Mortality Patterns Following Spruce Budworm Infestation in Unprotected Spruce-Fir Forests in Maine

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ABSTRACT: *Cumulative and annual mortality of red spruce* (Picea rubens *Sarg.) and balsam fir* [Abies balsamea *(L.) Mill.*] *were examined over a 10 yr period to follow the mortality patterns in unprotected spruce-fir forests in northern Maine. Different mortality patterns were determined based on stand composition classes and merchantability classes. In general, balsam fir was more vulnerable to budworm attack, and reached 92–100% basal area mortality and 84–97% stem density mortality 12 yr after the start of the outbreak. Red spruce, in contrast, had approximately 32–59% basal area mortality and 30–66% stem density mortality during the same time period. Balsam fir mortality started 1 to 2 yr before spruce, while spruce mortality continued 2 to 3 yr after fir mortality was completed. Higher mortality was found in smaller trees than sawtimber-sized trees. Stands with hardwood components (30–70% in basal area) had the lowest mortality rate for both species. Furthermore, Schnute growth function (Schnute 1981) was used to characterize the cumulative mortality trajectories after the defoliation of spruce and fir by stand composition classes. The models estimated the time when annual mortality achieved maximum, the cumulative mortality at that time, and the asymptotic mortality over a long time period after the start of the attack. The information can provide guidelines for predicting protection strategies and scheduling salvage harvests. North. J. Appl. For. 20(4):148–153.*

Key Words: Budworm, defoliation, tree mortality, red spruce, balsam fir.

Spruce budworm (*Choristoneura fumiferana* Clem.) has been the most destructive forest insect in the spruce-fir (*Picea-Abies*) region of New England, with increasing frequency, extent, and severity of outbreaks during the last century (Mog et al. 1982, Blais 1981, 1983a). The most recent budworm epidemic spread across northcentral Maine by 1971 and continued into the 1980s. The resulting growth loss and spruce-fir mortality warranted research into the natural progression of the spruce budworm attack to aid in the development of protection strategies and harvest scheduling of affected areas.

Mortality patterns in the spruce-fir forests are usually reported from spruce budworm case history studies. With balsam fir [*Abies balsamea* (L.) Mill.] more vulnerable to attack than red spruce (*Picea rubens* Sarg.), mortality usually begins 4 to 6 yr after the start of continuous heavy defoliation (Westveld 1946, McLintock 1948, Belyea 1952, Baskerville and MacLean 1979, Blais 1985a, 1985b, Raske and Alvo 1986). Mortality usually increases with increasing severity and duration of the outbreak (Swaine et al. 1924, McLintock 1955, Burke 1979, Moody 1981, MacLean 1985, Solomon 1985) and with increasing stand maturity (MacLean 1980, Blais 1983b). Additionally, mortality generally increases in-extensive stands having a high proportion of the basal area in mature host species (Seymour 1980, Blais 1983b, Raske and Alvo 1986, Solomon and Brann 1992) and in stands with an open structure where spike tops of host species protrude above the forest canopy (Witter et al. 1983, Johnston 1986). Finally, mortality is usually reduced in stands in which host species are overtopped by hardwoods (Blum and MacLean 1985, Witter 1985, Bergeron et al. 1995, Su et al. 1996, Needham et al. 1999).

For modeling mortality patterns, researchers commonly used logistic regression models to predict the probability that a tree would die, which is usually related to tree, stand, and site

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variables (e.g., Monserud 1976, Hamilton 1986, Coyea and Margolis 1994, Dobbertin and Brang 2001). Other statistical techniques or models were also used for analyzing tree and stand mortality data. Crow and Hicks (1990) applied linear discriminant function analysis to examine tree mortality levels in relation to years of defoliation and stand and site conditions for mixed oak stands. Volney (1998) developed a nonparametric proportional hazards model to evaluate the relative risk of individual trees dying following a jack pine budworm outbreak in Saskatchewan. Negron (1998) used regression trees to model tree infestation and mortality caused by the Douglas-fir beetle in the Colorado Front Range. Bergeron et al. (1995) utilized multiple linear regression to assess the respective effects of stand structure, species composition, site characteristics, and the forest composition surrounding the stand on the observed mortality of balsam fir stands in northwestern Quebec.

The objective of this study was to describe and examine the differences in the mortality patterns of red spruce and balsam fir trees over a 10 yr period following an uncontrolled budworm outbreak in northern Maine. The study covered a range of forest stands, with defoliation varying with respect to the concentration susceptible and vulnerable species.

Data and Methods

Fourteen study plots (0.05 to 2.02 ha in size) were established in a 60–90 yr old red spruce-balsam fir stand in the Baxter State Park, Maine in 1977 by the USDA Forest Service, Northeastern Research Station, to follow the natural progression of spruce budworm defoliation and tree mortality. The main plots were divided into (10 × 10 m) subplots. The diameters at breast height (dbh) of all trees (>1.37 m in height) were measured, and other information such as species and merchantability class (i.e., sawtimber, >24 cm; pulpwood, 10–24 cm; and nonmerchantable, ≤10 cm) were also recorded. Based on the initial species basal area in 1977, the subplots were grouped into four stand composition classes: high fir (>70% balsam fir), high spruce (>70% spruce), mixed spruce-fir (>70% combined spruce and fir), and mixed-wood (>30% but <70% hardwood) (Table 1). Tree mortality was monitored annually from 1978 to 1987 and tallied by species, merchantability classes, and cause of death (blowdown, budworm related). The year 1978 was considered as the seventh year after the start of defoliation in 1971. Cumulative (1978 to 1987) mortality was calculated as a percentage of both initial basal area and initial stem density (number of stems per unit area), and was determined for stand composition classes and merchantability classes. Annual mortality was computed as a percentage of total basal area to examine if species composition and merchantability had influence on the timing of mortality.

Instead of using a traditional logistic regression model, we chose Schnute growth function (Schnute 1981) to model the pattern of cumulative mortality over time of red spruce and of balsam fir by stand composition classes. The Schnute function is a generalized growth model based on biological principles. Other growth functions, such as the logistic model, are special cases of the Schnute function. However, we did not intend to develop a prediction model for tree mortality or survival in this study. Rather we were more interested in the characteristics of the mortality patterns of the two species, particularly the time when annual mortality achieves its peak and the maximum percent mortality at that time.

The Schnute growth function is expressed as:

$$Y(t) = \left[y_1^{\,b} + \left(y_2^{\,b} - y_1^{\,b} \right) \frac{1 - e^{-a(t-t_1)}}{1 - e^{-a(t_2-t_1)}} \right]^{(1/b)} \qquad (1)$$

where $Y(t)$ is cumulative mortality at time t; y_1 and y_2 are cumulative mortality at time t_1 (t_1 = 7) and t_2 (t_2 = 15), respectively; a and b are rate coefficients. In Equation (1) time t is defined as years after the budworm outbreak in 1971. Therefore, year 1978 (t_1) is referred as the seventh year after the attack and year 1986 (t_2) as the fifteenth year after the attack. The y_1, y_2, a and b in Equation (1) were estimated from data. The Schnute function represents a family of nonlinear curves depending on the two rate coefficients, a and b. Other characteristics of the cumulative mortality curves, such as the time of curve inflection (t^*), the cumulative mortality at t^* (y^*), and the asymptotic mortality when time approaches infinite (y_∞), can be computed by the following equations (Schnute 1981):

$$t^* = t_1 + t_2 - \frac{1}{a} \log \left[\frac{b(e^{at_2} y_2^{\,b} - e^{at_1} y_1^{\,b})}{y_2^{\,b} - y_1^{\,b}} \right] \qquad (2)$$

$$y^* = \left[\frac{(1-b)(e^{at_2} y_2^{\,b} - e^{at_1} y_1^{\,b})}{e^{at_2} - e^{at_1}} \right]^{(1/b)} \qquad (3)$$

$$y_\infty = \left[\frac{e^{at_2} y_2^{\,b} - e^{at_1} y_1^{\,b}}{e^{at_2} - e^{at_1}} \right]^{(1/b)} \qquad (4)$$

Table 1. Mean spruce-fir initial (1977) basal area and stem density and cumulative (1978 to 1986) percent mortality by stand composition classes.

		Balsam fir				Spruce			
		Basal area		Stem density		Basal area		Stem density	
Stand class	Subplots (no.)	Initial (m^2/ha)	Mortality (%)	Initial (no./ha)	Mortality (%)	Initial (m^2/ha)	Mortality (%)	Initial (no./ha)	Mortality (%)
High fir	119	33	97	3,647	95	4	52	370	39
High spruce	143	6	100	710	97	41	59	2,259	66
Mixed spruce-fir	234	20	98	1,606	95	21	55	893	59
Mixedwood	169	14	92	1,176	84	7	32	566	30

The inflection point t^* represents the time when annual mortality achieves its maximum.

Results and Discussion

Cumulative Mortality

Regardless of stand composition classes, balsam fir cumulative basal area mortality was ≤92% of the initial balsam fir basal area (Table 1). As a percentage of initial stem density, balsam fir cumulative mortality was ≥95%, except in mixed-wood (mixed softwood and hardwood) stands, in which mortality was 84%. This may be due to a "buffering effect" of hardwoods during the first years of budworm infestation (Su et al. 1996). Differences between basal area and stem density mortality percentages may be accounted for by the size of dead trees. The death of smaller trees had a greater impact on stem density mortality than on basal area mortality. Balsam fir cumulative basal area mortality was ≥83% for each combination of stand composition classes and merchantability classes (Table 2). For each stand composition class, fir mortality was lower for sawtimber than for the other merchantability classes. In terms of stem density, balsam fir mortality was lowest in the sawtimber class for high fir and high spruce stands. In mixed spruce-fir and mixed-wood stands, however, stem density mortality was lowest in the nonmerchantable class (Table 2).

Spruce cumulative mortality percentages were less than those of balsam fir. The highest basal area and stem density mortalities (59 and 66%, respectively) occurred in high spruce stands (Table 1). Again, basal area (32%) and stem density (30%) mortalities were lowest in mixed-wood stands. Spruce basal area mortality ranged from 26 to 82% for all combinations of stand composition classes and merchantability classes (Table 2). Mortality was lowest in the sawtimber class for each of the four stand composition classes. Spruce stem density mortality was highest in the pulpwood class, except in high spruce stands in which mortality was highest in the nonmerchantable class.

The time trajectories of the cumulative mortality for balsam fir and spruce were modeled using Equation (1) by stand composition classes (i.e., high fir, high spruce, mixed spruce-fir, and mixed-wood). The estimated parameters (y_1, y_2, a, b, t^*, y^*, and y_∞) are provided in Table 3, and simulations from the models were demonstrated in Figure 1. The parameter b was negative in all cases, indicating an *S*-shaped mortality

Table 2. Mean spruce-fir initial (1977) basal area and stem density and cumulative (1978 to 1986) percent mortality by stand composition and merchantability classes.

		Balsam fir				Spruce			
		Basal area		Stem density		Basal area		Stem density	
Stand class Merchantability	Subplots (no.)	Initial (m^2/ha)	Mortality (%)	Initial (no./ha)	Mortality (%)	Initial (m^2/ha)	Mortality (%)	Initial (no./ha)	Mortality (%)
High fir	119								
Sawtimber		4	90	66	90	1	32	14	31
Pulpwood		23	98	1,371	98	3	59	138	63
Nonmerchantable		6	100	2,206	93	<1	43	218	24
High Spruce	143								
Sawtimber		<1	89	8	91	11	52	176	53
Pulpwood		4	100	312	100	27	60	1,326	61
Nonmerchantable		1	100	390	95	3	82	757	78
Mixed Spruce-Fir	234								
Sawtimber		3	93	51	93	9	45	130	47
Pulpwood		15	99	790	98	11	63	478	67
Nonmerchantable		2	100	764	91	1	69	285	52
Mixedwood	169								
Sawtimber		2	83	48	83	2	26	28	25
Pulpwood		10	95	476	95	4	33	210	33
Nonmerchantable		2	90	650	76	1	36	328	29

Table 3. Model parameters and characteristics of Equation (1) for balsam fir and spruce cumulative mortality by stand composition classes.

	Basal area							Stem density						
Stand class	y_1	y_2	a	b	y_∞	t^*	y^*	y_1	y_2	a	b	y_∞	t^*	y^*
Balsam fir														
High fir	15.25	97.53	1.4686	−1.7718	97.54	8.82	54.86	18.46	94.51	1.7099	−2.6890	94.52	8.98	58.17
High spruce	23.24	100.0	2.0061	−3.2484	100.0	8.78	64.26	23.68	97.19	1.3866	−1.7890	97.20	8.34	54.78
Mixed spruce-fir	13.96	98.23	1.5604	−1.8952	98.24	8.94	56.06	18.37	94.74	1.4068	−1.9379	94.76	8.76	54.34
Mixedwood	4.10	92.70	1.2217	−1.0150	92.82	9.54	46.54	6.95	83.75	1.2093	−1.4807	83.89	9.70	45.42
Spruce														
High fir	0.90	51.19	2.3290	−2.4638	51.19	10.89	30.92	1.20	38.24	2.4137	−3.0555	38.27	10.92	24.20
High spruce	2.93	58.97	1.6558	−2.4400	59.04	10.88	35.58	5.92	65.67	1.5298	−2.7498	65.76	10.67	40.67
Mixed spruce-fir	1.69	54.64	1.6640	−2.0941	54.70	10.93	31.90	3.17	58.45	1.8500	−2.7901	58.48	10.84	36.27
Mixedwood	1.42	30.66	1.9715	−3.6500	30.75	12.04	20.18	2.98	30.02	1.0298	−2.2928	30.74	11.39	18.28

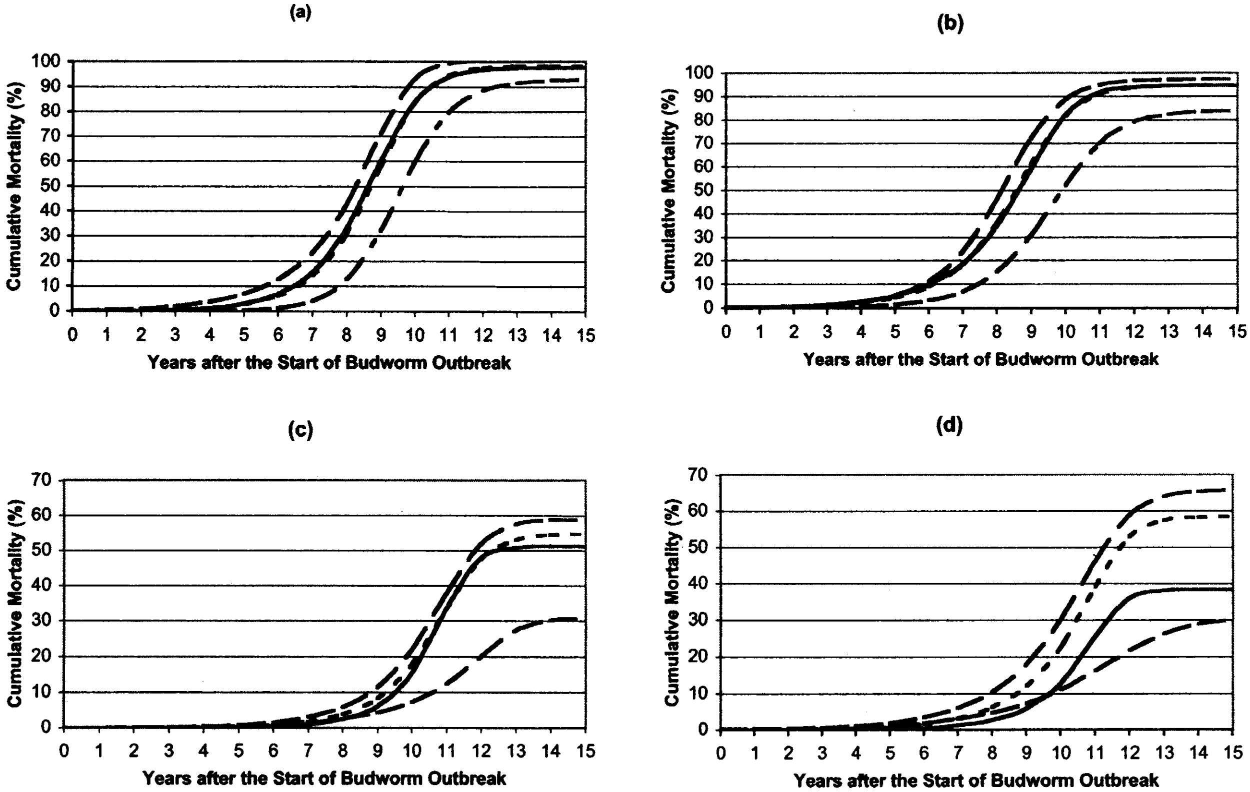

Figure 1. Cumulative mortality (%) by stand composition classes: high fir (———), high spruce (— — —), mixed spruce-fir (- - -), and mixed-wood (— · —). (a) basal area mortality for balsam fir, (b) stem density mortality for balsam fir, (c) basal area mortality for red spruce, (d) stem density mortality for red spruce.

curve with a gradual increase in tree mortality a few years after the budworm attack (Schnute 1981, curve 8). Balsam fir basal area annual mortality peaked about 8.8–8.9 yr *(t^*)* after the attack in high fir, high spruce, or mixed spruce-fir stands. At this time the cumulative mortality ranged between 55 to 64% *(y^*)* in these stands (Table 3). In mixed-wood stands balsam fir basal area annual mortality peaked 9.5 yr after the attack, with the cumulative mortality about 46% (Table 3). Similarly, balsam fir stem density annual mortality peaked about 8.3–9 yr *(t^*)* after the attack in high fir, high spruce, or mixed spruce-fir stands. At this time, the cumulative mortality ranged between 54 and 58% *(y^*)* (Table 3). In mixed-wood stands balsam fir stem density annual mortality peaked 9.7 yr after the attack, with the cumulative mortality about 45% (Table 3). Figures 1(a) and 1(b) showed similar trajectory patterns of basal area and stem density mortality among the four stand composition classes for balsam fir.

In contrast, spruce basal area annual mortality peaked 10.9 yr after the attack in high fir, high spruce, or mixed spruce-fir stands and 12 yr in mixed-wood stands. At this time, the cumulative mortality ranged from 20 to 36% depending on the stand types (Table 3). For stem density annual mortality, spruce peaked 10.7–10.9 yr after the attack in high fir, high spruce or mixed spruce-fir stands and 11.4 yr in mixed-wood stands. At this time the cumulative mortality ranged from 18 to 41% depending on the stand types (Table 3). Figures 1(c) and 1(d) illustrated different trajectory patterns of basal area and stem density mortality among the four stand composition classes for red spruce.

Over a long time period after the attack (i.e., when time approaches infinite), spruce species suffered much less cumulative mortality (average y_∞ was 41% across the four stand composition classes) than balsam fir (average y_∞ was 97% across the four stand composition classes) (Table 3). Using the model parameters in Table 3, forest managers can predict the cumulative mortality after budworm outbreak for balsam fir and spruce species.

Annual Mortality

Annual mortality was computed as a percentage of total basal area and used to examine the influence of species composition and merchantability on the timing of mortality. Prior to a spruce budworm outbreak, the annual net natural mortality ranged from 1.0 to 3.8% per year for balsam fir (Seegrist and Arner 1982). Balsam fir maximum annual mortality (25 to 27%) occurred in 1980 or 1981 for the four stand composition classes, with mortality essentially completed by 1983, i.e., 12 yr after the start of the outbreak. This result was consistent with the findings by MacLean (1980). Maximum annual mortality in mixed-wood stands appeared to lag about 1 yr behind the other stand composition classes (Table 4). Table 5 indicated that maximum annual mortality of sawtimber-sized fir generally occurred in 1981 (i.e., 10 yr after the start of the outbreak), which was later than pulpwood in 1980 (i.e., 9 yr after the start of the outbreak) and nonmerchantable in

Table 4. Annual spruce-fir percent basal area mortality by stand composition classes.

Stand class	1978	1979	1980	1981	1982	1983	1984	1985	1986
					(%)				
Balsam fir									
High fir	15	20	26	25	10	3	<1	0	0
High spruce	21	24	24	25	6	1	0	<1	0
Mixed spruce-fir	14	18	27	27	12	3	<1	<1	0
Mixedwood	4	9	23	26	24	12	1	1	1
Spruce									
High fir	4	4	4	15	41	24	8	1	<1
High spruce	4	5	13	12	30	23	9	2	2
Mixed spruce-fir	3	4	10	12	33	24	9	4	2
Mixedwood	4	4	10	6	12	31	21	6	8

1978 (i.e., 7 yr after the start of the outbreak). The slower mortality pattern for the sawtimber class may be attributed to greater vigor of sawtimber-sized fir. Baskerville and MacLean (1979) reported peak mortality in smaller balsam fir stands in the sixth and seventh yr of an outbreak.

Prior to a spruce budworm outbreak, the annual net natural mortality ranged from 0.5 to 0.9% per year for spruce (Seegrist and Arner 1982). Spruce annual mortality lagged 2 to 3 yr behind that of balsam fir (Table 4). It is more likely that spruce was better able to withstand the defoliation than fir. Erdle and MacLean (1999) showed that similar growth loss and defoliation relationships between fir and spruce, but quite different mortality and defoliation relationships between the two species (fir had higher mortality for a given level of defoliation). Furthermore, the depletion of stored reserves from continuous defoliation may have been delayed for spruce since spruce has an average of 12 age classes of needles, compared to eight classes for fir. Spruce annual mortality was similar for three of the four merchantability classes, except in high fir stands (Table 5). Maximum annual mortality occurred

Table 5. Annual spruce-fir percent basal area mortality by stand composition and merchantability classes.

Stand class / Merchantability class	1978	1979	1980	1981	1982	1983	1984	1985	1986
					(%)				
Balsam fir									
High fir									
Sawtimber	3	2	37	25	22	12	0	0	0
Pulpwood	13	21	27	27	10	2	1	0	0
Nonmerchantable	29	26	19	20	4	2	<1	0	<1
High spruce									
Sawtimber	30	0	0	27	42	0	0	0	0
Pulpwood	19	25	27	26	3	1	0	0	0
Nonmerchantable	27	27	22	19	4	2	0	1	0
Mixed spruce-fir									
Sawtimber	6	7	26	33	24	4	0	1	0
Pulpwood	13	19	28	27	10	3	<1	0	0
Nonmerchantable	27	25	22	17	7	3	<1	<1	0
Mixedwood									
Sawtimber	0	7	27	30	18	17	2	0	0
Pulpwood	4	9	24	26	26	10	1	1	1
Nonmerchantable	9	12	16	24	19	15	3	1	1
Spruce									
High fir									
Sawtimber	19	0	0	0	27	39	15	0	0
Pulpwood	1	4	4	16	45	21	8	1	1
Nonmerchantable	3	11	6	24	28	24	1	3	0
High spruce									
Sawtimber	2	3	12	10	31	26	14	2	2
Pulpwood	4	5	13	13	31	22	9	2	2
Nonmerchantable	10	12	15	17	21	19	3	2	1
Mixed spruce-fir									
Sawtimber	2	5	10	9	30	27	10	6	1
Pulpwood	3	4	10	13	35	23	9	3	2
Nonmerchantable	11	8	13	19	29	15	3	1	2
Mixedwood									
Sawtimber	0	0	0	0	24	29	27	9	10
Pulpwood	5	3	12	6	8	34	23	4	7
Nonmerchantable	7	9	13	17	12	21	6	9	5

in 1982 in high spruce and mixed spruce-fir stands for each merchantability class. In mixed-wood stands, maximum annual mortality occurred in 1983 for each merchantability class. In high fir stands, maximum annual mortality occurred in 1982 for pulpwood and nonmerchantable classes, while a 1 yr lag in mortality occurred for spruce sawtimber.

Conclusions

During the spruce budworm attack in the unprotected spruce-fir forests in Maine, the more vulnerable balsam fir reached 92–100% basal area mortality and spruce approximately 32–59% basal area mortality 12 yr after the start of the outbreak. Balsam fir mortality started 1 to 2 yr before spruce, and spruce mortality continued 2 to 3 yr after fir mortality was completed. Small differences in mortality occurred across merchantability classes for each of the species groups. Smaller and more stressed trees died first, indicating trees with more crown competition died sooner. Nonmerchantable class had the highest mortality rate followed by pulpwood and then sawtimber. Sawtimber mortality peaked and continued 2 to 3 yr after the smaller trees died in high fir, high spruce, and mixed spruce and fir. However, the fir, spruce, and combined spruce and fir mortality patterns for the merchantability classes were similar in mixed-wood stands, with spruce mortality delayed 2 to 3 yr later than fir.

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