

## Tree mortality in a semi-natural beech forest in SW Sweden

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To provide a better understanding of natural stand dynamics of Scandinavian broadleaved forests we studied pattern of tree mortality in a semi-natural beech *Fagus sylvatica* forest at Biskopstorp, SW Sweden. The primary goals were 1) to assess beech mortality rates of different tree condition classes (TCC) and transition probabilities between them, and 2) to suggest likely mortality drivers in the studied beech population. Mortality rates and transition probabilities were calculated between pairs of six TCC (live trees, live high stumps, dead trees, dead high stumps, stumps, and logs) by using data from two complete censuses of a 3.9 ha stand ( $n_{\text{trees}} = 1189$ ) over a ten year interval (1996–2006). The total beech mortality rate reached  $2.0\% \text{ yr}^{-1}$  following two main pathways: 1) stem breakage leading to instantaneous death ( $1.1\% \text{ yr}^{-1}$ ), and 2) stem breakage leading to partial crown removal, resulting in formation of a living high stump,  $\text{HST}_L$  ( $10.5\% \text{ yr}^{-1}$ ) which was characterized by an increased mortality rate ( $11.5\% \text{ yr}^{-1}$ ).  $\text{HST}_L$  made up ca 10% of the living trees in both censuses indicating the importance of this feature in the dynamics of the beech forest. Only two uproots were recorded ( $0.04\% \text{ yr}^{-1}$ ), despite of two hurricanes (in 1999 and 2005) that occurred during the study period. Mortality was significantly higher in trees above 60 cm DBH than in smaller trees ( $4.0$  vs  $0.7\% \text{ yr}^{-1}$ , respectively) and no differences were found among smaller DBH classes. Trees with fungal fruit bodies (FFB) had a significantly higher mortality than trees lacking FFB ( $7.6$  vs  $1.1\% \text{ yr}^{-1}$ , respectively). Our results highlight the role of the living high stump stage in the dynamics of the beech forest and suggest that the combination of wind and fungal infection of *Fomes fomentarius* are the main drivers of mortality in the studied stand.

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Tree mortality is a fundamental element of natural forest dynamics. Typically, annual overall tree mortality rates of canopy trees are in a range within 0.5 and 2% with only small variation between tree species (Runkle 1985, 2000, Wolf et al. 2004, Drobyshev et al. 2009). Insights into mortality dynamics often come from the studies of natural disturbance regimes (Runkle 1985, 2000, Clark 1991, Esseen 1994, Wolf et al. 2004, Chapman et al. 2008). A number of studies have addressed variation in mortality rates as a function of tree characteristics and, particularly, tree size (Franklin et al. 1987, Mueller-Dombois 1987, Waring 1987, Dobbertin and Biging 1998). Small trees under closed canopies and during the early successional

stages are often subject to high mortality due to self-thinning and limited amounts of light. A low mortality period tends to be associated with intermediate diameter classes, followed by an age- and size-related increase in mortality rate (Franklin et al. 1987). This general pattern, however, may vary as a function of tree life strategy in the community (Shimatani et al. 2008, Drobyshev et al. 2009).

Mortality factors for canopy trees differ among ecosystems. In deciduous high canopy forests wind disturbance is often the dominant mortality factor and the main stem capacity to withstand breakage and uprooting are principal determinants of trees' survival rates (Peterson and Pickett 1991, Ulanova 2000). To assess mortality levels, large da-

datasets and/or long observation periods are typically needed to arrive at reliable mortality estimates, especially in the cases when these rates are low.

In Sweden, European beech *Fagus sylvatica* grows in mixed or pure stands to a latitude of ca 58°N (Dahl 1998). The importance of this species in maintaining regional biodiversity has been increasingly acknowledged (Nilsson 1997, Brunet et al. 2010, Fritz and Brunet 2010), however, our understanding of natural stand dynamics of beech-dominated forests in Scandinavia remains limited. In this study, we explored canopy dynamics and tree mortality in one of the few remaining multi-cohort semi-natural beech stands in southern Sweden, located in the Biskopstorp nature reserve (Fig. 1, Fritz 2006). By inventorying > 1000 beech trees twice over a 10 yr interval we estimated transition probabilities among seven tree condition classes and, for the most abundant classes, the importance of tree diameter in affecting these probabilities. By recording presence of fungal bodies of *Fomes fomentarius* on tree stems, we attempted to evaluate the role of fungi infection in modifying the mortality rates. To further project the impact of mortality on stand properties, we assessed the contribution of beech mortality into the deadwood pool of the studied stand. Finally we draw a conceptual picture of the disturbance regime in the studied forest by highlight-

ing the most important mortality factors and the differences between our findings and the previously published results from similar European forests.

## Materials and methods

### Study area and the stand inventoried

The nature reserve Biskopstorp lies in the county of Halland, southern Sweden (56°48'N, 12°52' E, Fig. 1). The area encompasses around 900 ha, almost completely covered by forest, and the broadleaved forests (beech and oak-dominated) make up ca 30% of the total forest cover (Fritz 2006).

The climate of the area is characterized by strong oceanic influence, mild winters, and cool summers with annual average temperature and precipitation of 7°C and 1100–1200 mm, respectively. Average temperature reaches –1.6°C in January and 15.5°C in July. The topography ranges from exposed bedrock on hill sides to gentle slopes typically covered by sandy moraines of glacial origin (SGU 1988).

According to the locally developed pollen diagrams (Karlsson 1996, Hannon 2002), beech has been present

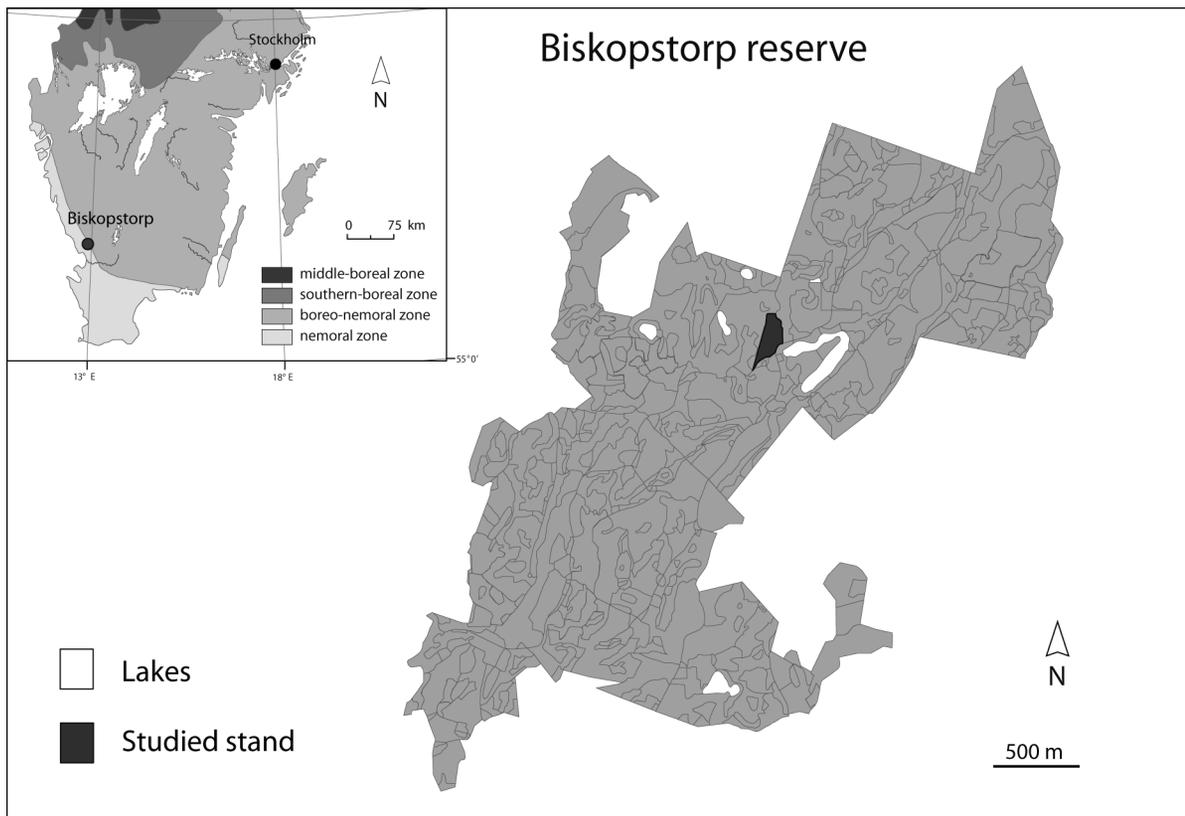


Figure 1. Study area and location of the sampled site, Holkåsen.

in the area for > 1500 yr. It increased in importance since AD 1350, presumably due to human-related disturbance of natural forest vegetation. In this same period the abundance of oak (*Quercus* spp.) and lime (*Tilia* spp.) pollen decreased. Beech and alder (*Alnus* spp.) pollen continued to hold a dominant position in the pollen spectra until the last century when *Picea* spp. increased its importance as a result of modern forestry practices (Karlsson 1996, Hanon 2002). Currently, beech remains the dominant broad-leaved species within the reserve. The reserve is known for its long forest continuity, and high number of threatened and red-listed species of bryophytes, fungi, epiphytic lichens and saproxylic insects (Heilmann-Clausen 2005, Fritz 2006).

The study was conducted in Holkåsen, a 3.9 ha beech stand within the Biskopstorp reserve. The stand is dominated by beech (90% of the total basal area) and the remaining 10% are accounted by spruce *Picea abies*, birch *Betula pendula*, Scots pine *Pinus sylvestris*, oaks *Quercus robur* and *Q. petraea*, rowan *Sorbus aucuparia*, and juniper *Juniperus communis*. The beech population in the forest canopy is composed of two cohorts: a younger cohort originated around 1940–1950 and an older cohort dating back to 1730–1760 (Niklasson et al. 2005, Churski and Niklasson 2010). The youngest cohort is distributed in clusters and the oldest cohort is more regularly spaced across the stand (Fuentes unpubl.). The presence of oak, juniper, and birch may indicate past openings in the stand, which were likely grazing-related. The stand is one of the most valuable beech stands in southern Sweden, considering its long forest cover continuity (Fritz and Brunet 2010).

### Tree inventory

Trees >1 cm in stem diameter and higher than 1 m in height were mapped and their characteristics were recorded during June–August 1996 (Karlsson 1996). In 2006 we identified 1189 of previously inventoried trees (98%). The following variables were recorded for each tree: species identity, status (alive or dead), tree condition class (TCC), diameter at breast height (DBH), presence of fungal fruit bodies (FFB, also called basidiocarps, Baum et al. 2003), and presence of any crown damage as defined in Karlsson (1996). We considered a tree dead when no green leaves or sprouts were present in any portion of the stem and no cambium activity was found after visual inspection (presence of green and moist cambium layer under the bark). The following TCC classes were identified: living, complete, unbroken and healthy tree (LTH); living tree with damaged crown (LTD); dead, unbroken and standing tree (DS); high stump with living branches and >1.3 m in height (HST<sub>L</sub>); high stump with no living branches and >1.3 m in height (HST<sub>DE</sub>); stump with living branches and <1.3 m in height (LST<sub>L</sub>); stump with no living branches and <1.3 m in height (LST<sub>DE</sub>); coarse woody debris with

minimum diameter of 10 cm at both ends of the log. An additional tree condition class, TRACES, was used during the 2006 census only and included remains of the deadwood originated from material recorded as stumps or logs in 1996 and currently present in a high decay stage, equivalent to decay class 5, according to Heilmann-Clausen and Christensen (2003). Trees that fell with their root system exposed were classified as uprooted.

### Mortality estimation

Transition rates between different pairs of TCC, including mortality rates, were calculated as

$$C = 1 - (C/N_0)^{1/y}, \quad (1)$$

where  $C$  is the number of currently recorded living trees,  $N_0$  original number of living trees,  $y$  – number of years between resamples (Sheil et al. 1995, von Oheimb et al. 2007). To estimate the variability of these rates we used the bootstrap approach (Efron and Tibshirani 1994). For each of the data sub-sets representing success/failure of transition between two states of TCC, we resampled original data with replacement 1000 times to produce confidence thresholds around the central 95% of respective distribution.

To assess the contribution of different DBH classes in the flux between different TCC during the observation period, we used inverse survivorship functions. This procedure took into account a) the DBH class – specific transition rates and b) the actual abundance of different DBH classes in the beech population. In contrast to the traditional version of the analysis operating with survival times during complete or censored (incomplete) time periods, we used diameter gradient and considered survival probabilities (transition probabilities in our case) not along a time, but a size axis. To assess site survivorship function, describing the probability for a tree to escape transition into another class during a given diameter interval, we used the Kaplan-Meier estimator (Kaplan and Meier 1958):

$$S(d) = \prod_{j=1}^d [(n-j)/(n-j+1)]^{s_j}, \quad (2)$$

where  $S(d)$  is the site survivorship function estimated for a diameter  $d$ ;  $n$  is the total number of observations;  $\prod$  is the geometric sum across all cases less than or equal to  $d$ ; and  $(j)$  is a constant that is either 1 if the  $j$ th case is uncensored (complete); and 0 if it is censored (incomplete).

To summarize the transition rate estimates, we grouped the data into 20-cm diameter classes and used the Gompertz distribution to develop a function relating each diameter class to the respective transition rate. Selection of this distribution was based on the fact that it is commonly used to describe systems with increasing probability of mortality over the selected gradient (commonly, a time

gradient). The probability density function for the Gompertz distribution is written as

$$f(x; a, b) = b \cdot e^{ax} \cdot \exp\left[\frac{b}{a}(1 - e^{ax})\right], \quad (3)$$

where  $0 < x < \infty$ ,  $a > 0$  (scale parameter) and  $b > 0$  (shape parameter) (Johnson et al. 1995). The  $\chi^2$ -values were computed as a function of the log-likelihood to evaluate statistical significance of the estimated function parameters.

In the analysis of fungal fruit body (FFB) frequency, we used the two-sided t-test for independent samples.

The Cox-Mantel Test was used to assess the significance of differences between two survivorship functions (Lee et al. 1975).

In this study we did not analyze growth dynamics in connection to mortality events. Although shown to be informative for predicting the fate of individual trees (Bigler et al. 2004, Wolf et al. 2004), this element fell outside the scope of the current paper.

### Calculation of beech deadwood volumes

To further explore the effects of beech mortality on stand characteristics, we translated beech mortality into deadwood dynamics. The fact that the stand's canopy was close to mono-dominant allowed us to exclude other species from consideration.

The volume of coarse woody debris was estimated following Nilsson et al. (2003):

$$V = 1/3 \times L \times (br + bt + (br \times bt)^{0.5}), \quad (4)$$

where  $L$  is the length of the log section,  $br$  is the basal area at the base of the wood piece and  $bt$  is the basal area at the top.

The top diameter of the high stumps was measured directly when it was within reach. Otherwise, it was estimated with the following formula:

$$d_{\text{top}} = \text{DBH} - (1.26 \times H), \quad (5)$$

where  $d_{\text{top}}$  is the diameter at the top of the piece, DBH is the diameter at 1.3 m height, the factor 1.26 is a stem-diameter reduction factor estimated from formula 7, and  $H$  is the height of the high stump minus 1.3 m.

The volume of the stumps was calculated as

$$V = \pi/40000 \times d^2 \times h \quad (6)$$

where  $\pi$  is the *pi* constant,  $d$  is the DBH, and  $h$  is the height of the stump (modified after Lombardi et al. 2008).

To estimate the height of dead unbroken trees we used a database of 473 trees with accurate height and diameter

measurements, obtained within the same nature reserve (Niklasson et al. 2005). We fit a polynomial curve, which explained 90.7% of the variation in height, as a function of tree DBH:

$$y = -0.0064x^2 + 0.8114x + 1.3667, \quad (7)$$

where  $x$  is the diameter, in cm, and  $y$  is the estimated height, in meters.

## Results

### Mortality and transition probabilities of different TCC

Out of the 1189 living trees (including living high stumps) recorded in 1996, 971 remained alive in 2006 (Table 1 in Appendix). This equaled an annual mortality rate of 2.0%  $\text{yr}^{-1}$ . However, mortality rates varied considerably among different TCC of living trees. Beech trees that were undamaged in 1996 had an annual mortality rate of 1.1%, while trees damaged in 1996 had a rate of 10.2%. Mortality rates for high and low stumps were even greater 10.5 and 17.5%, respectively (Table 1).

Canopy tree removal occurred through 1) stem breakage leading to instantaneous death (1.1%  $\text{yr}^{-1}$ ), and 2) stem breakage leading to partial crown removal, resulting in formation of a living high stump,  $\text{HST}_L$  (10.5%  $\text{yr}^{-1}$ ).  $\text{HST}_L$  was characterized by an increased mortality rate (11.5%  $\text{yr}^{-1}$ ). The average heights of living and dead high stumps were 8.0 ( $\pm 3.8$  SD) and 6.0 m ( $\pm 3.9$  SD), respectively.  $\text{HST}_L$  originated mainly from large trees: <5% of  $\text{HST}_L$  came from trees below 40 cm DBH. Input into the living high stump pool increased significantly with the tree size, reaching 56% for trees in the 60–80 cm DBH class (Table 2, Fig. 3). Living high stumps often survived for > 10 yr; of 147  $\text{HST}_L$  recorded in 1996, 40 were still alive in 2006 (12.2%  $\text{yr}^{-1}$  moved to other TCC, Table 1 in Appendix). As a result, the stand had a relatively constant share of living high stumps at the time of the two inventories (9% in 1996 and 12% in 2006, Table 1 in Appendix). Uprooting with a root plate exposed was a rare event. Only three uprooted trees were recorded in the 1996 census, and two between 1996 and 2006, corresponding to an annual rate of 0.04%.

There was no significant variation in mortality rates of undamaged living trees along the diameter gradient, with the exception of trees larger 60 cm DBH (Table 2). Living trees >60 cm DBH became living high stumps ( $\text{HST}_L$ ) significantly more frequently than trees <40 cm DBH. In turn, mortality of living high stumps was significantly higher for the 20–60 cm DBH classes, than for the >60 cm DBH class. Particularly, all dead trees within the 20–40 cm DBH class became stumps during the observation pe-

Table 1. Transition rates ( $\text{yr}^{-1}$ ) between different TCC in the studied beech stand during the 1996–2006 period. Variability in estimates was assessed by the bootstrap method. LT and  $\text{LT}_{\text{FB}}$  are living trees without and with fungal fructiferous bodies (usually of *Fomes fomentarius*) present on the stem at the time of the 1996 census, respectively.  $\text{HST}_{\text{L}}$  and  $\text{HST}_{\text{LFB}}$  are living high stumps with fungal fructiferous bodies absent or present on the stem in 1996.  $\text{TCC}_{\text{DEAD}}$  indicates any tree found dead in 2006. See Table 1 in the Appendix for further explanation of TCC abbreviations. CL are distribution confidence limits.

TCC transition rates	Mean	Standard deviation	2.5% CL	97.5% CL
LT into DS	0.011	$1.13 \times 10^{-6}$	0.009	0.013
$\text{HST}_{\text{L}}$ into $\text{HST}_{\text{DE}}$	0.115	$1.32 \times 10^{-4}$	0.093	0.137
$\text{LST}_{\text{L}}$ into $\text{LST}_{\text{DE}}$	0.175	0.059	0.04	1
LT into Logs	0.001	$4.94 \times 10^{-8}$	$9.67 \times 10^{-05}$	0.001
LT into $\text{HST}_{\text{L}}$	0.009	$9.33 \times 10^{-7}$	0.007	0.011
(DS or $\text{HST}_{\text{DE}}$ ) into $\text{LST}_{\text{DE}}$	0.134	$3.63 \times 10^{-4}$	0.1	0.177
$\text{LT}_{\text{FB}}$ into $\text{TCC}_{\text{DEAD}}$	0.076	0.004	0.013	0.188
LT into $\text{TCC}_{\text{DEAD}}$	0.011	$1.04 \times 10^{-6}$	0.009	0.013
$\text{HST}_{\text{LFB}}$ into $\text{TCC}_{\text{DEAD}}$	0.146	0.001	0.098	0.21
$\text{HST}_{\text{L}}$ into $\text{TCC}_{\text{DEAD}}$	0.105	$1.68 \times 10^{-4}$	0.082	0.131

riod, making this DBH class significantly different from all other DBH classes (Table 2). Transition of living undamaged trees to logs was consistently low across all DBH classes ( $0.1\% \text{ yr}^{-1}$ , Table 2).

### Cumulative functions

An undamaged living tree below 20 cm had 7.8% probability of mortality, or, in other words, 92.2% probability to reach the following class during its lifespan (Fig. 3A). Mortality increased only marginally in the following DBH class, 20–40 cm DBH (91.1% survival probability or 9.9% chance of mortality). Survival probability decreased down to 79% for the 40–60 cm DBH class and down to 53.3% for the largest DBH class (>60 cm). Although cumulative transition curves (Fig. 3) and calculation of size-specific transition rates (Table 2) were obtained on different sets of data (transition rates and abundance data in the first case, and transition rates only in the second case), both analyses showed mutually consistent results.

The lack of significant diameter effects on canopy beech mortality for trees <60 cm DBH was also reflected in a close-to-linear increase in the cumulative function (Fig. 3A), suggesting that all DBH classes except the >60 cm class provided generally similar contributions to the pool of deadwood.

Significant differences in transition probabilities between DBH classes were observed for transitions involving high stumps (Table 2). This effect was expressed as non-linearity in the respective cumulative functions (Fig. 3B, C). For example, an undamaged living tree had only 3.4% probability to become a living high stump before reaching 20–40 cm DBH class (Fig. 3B). This probability increased to 55.5% for the largest DBH class (trees >60 cm DBH). For the transitions involving standing deadwood (DS and  $\text{HST}_{\text{DE}}$ ) into logs, we observed three size groups (<20 cm, 20–60 cm, and >60 cm DBH classes) with significantly different transition probabilities (Fig. 3D, Table 2). In this case, the non-linearity was associated with little difference between probabilities for 20–40 and 40–60 cm DBH classes.

Table 2. Summary of transition rates between TCC classes. Letters in the cells indicate significant differences ( $p < 0.05$ ) in transition rates between the focal cell and a cell from a row denoted by respective letter within the same row. See Table 1 in Appendix for explanation of abbreviations. Total n used to calculate particular transition probability is given in brackets.

Diameter classes		LTH into any TCC representing dead trees	LTH into $\text{HST}_{\text{L}}$	LTH into Logs	$\text{HST}_{\text{L}}$ into any TCC representing dead trees	DS or $\text{HST}_{\text{DE}}$ into $\text{LST}_{\text{DE}}$
<21	a	0.001 (464) d	0.014 (524)	0.007 (524)	0.028 (4)	0.153 (21) b
21–40	b	0.005 (227) d	0.004 (232)	0.000 (232)	0.157 (22) d	1.000 (6) acd
41–60	c	0.024 (207)	0.012 (210)	0.000 (210)	0.132 (82) d	0.118 (35) b
>60	d	0.040 (72) ab	0.022 (69)	0.000 (69)	0.082 (40) bc	0.093 (8) b

## DBH distributions of living trees and deadwood pools

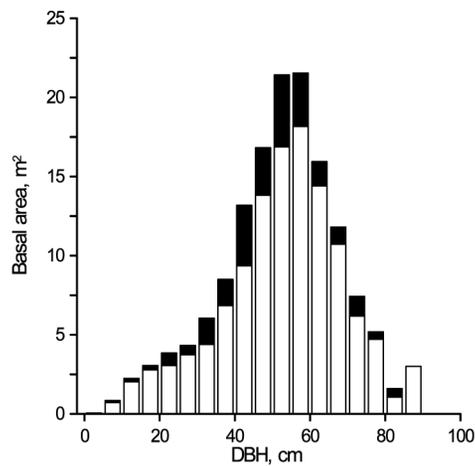
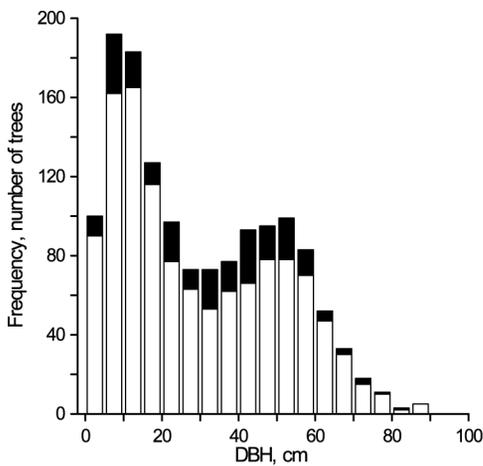
In 1996, most of the basal area of both living and dead beech trees was within a range of 40–70 cm DBH (79.0 and 81.2% respectively, Fig. 2). In 2006, the contribution of these diameter classes to the basal area of living trees decreased to 63.7%, whereas logs and stumps of such dimensions became even more dominant in the total deadwood pool (change from 81.2 to 90.4%).

In comparison to the 1996 inventory, the total deadwood volume had nearly doubled by 2006 – from 27.9

to 53.8 m<sup>3</sup> ha<sup>-1</sup> (Table 3). Mortality of living high stumps (HST<sub>L</sub>) was the major cause in this increase, contributing with 18 m<sup>3</sup> ha<sup>-1</sup> over the 10-yr period. Deadwood DBH distribution did not change though – a shift towards larger diameter deadwood was non-significant (Wilcoxon matched-pairs test on DBH class frequencies  $T = 56.00$ ,  $z = 0.621$ ,  $p = 0.535$ ).

We observed large differences in the abundance of different deadwood types between the inventories. The volume of dead low stumps (LST<sub>DE</sub>) increased by a factor of five between the inventories (from 1.2 to 6.2 m<sup>3</sup> ha<sup>-1</sup>). Dead high stumps (HST<sub>DE</sub>) doubled their volume dur-

1996



2006

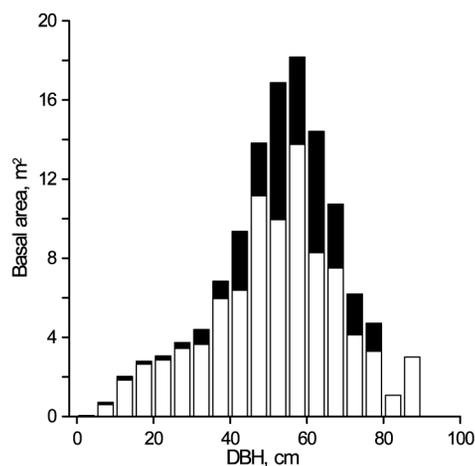
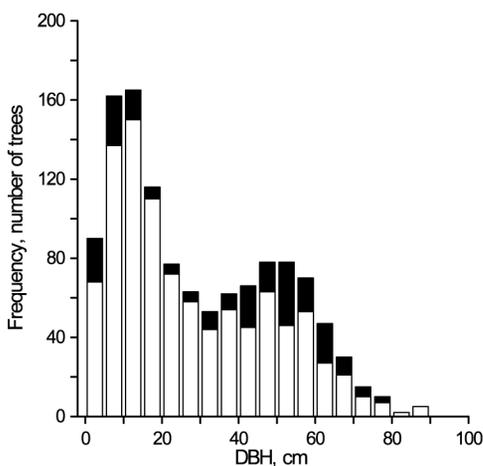


Figure 2. DBH and basal area distributions of live (open bars) and dead (filled bars) beech trees in the studied stand in 1996 and 2006.

Table 3. Dead wood volumes in different TCC classes for the 1996 and 2006 censuses, in  $\text{m}^3 \text{ha}^{-1}$ . See Table 1 in Appendix for explanation of abbreviations.

Year of survey	Standing dead wood			Lying dead wood			Total
	HST <sub>DE</sub>	DS	Standing deadwood (%)	LST <sub>DE</sub>	Log	Lying dead wood (%)	
1996	14.2	1.8	57.3	1.2	10.7	42.6	27.9
2006	32.2	0.35	60.5	6.2	15	39.4	53.8

ing the study period (14.2 vs 32.2  $\text{m}^3 \text{ha}^{-1}$ ). Log volume increased by 30% (from 10.7 to 15  $\text{m}^3 \text{ha}^{-1}$ , Table 3), with a major contribution from high stumps recorded as living in 1996. Dead standing trees (DS) were overall rare and were almost exclusively found in the size class below 21 cm (Table 1, 2 in Appendix). Over 1996–2006, the volume of dead standing trees decreased by 80% (from 1.8 to 0.35  $\text{m}^3 \text{ha}^{-1}$  respectively, Table 3).

### Relationship between fungal presence and mortality rate

Fungal fructiferous bodies (FFB) were present on 4.3 and 7.0% of the total number of living beech trees in 1996 and 2006, respectively (difference significant at  $p = 0.006$ , Table 3 in Appendix). In the presence of FFB the mortality rates increased both for trees and high stumps. For unbroken trees with FFB present the mortality rate was 7.6% (vs 1.1% with no FFB present) and for high stumps 14.6% (vs 10.5% with no FFB present). Low numbers of trees with FFB decreased the statistical power of the test: the effect of FFB presence was non-significant both for trees ( $p = 0.069$ ) and for high stumps ( $p = 0.488$ ). However, analysis of the survivorship function, which took into account the DBH distribution of trees with and without FFB, showed significantly higher survival rate of trees without FFB (Cox-Mantel Test statistics = 5.34,  $p < 0.001$ ). The difference in survival rates started to accumulate at a DBH of approximately 30 cm (Fig. 4).

## Discussion

The analysis of re-inventory data from our study area Holkåsen enabled us to quantify the temporal dynamics of semi-natural beech forest and to trace the main “mortality pathways” of beech canopy trees. As with any tree mortality study, our results may contain methodological biases, which are important to mention before discussing the study results. First, the analyzed 10-yr period represented ca 3% of the potential life span of beech in the region (Niklasson and Fritz 2003), implying that our results might be biased towards certain environmental conditions and a particular age structure of the stand ob-

served during the period between two censuses. Indeed, the significantly higher mortality rate of trees above 60 cm DBH (see below) implies that the proportion of larger and, probably, older trees could have a direct effect on the overall mortality rates. Secondly, large disturbance events provide a major impact on forest canopies (Peterson 2000, Chapman et al. 2008) with time intervals often exceeding the period between inventories. In our study, two large windstorms occurred in the area between the first and the second inventory, which might eliminate a potential bias due to sampling during a disturbance-free period. Both windstorms, however, took place during the dormant periods (7–8 January 2005 and 3–4 December 1999, SMHI 2005), when the trees were potentially less prone to wind disturbance due to absence of a leaved canopy. Thirdly, by pooling data from the whole stand during statistical analyses we assumed no spatial dependences between mortality patterns and patches of different age cohorts. In our study, this was justified by 1) the size of the area inventoried (3.9 ha) exceeding the scale of the patch mosaic, and 2) the lack of a clear spatial structuring with older trees being spaced among younger cohorts (Fuentes et al. unpubl.).

The studied stand was left unmanaged since at least the 1940s (S. Bengtsson pers. comm.) and the reported mortality and transition rates should be considered as not directly affected by human activities, and, therefore, largely natural. This makes the study the first attempt to quantify mortality dynamics of European beech on a large dataset originating from a semi-natural forest in Scandinavia. Discussion on the mortality of beech presented below could, therefore, contribute to better silvicultural strategies aimed at management and biological conservation in north European beech forests.

### Pattern of beech mortality

Four main features of beech stand dynamics were 1) a very low frequency of canopy tree uprooting, 2) a relatively high frequency of snapping events, resulting in about one tenth of all trees being high stumps, 3) a low mortality rate (1.1%  $\text{yr}^{-1}$ ) of unbroken canopy trees as compared to a high mortality rate (10.5–14.6%  $\text{yr}^{-1}$ ) of high stumps, and finally 4) the potentially important role of fungal infec-

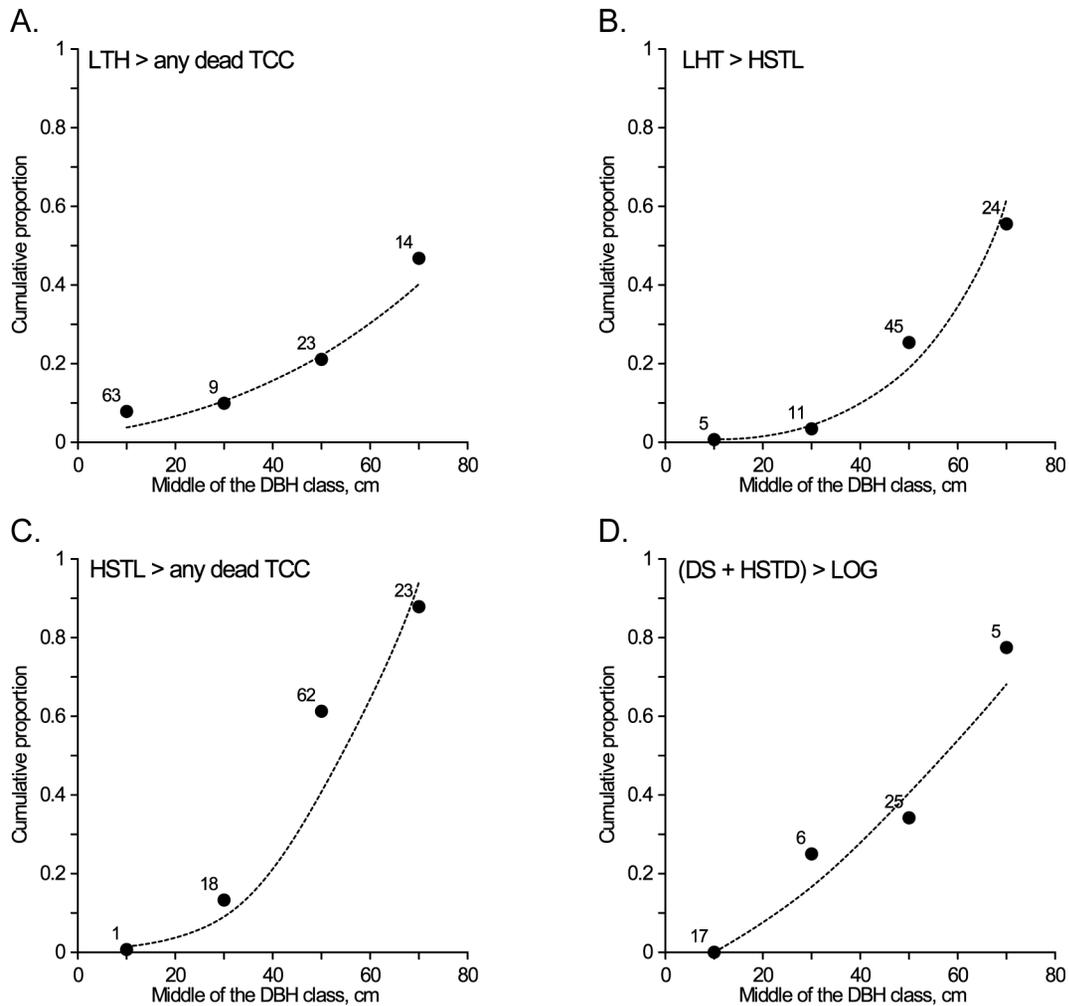


Figure 3. Cumulative transition probabilities between different TCC, estimated as inversed survivorship function for 20-cm DBH classes. Cumulative proportion is the cumulative percent of surviving trees reaching respective DBH class. Number of actual transitions between respective TCC is indicated for each point on the graphs.

tions in regulating beech mortality. Below we discuss these features and their implications for long-term dynamics of the studied stand.

The overall annual mortality rate (1.1%) of unbroken canopy trees was well in line with other studies of mortality, both in beech and in other deciduous species (Runkle 1985, Wolf et al. 2004, Drobyshev et al. 2008). European and American studies point to the range of beech mortality rates within 0.5 and 2% annually (Foré et al. 1997, Wolf et al. 2004, Wunder et al. 2008), differences in the age and size of the trees and disturbance regime being likely

responsible for this variation. In our study, diameter did not influence the mortality of undamaged healthy trees <60 cm DBH, although significantly higher mortality was observed above this size threshold. These results agree with previous studies where higher mortality was generally associated with the largest trees in the population (Peterson 2000, Runkle 2000, Lorimer et al. 2001, Wolf et al. 2004). The shade-tolerance of beech and the size threshold chosen to include trees in the inventory (>1 cm DBH) excluded very small beeches experiencing high mortality rates due to resource limitation (primarily light).

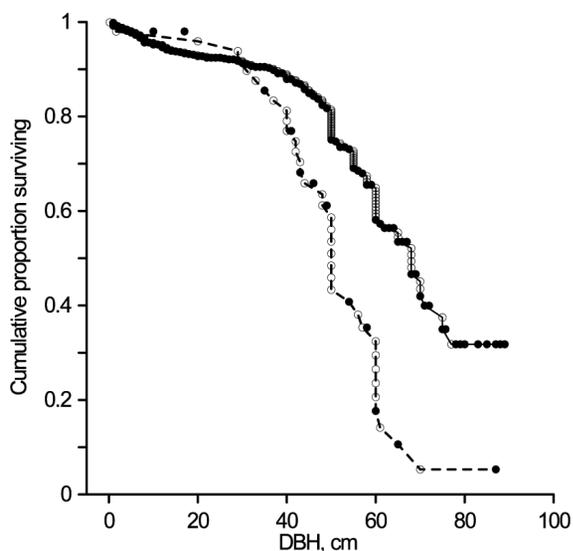


Figure 4. Cumulative proportion of surviving trees along diameter gradient for two sub-populations of trees, with fungal fruit bodies absent (solid line) or present (dashed line). Dead trees are indicated with empty circles and living trees with filled circles. Data from the 10-yr period 1996–2006.

Tree uprooting, involving exposure of roots and mineral soil, was a rare event in the studied forest. This is especially noteworthy considering that two major hurricanes passed over the area in 1999 and 2005. During the storm (“Gudrun”) 8–9 January 2005 wind speeds exceeded  $33 \text{ m s}^{-1}$  in the study area (Alexandersson and Edqvist 2007). In contrast to beech stands, we witnessed heavy damaged neighboring spruce forests, with uprootings being the typical disturbance event. Similar to our results, a study of an old-growth mixed beech forest in Poland found a low rate of uprootings and more frequent stem breaks (Szwagrzyk and Szewczyk 2001). Beech uprootings were, however, common in a natural lowland beech forest in France, although stem breaking was also noted as a typical type of tree damage (Pontailler et al. 1997). We consider soil conditions as one important factor affecting uprooting rates: most Swedish moraines are rich in stones and boulders and likely aid in anchoring the trees in comparison with fine-textured soils. Such fine-textured soils may be occasionally waterlogged, which would further enhance tree instability through mortality of fine roots in anaerobic conditions (Abrazhko 1988). Another factor which could favor stem break before uprooting is stem infection by saprophytic fungi, which we discuss in the following section.

An important feature of the disturbance dynamics was the formation of high stumps, resulting in trees avoiding direct mortality in cases when the stem breaking point was located above living branches. Although the mortality rate was elevated for high stumps ( $11.5\% \text{ yr}^{-1}$ ), many of them survive over several decades as suggested by our observations of totally hollowed high stumps with a vigor-

ous thick new crown and the fact that ca 10% of all living trees in both censuses were living high stumps. Such a survival strategy was also noted by Runkle (1998) and Peterson (2000), who both suggested that sprouting could be an important process for post-disturbance tree recruitment into the canopy. Similarly high mortality of living but injured trees was recorded by Runkle (1998,  $7\% \text{ yr}^{-1}$ ) in temperate forests of eastern North America.

Since age structure was not explicitly studied in this study, we could not adequately assess the role of this factor in affecting stand mortality rates. Age reconstruction studies from the central part of the Holkåsen stand have shown that the majority of trees  $>20 \text{ cm}$  DBH belonged to a cohort of 219–279 yr of age (Karlsson 1996, Niklasson et al. 2005, Churski and Niklasson 2010). One could expect an increase in mortality rates in the coming 50 yr, when the age of the dominate cohort would start approaching the maximum lifespan of beech (350–400 yr, Niklasson and Fritz 2003), resulting in cohort dieback (Mueller-Dombois 1987, Ogden et al. 1988).

## Deadwood

The total volume of dead wood in Holkåsen during the 2006 inventory ( $53.8 \text{ m}^3 \text{ ha}^{-1}$ ) was considerably lower than the average of  $131 \text{ m}^3 \text{ ha}^{-1}$  reported from long-established lowland/submontane European beech forest reserves in a recent review study by Christensen et al. (2005). Local and regional differences in tree size distribution, soil conditions, and wind climate may be important factors affecting the deadwood pool of beech stands. A low site index and high decomposition rates due to humid climate and small log diameter may explain the relatively low amounts of CWD in our study area. The large difference in deadwood volumes between the two inventories is likely explained by the effect of two recent windstorms taking place in the winters of 1999 and 2005. Instead, a storm-free period prior to the 1996 inventory lasted for more than two decades, with the latest windstorms recorded during the autumns of 1967 and 1969 (Nilsson et al. 2004).

The beech stand at Holkåsen showed a dominance of standing deadwood (59.9% of total deadwood volume), which was twice as high than the 29% of deadwood reported as snags in Christensen et al. (2005). In our study, such a large proportion of deadwood represented by high stumps could be explained by the high abundance of rot fungi. Infection of live trees by *F. fomentarius* (Baum et al. 2003) may cause deterioration of the trees’ mechanical properties, leading to an increased frequency of stem breakages.

## Role of fungal infection

Although fungal fruit bodies (FFB) are not very common on living and undamaged trees in the Biskopstorp

forest (4–7% in our data), we believe fungi may play a crucial role in shaping beech mortality. Trees with FFB in our study had a significantly lower survivorship rate than FFB-free trees (Table 1, Fig. 4), suggesting that the occurrence of fungi colonizing trees has a direct, though probably time-lagged, effect on beech mortality. In particular *F. fomentarius*, which is an important wood decomposer of both beech and *Betula* spp. in this region (Heilmann-Clausen 2005), may colonize trees and remain dormant, not producing fruit bodies during many years (Chapela and Boddy 1988). Sudden changes in water availability, wood oxygen and nutrient levels may trigger the activity of the fungus and its fructification (Baum et al. 2003). Since our results are based on observations of the presence/absence of FFB growing on stems of living beech trees, it is likely that a higher number of trees than those with visible fruit bodies might have been affected by fungi. Given proper identification of fungal infection on trees without fungal fruit bodies, the actual mortality rates of fungi-infected trees may differ from the reported ones.

## Conclusions

Our study shows a large variation in beech mortality rates among different tree condition classes (TCC) and no effect of tree diameter on mortality rates for undamaged living trees <60 cm DBH. This suggests that overall mortality rates integrating over different TCC may be misleading without information about abundance of different TCC in a forest under consideration. Most beech trees in the studied stand were killed through stem breakage (snapping) and about half of all snapped trees could survive as living high stumps due to location of the breakage point above the lowest living branches. A combination of wind disturbance and fungal infection of tree stems appears to be the dominant mortality factor and apparently explains commonness of high stumps. Such stumps, characterized by an increased mortality rate (ca 10% annually), may present a regional feature of beech dominated forests developed on stony moraines. Living high stumps, being of high conservational value for both invertebrates and epiphytes (Brunet and Isacson 2009, Fritz and Brunet 2010), should receive proper attention in conservation-oriented management plans for southern Swedish beech forests.

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## Appendix

Table 1. Summary of the census data for the trees recorded as living during the 1996 census. For each category absolute number of trees and number of trees per ha (in brackets) are given. TCC are: LTH, healthy living trees; LT<sub>DA</sub>, damaged living tree; a tree with up to 50% of branches lost in the upper crown; DS, dead standing tree; HST<sub>L</sub>, living high stump; HST<sub>DE</sub>, dead high stump; LST<sub>L</sub>, living low stump; LST<sub>DE</sub>, dead low stump; LOG, a lying trunk or fragments of the tree bole. Traces are woody detritus remaining after decomposition of a stump or log. Uprooted are fallen trees with root plate exposed. Not found are trees recorded in 1996 but not found in 2006.

Diameter class, cm	TCC	Total count and density 1996	LTH	LT <sub>DA</sub>	DS	HST <sub>L</sub>	HST <sub>DE</sub>	LST <sub>L</sub>	LST <sub>DE</sub>	LOG	Traces	Uprooted	Not found
<21	LTH	528 (133.3)	364 (91.9)	97 (24.5)	13 (3.3)	4 (1.0)	3 (0.8)	–	12 (3.0)	4 (1.0)	13 (3.3)	–	18 (4.5)
<21	LT <sub>DA</sub>	12 (3.0)	3 (0.8)	7 (1.8)	–	–	–	–	2 (0.5)	–	–	–	–
<21	HST <sub>L</sub>	6 (1.5)	1 (0.3)	–	–	3 (0.8)	1 (0.3)	–	1 (0.3)	–	–	–	–
<21	LST <sub>L</sub>	6 (1.5)	–	–	–	–	–	2 (0.5)	4 (1.0)	–	–	–	–
21–40	LTH	213 (53.8)	164 (41.4)	36 (9.1)	–	6 (1.5)	3 (0.8)	–	2 (0.5)	1 (0.3)	–	1 (0.3)	–
21–40	LT <sub>DA</sub>	10 (2.5)	3 (0.8)	2 (0.5)	–	1 (0.3)	3 (0.8)	–	1 (0.3)	–	–	–	–
21–40	HST <sub>L</sub>	26 (6.6)	–	–	–	3 (0.8)	5 (1.3)	1 (0.3)	12 (3.0)	2 (0.5)	1 (0.3)	–	2 (0.5)
41–60	LTH	189 (47.7)	103 (26.0)	48 (12.1)	1 (0.3)	20 (5.1)	15 (3.8)	–	1 (0.3)	–	–	1 (0.3)	–
41–60	LT <sub>DA</sub>	31 (7.8)	–	18 (4.5)	–	8 (2.0)	4 (1.0)	–	1 (0.3)	–	–	–	–
41–60	HST <sub>L</sub>	93 (23.5)	–	1 (0.3)	–	20 (5.1)	35 (8.8)	1 (0.3)	29 (7.3)	4 (1.0)	2 (0.5)	–	1 (0.3)
>60	LTH	44 (11.1)	15 (3.8)	17 (4.3)	–	4 (1.0)	8 (2.0)	–	–	–	–	–	–
>60	LT <sub>DA</sub>	9 (2.3)	2 (0.5)	1 (0.3)	–	2 (0.5)	4 (1.0)	–	–	–	–	–	–
>60	HST <sub>L</sub>	22 (5.6)	–	–	–	14 (3.5)	7 (1.8)	–	1 (0.3)	–	–	–	–
Total		1189 (300.3)	655 (165.4)	227 (57.3)	14 (3.5)	85 (21.5)	88 (22.2)	4 (1.0)	66 (16.7)	11 (2.8)	16 (4.0)	2 (0.5)	21 (5.3)

Table 2. Summary of the census data for dead trees of the 1996 census. For each category, absolute number of trees and number of trees per ha (in brackets) are given. TCC are DS, dead standing tree; HST<sub>DE</sub> dead high stump; LST<sub>DE</sub> dead low stump. See Table 1 in the Appendix for explanation of other abbreviations.

DBH class, cm	TCC	Count and density	DS	HST <sub>DE</sub>	LST <sub>DE</sub>	LOG	Traces	Uprooted	Not found
<21	DS	21 (5.3)	1 (0.3)		16 (4.0)	1 (0.3)	2 (0.5)		1 (0.3)
<21	LST <sub>DE</sub>	25 (6.3)		1 (0.3)	22 (5.6)				2 (0.5)
<21	Uprooted	3 (0.8)				2 (0.5)		1 (0.3)	
<21	LOG	36 (9.1)				36 (9.1)			
21–40	HST <sub>DE</sub>	12 (3.0)		1 (0.5)	9 (2.3)	1 (0.3)			
21–40	LST <sub>DE</sub>	14 (3.5)			13 (3.3)				1 (0.3)
21–40	LOG	50 (12.6)				50 (12.6)			
41–60	HST <sub>DE</sub>	32 (8.1)		9 (2.3)	22 (5.6)	1 (0.3)			
41–60	LST <sub>DE</sub>	14 (3.5)			13 (3.3)	1 (0.3)			
41–60	LOG	15 (3.8)				15 (3.8)			
>60	DS	1 (0.3)		1 (0.3)					
>60	HST <sub>DE</sub>	4 (1.0)		2 (0.5)	2 (0.5)				
>60	LST <sub>DE</sub>	2 (0.5)			1 (0.3)				1 (0.3)
>60	LOG	1 (0.3)				1 (0.3)			
Total		230 (58.1)	1 (0.3)	15 (3.8)	98 (24.7)	108 (27.3)	2 (0.5)	1 (0.3)	5 (1.3)

Table 3. Summary of the census data for the trees recorded as living and with no fungal fruit bodies during 1996 census. For each category the absolute number of trees and number of trees ha<sup>-1</sup> (in brackets) are given. TCC follows the abbreviations used as in Table 1 in the Appendix: TCC<sub>FB</sub> are the number of TCC with fungal fructiferous bodies on the stem.

DBH class (cm)	TCC alive 1996			TCC <sub>FB</sub> in 2006							
	TCC	Total TCC <sub>FB</sub> 1996	Infected	LT <sub>DA</sub>	HST <sub>L</sub>	HST <sub>DE</sub>	LST <sub>L</sub>	LST <sub>DE</sub>	Log	Traces	Uprooted
<21	LT	–	2 (0.5)	–	–	1 (0.3)	–	–	–	1 (0.3)	–
<21	HST <sub>L</sub>	–	5 (1.3)	1 (0.3)	2 (0.5)	1 (0.3)	–	1 (0.3)	–	–	–
<21	LST <sub>L</sub>	–	1 (0.3)	–	–	–	1 (0.3)	–	–	–	–
21–40	LT	3 (0.7)	13 (3.3)	3 (0.8)	3 (0.8)	5 (1.3)	–	1 (0.3)	–	–	1 (0.3)
21–40	HST <sub>L</sub>	11 (2.8)	8 (2.0)	–	–	4 (1.0)	1 (0.3)	3 (0.8)	–	–	–
41–60	LT	4 (1)	46 (11.6)	6 (1.5)	22 (5.6)	16 (4.0)	–	2 (0.5)	–	–	–
41–60	HST <sub>L</sub>	29 (7.3)	50 (12.6)	–	9 (2.3)	31 (7.8)	1 (0.3)	6 (1.5)	3 (0.8)	–	–
>60	LT	1 (0.3)	17 (4.3)	4 (1.0)	4 (1.0)	9 (2.3)	–	–	–	–	–
>60	HST <sub>L</sub>	2 (0.5)	15 (3.8)	–	10 (2.5)	5 (1.3)	–	–	–	–	–
Total		50 (12.6)	157 (39.6)	14 (3.5)	50 (12.6)	72 (18.2)	3 (0.8)	13 (3.3)	3 (0.8)	1 (0.3)	1 (0.3)