990). For identification, a minimum of 95% sequence identity to an ITS sequence of at least 450 bp from a known specimen in the database was required. Those samples with 97–100% identity match to a known species were considered a match and named to the species level.

2.5. Statistical analyses

Data were initially inspected by constructing scatter matrices to visualise the relationships between percentage sapstain, percentage outer sapwood moisture content, percentage inner sapwood moisture content, disc diameter and disc height for all the data together and after separating out the rooting type (rooted or severed) and the sample times. Degrees of relationship among these variables were evaluated by means of Pearson's correlation coefficients, distinguishing between rooting type and sampling times.

A number of different models aimed at predicting the progress of sapstain and moisture content over time were investigated. Independent predictor variables were considered in both models relating to whether the tree was rooted or severed, and to disc diameter and position (the height of the sampled disc). Examination of the response variables revealed that most differences were between the basal disc and the remaining upper discs. Hence an indicator variable was introduced to specify whether the disc was a basal disc or one of the upper discs. Sapwood moisture content was modelled as a function of time with a linear mixed model using PROC MIXED (SAS, 2008) while the prediction of the proportion of stem with sapstain and the isolation frequency of decay fungi were both modelled using a generalized linear mixed model with a binomial distribution and a logit link function in PROC GLIMMIX (SAS, 2008) (Littell et al., 2006). In all models, site and trees within site were considered as random effects, and autocorrelation of discs sampled from the same tree was accounted for in all models with a first order auto-regressive (AR(1)) error structure. Error terms were appropriate to the correct hierarchy associated with the data.

Models were assessed in terms of the root mean square error (RMSE; Eq. (1)), the mean error (ME; Eq. (2)) (Fehrmann et al., 2008), a loglikelihood R^2 (R^2_{LR}) (Eq. (3)) (Kramer, 2005) and an adjusted concordance correlation coefficient (r_c; Eq. (4)) (Vonesh et al., 1996) (Table S2). Criteria were based on predictions made without the inclusion of random effect predictions as these characteristics would be unknown for a new site.

The influence of beetle infestation on sapstain development was analysed by comparing differences in sapstain proportions in discs in relation to whether or not infestation had occurred. This was done by means of simple *t*-tests, using Satterthwaite's method for data with unequal variances (SAS, 1999), considering the two disc positions (1 and 4), with and without the adjacent log segment, for rooted and severed trees. Intensity of beetle infestation to the upper and lower surfaces of placed billets was analysed using analysis of variance (ANOVA); data were log transformed to meet assumptions of normality.

3. Results

3.1. Moisture content and sapstain

Moisture content of inner and outer sapwood decreased, and sapstain increased, during the course of the study (Table 1). Severed stems (Table 1a) dried more rapidly and developed sapstain more quickly than rooted stems (Table 1b). Mean percent sapstain of discs in severed trees was >15% 188 days (27 weeks) after the snow event, i.e. 154 days (22 weeks) after cutting in early spring, when mean moisture content was <120% (Table 1a; for site 2, affected by the wind storm, this period was 16 days longer). By contrast sapstain averaged <2% in discs from rooted trees during the same period, and mean sapwood moisture content was still >120%. The majority of rooted trees remained alive and retained green foliage for up to a year after windfall.

There was substantial variation in percent sapstain and moisture content between individual discs and trees as shown by high standard deviations (Table 1). This variability was even more apparent in the scatter matrices where few relationships were indicated (e.g. Fig. S1), and most Pearson correlation coefficient (r) values were low (less than 0.5).

The ratio of outer to inner sapwood moisture content was less than 1 in 75% of samples indicating a lower outer sapwood moisture content (Table 1). A paired *t*-test showed significant ($P < 0.001$) differences between the outer and inner moisture contents with the outer sapwood having an 11.4% lower MC than the inner sapwood, on average.

A number of models to predict moisture content loss and the progress of sapstain over time, that included various combinations of the dependent variables, were explored. Moisture content was modelled at the disc level. However, all references to position on the stem (e.g. disc diameter, relative diameter defined as the disc diameter divided by the diameter of the basal disc of the tree), were not significant, so were not included in the models. The models selected are shown below (Eqs. (5) and (6)), while the parameter estimates are provided in Table 2.

$$M_{ijk} = \beta_0 + \beta_1 \ln(T) + \beta_2 R_{ij} + \beta_3 D_{ijk} + \beta_4 D_{ijk} R_{ij} + \beta_5 \ln(T) R_{ij} + a_i + b_{ij} + \varepsilon_{ijk} \quad (5)$$

$$\text{logit}(p_{ijk}) = \gamma_0 + \gamma_1 \ln(T) + \gamma_2 R_{ij} + \gamma_3 D_{ijk} + \gamma_4 R_{ij} D_{ijk} + a'_i + b'_{ij} + \varepsilon'_{ijk} \quad (6)$$

where M_{ijk} is the moisture content of disc k from tree i at site j; p_{ijk} is the proportion of sapstain in disc k from tree i and site j; $\ln(T)$ is

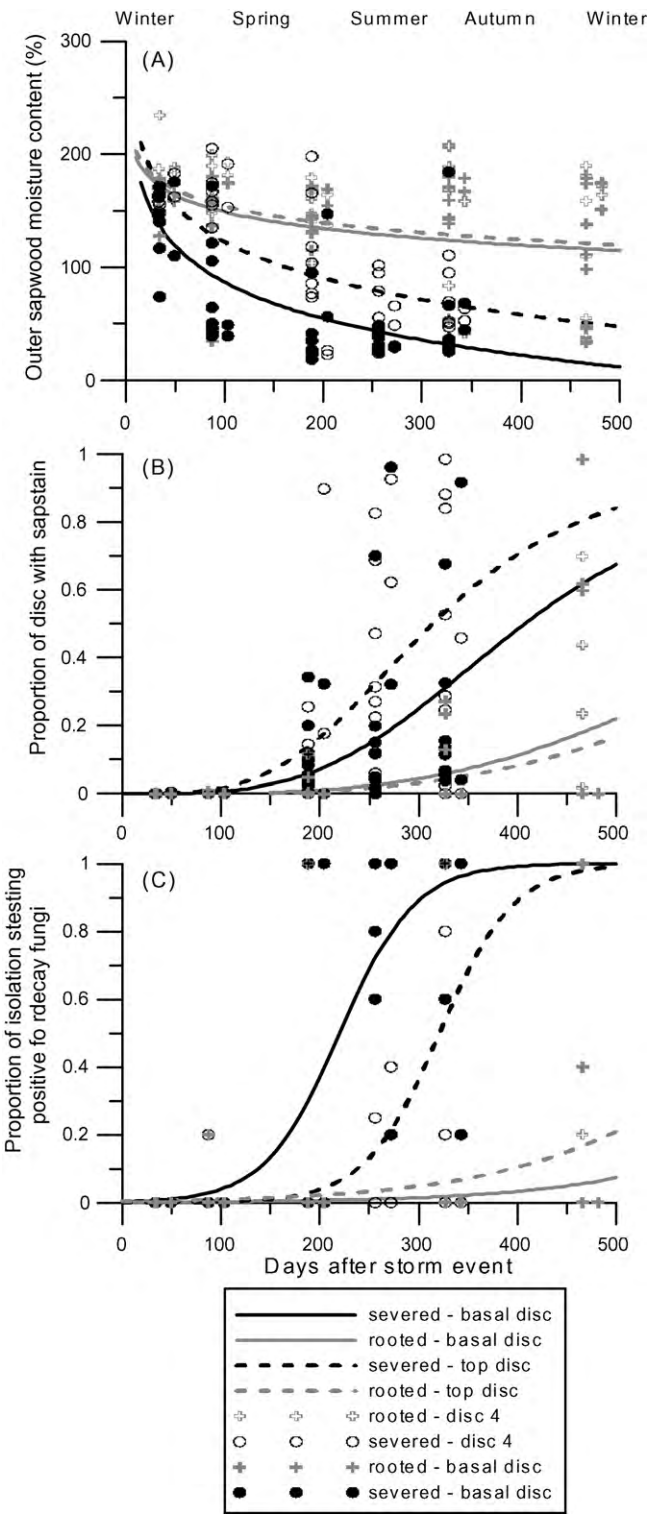

Fig. 1. Comparisons of model predictions of (A) outer sapwood moisture content, (B) sapstain, and (C) occurrence of decay fungi, for severed (black) and rooted (grey) trees. Symbols indicate observed data points for the basal disc 1 (solid symbol) or disc 4 (hollow symbol), the solid and broken curves being the predicted values for the basal disc and combined upper discs, respectively. Fit criteria are, respectively: model (A), ME, 0.44; RMSE, 46.54; R^2_{LR}: −2.73 and adjusted r_c: 0.58; model (B), ME: 0.00592; RMSE: 0.181; R^2_{LR}: 0.98 and adjusted r_c, 0.63; model (C), ME: 0.00674; RMSE: 0.247; R^2_{LR}: −0.98 and adjusted r_c, 0.69. The models for severed trees are derived from data for stems that were cut 34 or 50 days after the snow or windstorms, respectively.

Table 1
Mean percent sapstain, percent sapwood moisture content, and disc size, with standard deviations, of (a) severed stems, and (b) rooted trees, by time since windthrow event.

Sampling time	Date 2008–2009 (season)	Days after storm[a]	Sapstain (%)[b]		Moisture content (%)				Disc diameter (cm)	
			Mean	SD	Outer SW		Inner SW		Mean	SD
					Mean	SD	Mean	SD		
(a) Severed stems										
1	17 September (spring)	33	0.0	0.1	153	26	165	39	17.5	4.4
2	10 November (spring)	87	0.0	0.0	141	48	145	53	24.8	6.1
3	19 February (summer)	188	15.6	22.8	73	45	90	59	22.4	5.8
4	28 April (autumn)	256	37.5	29.6	65	46	81	57	23.6	4.9
5	8 July (winter)	327	45.8	34.6	67	46	78	68	23.9	4.8
6	24 November (spring)	466	–	–	–	–	–	–	–	–
(b) Rooted stems										
1	17 September (spring)	33	0.0	0.0	173	18	191	20	20.7	6.5
2	10 November (spring)	87	0.2	1.1	163	39	183	62	23.5	5.5
3	19 February (summer)	188	1.7	6.2	140	50	153	40	22.2	6.6
4	28 April (autumn)	256	–	–	–	–	–	–	–	–
5	8 July (winter)	327	2.5	6.1	127	67	125	67	22.9	5.4
6	24 November (spring)	466	16.1	27.6	120	65	125	71	24.0	5.7

[a] Applies to four sites that experienced snow damage; wind damage in the fifth site (site 2) occurred 16 days earlier. Severed stems sampled at times 2–6 were cut on 17–18 September, 34 or 50 (site 2) days after the storms.
[b] Percentage disc surface area affected.

the natural log of the number of days since the storm event, days >10); R_{ij} is an indicator variable indicating whether tree i from site j is severed or rooted (0 = severed; 1 = rooted); D_{ijk} is an indicator variable indicating whether disc k from tree i at site j was a basal disc or an upper disc (0 = upper disc; 1 = basal disc); β_0, β_1, β_2, β_3, β_4, γ_0, γ_1, γ_2, γ_3, and γ_4 are estimable parameters. a_i, b_{ij} a'_i and b'_{ij} are random variables associated, with the site and the trees within site, $a_i \sim N(0, \sigma_a^2)$, $b_{ij} \sim N(0, \sigma_b^2)$, $a'_i \sim N(0, \sigma_{a'}^2)$, $b'_{ij} \sim N(0, \sigma_{b'}^2)$; ε_{ijk} and ε'_{ijk} are random errors, $\varepsilon_{ijk} \sim N(0, \sigma^2)$, $\varepsilon'_{ijk} \sim N(0, \sigma'^2)$.

Fig. 1A and B show the mean model predictions for the basal disc and for the remaining upper discs taken together; also shown are the raw data for the basal disc and, as an example, for upper stem disc 4. Rooting type (rooted or severed), stem diameter and moisture content were significant in describing sapstain development. The models indicated that sapstain appeared mainly when moisture content had fallen below 120% (cf. Fig. S1). This occurred approximately 150 days after the storm (ca. 100 days after stems were severed; Fig. 1A and B). The random effects of site or trees within sites were not significant when predicting either percentage outer sapwood moisture content or proportion of sapstain over time. However, significant autocorrelation between discs from the same tree was found.

3.2. Bark beetles

There was no evidence of cerambycid colonisation of wood during the course of this study. The percentage of discs colonised by bark beetles increased significantly from sample time 3 to the final sample times on both severed (4% versus 42%) and rooted stems (2% versus 24%) ($P < 0.05$, $n = 50$, Fisher's exact test; Table S3). Over the full period, there was a significantly higher proportion of bee-

Table 2
Estimated parameters for the models used to predict (a) mean outer sapwood moisture content (Eq. (5)) and (b) the proportion of sapstain (Eq. (6)).

Parameter	Estimate	Standard error	*P* value
(a) Outer sapwood moisture content			
β_0	301.000	25.412	<.001
β_1	−46.533	4.893	<.001
β_2: If trees rooted (i.e. rooted = 1)[a]	−54.721	33.802	0.108
β_3: If considering upper discs (i.e. disc ≠ 1)[a]	35.695	6.378	<.001
β_4: If trees rooted and considering upper discs (i.e. rooted = 1 and disc ≠ 1)[a]	−30.679	9.020	<.001
β_5: If trees rooted (i.e. rooted = 1)[a]	25.379	6.544	<.001
σ_a^2	102.87	119.66	0.390
σ_b^2	98.746	89.169	0.268
AR(1)	0.400	0.0497	<.001
σ^2	2020.33	157.90	<.001
(b) Proportion of sapstain			
γ_0	−21.579	2.843	<.001
γ_1	3.590	0.505	<.001
γ_2: If trees rooted (i.e. rooted = 1)[a]	−1.998	0.458	<.001
γ_3: If considering upper discs (i.e. disc ≠ 1)[a]	0.934	0.222	<.001
γ_4: If trees rooted and considering upper discs (i.e. rooted = 1 and disc ≠ 1)[a]	−1.289	0.400	0.002
γ_0	−21.579	2.843	<.001
γ_1	3.590	0.505	<.001
γ_2: If trees rooted (i.e. rooted = 1)[a]	−1.998	0.458	<.001
γ_3: If considering upper discs (i.e. disc ≠ 1)[a]	0.934	0.222	<.001
γ_4: If trees rooted and considering upper discs (i.e. rooted = 1 and disc ≠ 1)[a]	−1.289	0.400	0.002
$\sigma_{a'}^2$	0.275	0.300	0.179
$\sigma_{b'}^2$	0.119	0.156	0.224
AR(1)	0.518	0.0479	<.001
σ'^2	0.257	0.0225	<.001

[a] If condition does not hold then parameter equals zero.

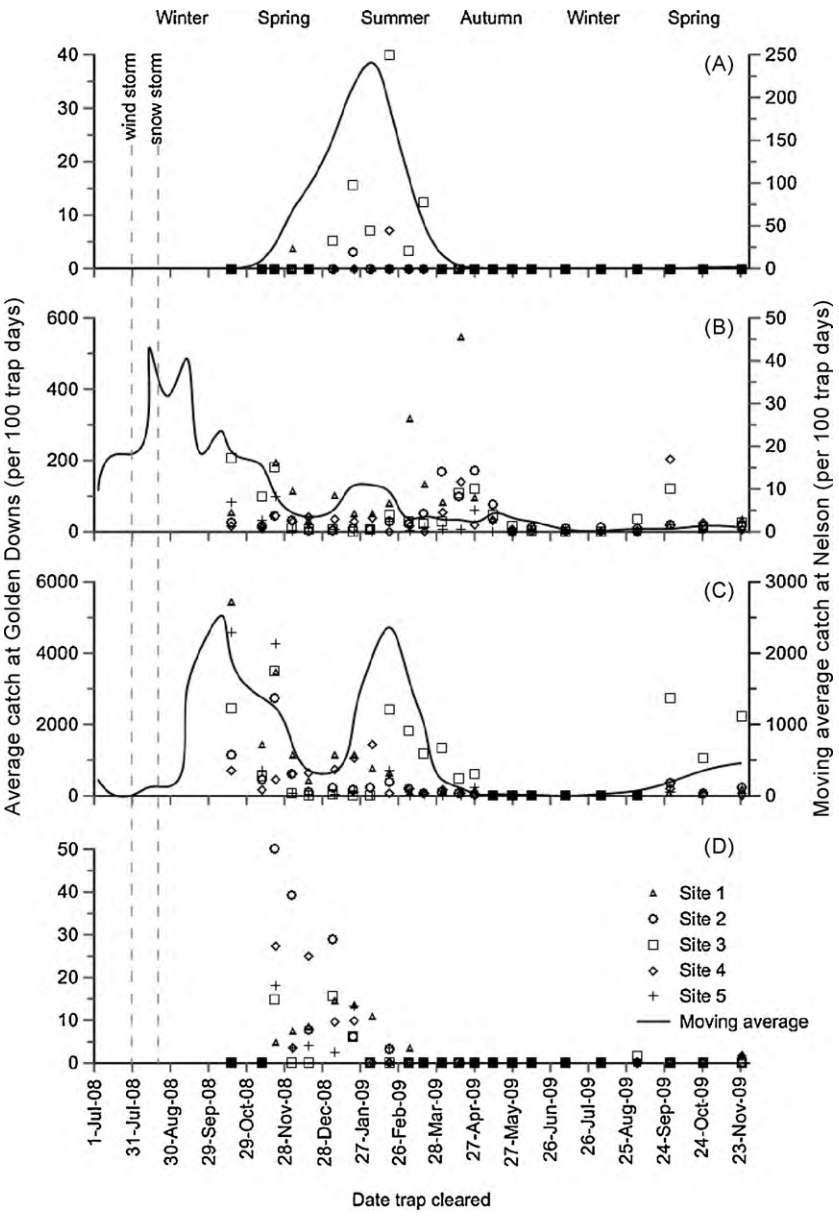

Fig. 2. Phenology of *Arhopalus ferus* (A), *Hylastes ater* (B), *Hylurgus ligniperda* (C), and *Pachycotes peregrinus* (D) across five trial sites in the storm-damaged forest (symbols) plotted against a smoothed 3 week moving phenology 'average' from semi-permanent beetle monitoring sites in the wider Nelson region. Trap clearing in the trial sites started on the 17th of October 2008. Note, no *P. peregrinus* were present at the Nelson sites.

tle attack in discs from severed stems (30%) than from rooted trees (13%; $P < 0.001$, $n = 150$). For most sample times there was no difference in percentage sapstain between discs with or without beetle attack, whether for the disc 1 or 4 position (inclusive of the upper adjacent stem segment) or for all discs taken together (Table S3). However, for rooted trees at sample time 6, the final sampling of the study, sapstain on all discs covered a significantly greater mean area (41%) when beetles were present at the assessment positions than when they were not (8%, $P = 0.006$; Table S3). Only 5.3% of discs without sapstain had evidence of beetle colonisation ($n = 131$). Windthrown trees lay mostly suspended across one another, and only 6.2% of all discs sampled had been in contact with the ground or adjacent fallen stems.

Seasonal abundance of beetle populations was monitored by trapping (with funnel traps) as an indicator of their availability to infest the study trees. Beetles were trapped in large numbers over the warmer months during spring and summer following the storms, after which there was a period of reduced abundance during the colder months (Fig. 2). *H. ligniperda* was the most abundant species representing 91.1% of all catches of the target borer species, followed by *H. ater* with 7.3%. Data from the long-term monitoring sites in Nelson indicated that *H. ater* was more active prior to, during, and immediately after the storms whereas *H. ligniperda* and *A. ferus* did not become active until late spring (September and November, respectively) (Fig. 2). Beetle abundance differed between sites, with the salvage-affected site (site 3) consistently experiencing higher counts, and others such as site 4 experiencing lower counts (Fig. 2).

Most of the small billet logs showed evidence of colonisation by *H. ater* and *H. ligniperda*, with an average of 7.1 adult bark beetles per billet at the time of the second assessment (10 November 2008, approximately 2 months after placement), but there were no signs of *A. ferus*. Colonisation by *H. ater* and *H. ligniperda* was more prevalent in the lower half of the billets that were in full contact

Table 3
Frequency of isolation of decay fungi by time from severed and still-rooted windthrown trees.

Sampling time	Days after storm[a]	No. isolation attempts	% attempts yielding isolates of:					
			Phlebiopsis gigantea[b]	*Stereum sanguinolentum*[b]	*Schizophyllum commune*[b]	Species α	Unspecified decay fungi	All species
(a) Severed stems								
1	33	100	0	0	0	0	0	0
2	87	90	0	0	0	0	1	1
3	188	99	4	6	0	5	0	15
4	256	98	20	31	0	2	0	53
5	327	100	14	45	7	0	0	66
6	466	–	–	–	–	–	–	–
(b) Rooted stems								
1	33	99	0	0	0	0	0	0
2	87	90	0	0	0	0	1	1
3	188	95	0	0	0	5	0	5
4	256	–	–	–	–	–	–	–
5	327	100	5	0	0	0	0[c]	5
6	466	99	11	7	0	0	0	18

[a] Applies to four sites that experienced snow damage; wind damage in the fifth site (site 2) occurred 16 days earlier. Severed stems sampled at times 2–6 were cut on 17–18 September, 34 or 50 (site 2) days after the storms.
[b] Culture codes, respectively: *P. gigantea*, 2, 5, (11), 12, (13), 35, 36, 38, 42, 55; *S. commune*, (2), 3, 20, 32, 36, 38, 42, 55; *S. sanguinolentum*, 2, 5, (11), 32, (36)/37, 39, 42/(43), 55; *S. sanguinolentum* is particularly variable in culture, with an uneven laccase reaction [it may equate to Y, DD, and EE in Hood and Gardner (2005)].
[c] Excludes 2 additional decay fungi obtained during isolation attempts for stain fungi (including Species ψ).

with the ground or woody debris (83% of beetles) than in the upper half (17% of beetles; $F = 8.91$, $P < 0.01$).

3.3. Stain and decay fungi

Decay fungi were first isolated 87 days (12 weeks) after the storms (53 days after cutting in severed stems), and the frequency of isolation increased steadily during the course of the study (Table 3). After 188 days (27 weeks), isolation frequency was significantly greater for severed stems than for rooted trees ($P < 0.05$, sample times 3 and 5; Fisher's exact test; Table 3a and b). The model constructed for predicting the isolation frequency of all decay fungi is shown in Eq. (7).

$$\text{logit}(p_{ijk}) = \beta_0 + \beta_1 T + \beta_2 D_{ijk} + \beta_3 R_{ij} + \beta_4 D_{ijk} R_{ij} + \beta_5 T R_{ij} + a_i + b_{ij} + \varepsilon_{ijk} \quad (7)$$

where p_{ijk} is the proportion of isolations with decay fungi in disc k from tree i and site j; T is the number of days since the storm event; D_{ijk} is an indicator variable indicating whether disc k from tree i at site j was a basal disc or an upper disc (0 = upper disc; 1 = basal disc); R_{ij} is an indicator variable indicating whether tree i from site j is severed or rooted (0 = severed; 1 = rooted); β_0, β_1, β_2, β_3, β_4, and β_4 are estimable parameters. a_i and a_{ij} are random variables associated, respectively, with the site and trees within site. $a_i \sim N(0, \sigma_a^2)$, $b_{ij} \sim N(0, \sigma_b^2)$; ε_{ijk} is the error associated with disc k from tree i and site j.

Table 4 shows the model parameter estimates together with standard errors, and Fig. 1C shows the mean predicted probability over time together with the data points associated with discs 1 and 4. The prediction curve followed a similar trend to that for sapstain percent. There were no differences between sites or trees within sites, and in addition, the autocorrelation between discs was not significant.

Three species of decay fungi were obtained repeatedly from the fallen stems (Table 3), these being *Phlebiopsis gigantea* (Fr.) Jülich, *Stereum sanguinolentum* (Alb. & Schwein.) Fr., and during the last sampling of severed stems, *Schizophyllum commune* Fr. Although morphologically variable in culture, these fungi were distinctive, each having a unique combination of macro- and microscopic identification features. However, one species group was only recognised as *S. sanguinolentum* after three representative cultures were diagnosed from DNA analysis (Table S4). This identification was later confirmed by comparison with isolates from basidiocarps on felled *P. radiata* trees in a central North Island pine plantation. Three identical, slightly atypical isolates from a single disc were accepted as *P. gigantea* after DNA analysis of one of the cultures (Table S4). However, the identities of Species α and ψ remain uncertain (Table S4). Cultures of the same decay or stain fungi were commonly isolated in series from several adjacent isolation points along a radius indicating that they occupied discrete zones within the inner or outer sapwood.

The most frequently isolated sapstain fungus was *D. pinea*, which was first obtained from severed stems 188 days (27 weeks) after windthrow (154 days after cutting) and after 327 days (47 weeks) in rooted trees. Cultures of this species were recognised from their identical macro- and micromorphology, and identification was verified by the production of fertile pycnidia in one isolate from each of 8 of the 23 sapstained discs from which this fungus was obtained (see below). Among trees of both rooting types, *D. pinea* was obtained from 92 of 165 isolation attempts, and was confirmed present in 23 of 33 stained discs from which isolations were attempted from 31 trees during sample times 3–6. Isolates of ophiostomatoid species were not obtained until 466 days (67 weeks; sample time 6), when 3 isolates of *Ophiostoma piceae* (Münch) Syd. & P. Syd. and 14 of *Grosmannia huntii* (Rob.-Jeffr.) Zipfel, Z.W. Beer & M.J. Wingf. were obtained from 40 isolation attempts from rooted trees. An additional isolate of *Ophiostoma* sp. was obtained in mixed culture with *D. pinea* from a rooted tree at sample time 6, but was not identified further. Other fungi associated with sapstain were *Strasseria geniculata* (Berk. & Broome) Höhn. and species of *Cladosporium*, *Phomopsis*, *Aureobasidium*, and *Scytalidium*. Most of these fungi (18 of 20 isolates) were obtained only from small patches of stain during the first two sample times when sapstain percent was still comparatively low. Mould fungi (species of *Trichoderma* and *Penicillium*) and basidiomycetes (e.g. Species ψ, Table S4) were occasionally also obtained during attempts to isolate stain fungi, the basidiomycetes occasionally mixed with *D. pinea*.

4. Discussion

Storms are a serious hazard to commercial forestry globally, and in New Zealand are considered to be the single greatest physi-

Table 4
Estimated parameters used to predict the isolation frequency of decay fungi as a function of disc moisture content and diameter (Eq. (7)).

Parameter	Estimate	Standard error	*P* value
β_0	−5.851	1.141	<0.001
β_1	0.0265	0.00437	<0.001
β_2: If considering upper discs (i.e. disc $\neq$ 1)[a]	−2.669	0.564	<0.001
β_3 If trees rooted (i.e. rooted = 1)[a]	−0.826	1.610	0.609
β_4: If trees rooted and considering upper discs (i.e. rooted = 1 and disc $\neq$ 1)[a]	3.889	0.926	<0.001
β_5: If trees rooted (i.e. rooted = 1)[a]	−0.0183	0.00510	<0.001
σ_a^2	0.657	0.877	0.227
σ_b^2	1.303	0.898	0.074
AR(1)	0.0248	0.106	0.815
σ^2	2.510	0.275	<0.001

[a] If condition does not hold then parameter equals zero.

cal risk to exotic forest plantations (Maclaren, 1993; MAF, 2009; Martin and Ogden, 2006; Pearce et al., 2001). This provides a compelling motivation for research into the biological degrade of fallen timber such as the investigation reported here. Our study of sapstain development after two storm events showed a substantial difference between severed trees and those that remained partly rooted following windthrow. In general, both the incidence of sapstain and the speed of drying increased more rapidly in severed stems than in rooted trees, and for both rooted and severed trees, colonisation and growth by sapstain and decay fungi occurred only after the mean tree wood moisture content had fallen below 120%. The model derived from this study predicts that under conditions similar to those in the forest studied during 2008–2009, very little sapstain will develop in partly rooted windthrown trees within 1 year following a storm in winter. This period is encouraging and agrees with earlier reports from New Zealand (Butcher and Drysdale, 1991; Childs, 1966; Wendelken, 1966), Great Britain (Grayson, 1989) and Germany (Eisenbarth, 1995). Green foliage persisted for many months on most rooted trees, and new flush developed in spring, suggesting there may be some residual physiological resistance to fungal and beetle infestation in the still living stem not present in snapped logs.

Severed stems dried and deteriorated more quickly than partly rooted trees. The model predicts that in stems snapped near ground level, sapstain will first appear in the 10 m long butt log portion (mean midpoint diameter 22.4 cm) about 3 months (90 days) after damage during conditions corresponding to early spring in the Nelson region. However, there is unlikely to be serious staining (more than 10% of the stem cross section) before about 4 months (120 days). For larger logs the onset of sapstain may occur still later (Gleason, 1982). This period is similar to that reported for standing fire-damaged pines (*Pinus elliottii* var. *elliottii* Engelm.) under warmer spring and summer conditions in southern Queensland, Australia, in which the vectored stain fungi were inoculated through the bark by the introduced North American bark beetle *Ips grandicollis* (Eichhoff) (Hood and Ramsden, 1997; Wylie et al., 1999). Cooler conditions at other times of the year would presumably favour slower drying, reduced fungal growth, low beetle populations, and more protracted development of degrade, but this must be resolved by further research. In our study there was also variation in sapstain development along the severed stems. The model predicts that stems will become stained to a level of 15% of their cross sectional area at least 50 days later at the basal disc position (mean diameter of 28.3 cm) than in the region occupied by the remaining upper discs (mean diameter of 20.9 cm) after a storm at a time corresponding to early spring in the Nelson region.

These predictions must be qualified because there is a high degree of between-tree variability so that a decision to terminate a salvage operation must be based on the merits of working to an average value versus selecting an acceptable maximum sapstain threshold for a certain percentage of stems. The degree to which sapstain may be tolerated also depends on the intended use and market for the log product type (saw log, post, pulpwood, chips, or residue; Gleason, 1982). The extensive variation in sapstain and moisture content between and within trees at different sites reflects the complexity of a system involving many hidden factors. Below the 120% moisture content threshold, fungal development may depend on such features as the local concentrations of nutrients and extractives, relative humidity, and possibly on circumstances affecting colonisation and establishment (Beal et al., 2010; Kay and Ah Chee, 1999; Seifert, 1993). Experimental factors such as the unavoidable destructive sampling of stems, localised measurement of moisture content on discs that may be drying unevenly (partly due to the sapstain fungi themselves; Beal et al., 2010), and the occasional inclusion of small amounts of heartwood, will tend to accentuate such variation.

Zeff (1999) devised an empirical Sapstain Danger Index designed to predict the safety period preceding the appearance of sapstain in commercially harvested *P. radiata* in New Zealand. The index uses the time of year, midday temperature, and days since the last rainfall to predict sapstain incidence. It remains to be seen whether the Sapstain Danger Index is applicable to fallen severed trees in storm-damaged stands where conditions are somewhat different. A substantial amount of bark is dislodged during the mechanical handling of harvested logs (Uznovic et al., 2004) which develop sapstain very rapidly (in less than 10 days during spring and summer). During our study there was little bark loss on the storm-damaged trees (as compared to commercially harvested stems), whether broken or still-rooted, which presumably slowed drying and reduced fungal invasion. In both rooted and severed trees, drying was significantly greater in the outer sapwood where sapstain is often first seen. This pattern agrees with results from several studies using different species of *Pinus*, but contrasts with behaviour in other conifer species (Beal et al., 2010; Hood and Ramsden, 1997). It is therefore important to sample sapwood moisture content consistently from the same relative position during similar studies to monitor developing sapstain.

Bark beetles and other phloeophagous and xylophagous insects are known to be potential vectors of sapstain (Paine et al., 1997; Romón et al., 2007; Suckling et al., 1999). Such insects can carry fungal spores on their surface or in specialised structures such as mycangia which evolved in bark beetles as a means of transporting spores of mutualistic fungi (Bleiker et al., 2009; Grebennikov and Leschen, 2010; Masuya et al., 2009; Reay et al., 2005, 2006b). However, in this study, although the incidence of beetle colonisation increased with time, no difference was found in the proportion of sapstain present in discs as a function of beetle colonisation until the last sample time, 67 weeks after the storms in rooted

trees. At this time, 55% of sapstain records occurred where beetles had colonised disc 1 and its adjacent segment near the base of still-rooted trees whereas sapstain was completely absent when no beetle colonisation was observed at the same position. Such a relationship might have occurred earlier had beetles played a greater role as vectors of the sapstain fungi, even allowing for growth of mycelium along the stem beyond the point where it was first inoculated into the tree. This result is consistent with the prevalence of *D. pinea*, which was the main stain fungus isolated from stained sapwood during the study. This species is well known as a ubiquitous wind- and rain-dispersed agent of degrade in *P. radiata* (Farrell et al., 1997; Uznovic et al., 2004) with no known vector relationship with bark beetles. By contrast, species of *Ophiostoma* as well as *G. huntii*, which have slimy spores that are vectored by bark beetles (Gibbs, 1993; Seifert, 1993; Reay et al., 2006a; Thwaites et al., 2004, 2005), were only isolated during the last sampling time when beetle infestation was most prominent. This pattern differs from behaviour in Queensland (Wylie et al., 1999) and the United Kingdom (Evans et al., 1989), where insect-vectored fungi were important after fire and wind, respectively, although *D. pinea* was also common in *P. nigra* var. *maritima* in the UK. *D. pinea* is considered responsible for ca. 70% of staining in harvested *P. radiata* logs in New Zealand, and was the most frequently isolated sapstain species at 100 forest sites throughout the country, even if the collective abundance of all ophiostomatoid fungi exceeded that of *D. pinea* (Farrell et al., 1997).

Trapping was conducted to monitor bark beetle flight activity during the project, and as anticipated, numbers increased in the warmer months of spring and summer, when adult flight periods typically peak, whereas there was little activity during winter (e.g. Reay and Walsh, 2001; cf. similar findings with *P. radiata* in Chile, Mausel et al., 2007). Only *H. ater* was present in any numbers in traps and billets at the time of the storms, while other species remained largely inactive until October 2008. These results also imply that beetles did not play an important role in vectoring sapstain fungi until later in the season, as suggested by the isolation and sapstain results. However, further study is needed to determine if beetles would be a major vector of sapstain fungi if storms occurred during spring or summer when flight activity is higher (Thwaites et al., 2004). Their significance may depend on the type of storm damage (breakage or uprooting) and on the prevailing environmental conditions in different seasons and regions, which may influence population numbers and the incidence with which they infest fallen wood. There is also the threat that a future introduction of a new exotic species capable of vectoring existing or alien stain fungi would greatly increase the transmission of sapstain and reduce the time available for timber recovery after storms (Brockerhoff et al., 2006b).

The billet logs demonstrated greater colonisation by *H. ater* and *H. ligniperda* where there was ground contact, which corroborates the results of an earlier study (Mausel et al., 2007). This provides an additional explanation for an initially low beetle colonisation rate on the fallen study trees, which were suspended above ground level for most of their stem length with a low incidence of contact. Bark beetle attacks eventually increased probably due to the seasonal increase in beetle numbers. Beetle host finding is facilitated by attractants such as ethanol and α-pinene emitted by the dying or recently dead study trees and the decline of defences such as the production of resin that obstruct beetle colonisation (Berryman et al., 1989; Paine et al., 1997).

The isolation frequency of basidiomycete fungi was initially low but increased with time in a manner that mirrored the trend shown by percentage sapstain. As with sapstain, yield frequencies were also greater in severed stems than in rooted trees after the first 5–6 months. These patterns are not surprising, given that the conditions that favour colonisation of the sapwood are similar for decay and non-decay fungi. Thus the rate of development of visible sapstain appears to provide a rough, indirect guide to the incidence of decomposer fungi (Gleason, 1982). The amount of sapstain may also serve as a crude indicator of the prevalence of the causal stain fungi, themselves (in addition to being a direct measure of degrade, itself), but this relationship is to some extent influenced by the rate that their hyphae become pigmented (Kay and Ah Chee, 1999). The presence of a low incidence of some decay fungi during the first 5 months after severance is probably of no concern, since their activity would cease when the salvaged timber was processed (Ah Chee et al., 1998; Cartwright and Findlay, 1958). It is also noteworthy that more than one species of decay or stain fungus was frequently present in the same disc wedge taken from severed stems, and that no autocorrelation was indicated between discs. This may indicate that colonisation was still at an early stage before the more dominant, competing species had occupied larger tracts of sapwood. The decay fungi most frequently cultured after 5 months (*P. gigantea* and *S. sanguinolentum*) are known early colonisers of *P. radiata* wood in pine forests in New Zealand (Butcher and Drysdale, 1991; Etheridge, 1967; Hood and Gardner, 2005; Uznovic et al., 2004). These fungi were also common in fallen pines in the United Kingdom, where they caused brown staining that was not acceptable in some markets (Dannatt and Garforth, 1989; Evans et al., 1989). In this study, a reddish-brown stain which may have been caused by *S. sanguinolentum* was occasionally observed at later sampling times. *S. commune*, another common earlier coloniser of newly felled trees, was isolated during sample time 5. It is not considered to have a high decay potential (Ah Chee et al., 1998; Cartwright and Findlay, 1958).

Most of the fungi isolated during this study are believed to spread spores by wind or rain, but it is not completely clear how or when they colonise the fallen stems. Evans et al. (1989) stated that *P. gigantea* and *S. sanguinolentum* invade freshly exposed sapwood by means of airborne spores, but this does not explain their presence during our study since extensive debarking did not occur. *D. pinea* is known to occur as a latent endophyte in healthy shoots, cones and seedlings of *Pinus* species (Flowers et al., 2001; Petrini and Fisher, 1988; Reay et al., 2006a; Smith et al., 1996; Stanosz et al., 1995), but it is not clear if this also applies to mature stems, and our results provide no evidence either way. Although functional sapwood is inhibitory to most fungi due to its water saturated, oxygen-depleted nature, any sapstain fungi present would grow and become apparent as conditions ameliorate when the cells die and become aerated as water is lost (Boddy and Heilmann-Clausen, 2008). Alternatively, it is possible that wind- or rain-borne spores may first establish in foci on or in the bark surface and invade through small crevices exposing the outer sapwood as it dries, as well as through broken ends (Boddy, 1994; Boddy and Heilmann-Clausen, 2008). The effectiveness of surface anti-sapstain chemical treatments in protecting logs destined for export markets implies that colonisation is mainly by invasion after bark is lost, but this question needs further research (Eden et al., 1997a,b; Seifert, 1993).

Breakage occurred in the wind-affected Nelson forest, but much of the damage was also caused by toppling and uprooting due to heavy snow. Although not quantitatively surveyed, breakage is thought to have been more widespread during the 1982 central North Island storm (Gleason, 1982; Somerville et al., 1989). This may explain the appearance of a low but significant level of sapstain in salvaged logs during the spring only 6 months after the 1982 storm (Gleason, 1982). Thus, the type of storm damage should be considered when planning wood recovery operations. Firstly, it is important to distinguish between stands where trees are predominantly snapped from those in which they are uprooted (Conway, 1959; Thomson, 1976). Stands with snapped and broken trees will deteriorate more rapidly and should be salvaged first, even where access to such stands may be more difficult (Grayson, 1989). Indeed,

one forest company in Canterbury, New Zealand, a region prone to recurring wind damage, reported that their policy was to manage their pine plantations in such a way as to allow for uprooting rather than breakage during gales (Somerville et al., 1989). This was done to increase potential log recovery, by lengthening the available salvage period and by reducing loss in wood volume through breakage. Secondly, it is necessary to consider the effect of season. It is not clear whether sapstain may have developed more rapidly in the central North Island, even to levels approaching that for normally harvested logs, had the 1982 storm occurred immediately prior to spring as in the forest used for our study, when temperatures were about to rise (Gleason, 1982). These are important issues, and further research clearly needs to investigate the effects of both time of year and climate region in which storm destruction occurs so that it will eventually be possible to provide reliable guidance to forest managers.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.07.044.

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