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White ash (*Fraxinus americana*) decline and mortality: The role of site nutrition and stress history

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ABSTRACT

Over the past century, white ash (*Fraxinus americana*) populations throughout its range have deteriorated as a result of declining tree health and increased mortality rates. Although co-occurring factors including site nutritional deficiencies and punctuated stress events (e.g., defoliations, drought) are hypothesized to trigger white ash decline, there are no empirical assessments of these factors at regional scales. In this study, we evaluated ash crown dieback, crown health condition, and mortality on 190 plots paired along a topographic gradient known to differ in site nutrition across a 3000 km^2 area of northwestern Pennsylvania, USA. Additionally, we assessed white ash foliar nutrient content and additional factors including defoliation history as potential explanatory variables at all sites. White ash populations on upper slopes consistently had significantly greater dieback, poorer crown condition, and greater mortality than populations in paired plots on lower slopes. Despite nearly two decades since the last major elm spanworm defoliation, this stressor further amplified the differences in health and mortality seen between slope positions. On the relatively cation deficient upper slope positions, crown dieback and crown condition improved with increasing foliar cation (Ca^{2+}, Mg^{2+}) concentration. Our results indicate that white ash health is strongly influenced by site nutrition, and defoliation can trigger declines in cation-deficient sites. Knowledge of how landscape position and nutrition influence white ash health may alter management responses to insect outbreak events.

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1. Introduction

Sudden, and often unexplained, episodes of dieback and mortality in forest tree species remain one of the most vexing and vital forest health issues facing managers and conservationists worldwide (Blank et al., 1988). In North America, ash species (*Fraxinus* spp.), and white ash (*F. americana*) in particular, have exhibited extensive dieback and increased mortality throughout their range since at least the 1920s (Hibben and Silverborg, 1978; Sinclair et al., 1990; Han et al., 1991). These episodes often decimate dominant or co-dominant tree populations with reported mortality reaching 48% (Castello et al., 1985) and reductions in live basal area as great as 60% (Morin et al., 2006). The collapse of these populations is critical as ash is an important component of eastern deciduous forests and a valued timber species with an estimated 1.25 billion trees ($\geqslant$5 in. DBH) growing throughout the upper midwestern and northeastern United States (USDA Forest Service, 2010).

Although episodic and extensive *Fraxinus* spp. mortality is occasionally linked to individual and readily identifiable endogenous (e.g., synchronous cohort senescence; Ward, 1982) or exogenous factors (e.g., pathogens; Castello et al., 1995), more often the exact cause is unknown (Hibben and Silverborg, 1978; Mueller-Dombois, 1987; Woodcock et al., 1993). Stand age, drought, landscape position, pests, pathogens, and phytoplasmas are hypothesized to act in concert to incite ash decline, but, evidence for any of these factors remains equivocal (Tobiessen and Buchsbaum, 1976; Hibben and Silverborg, 1978; Castello et al., 1985; Woodcock et al., 1993; Sinclair and Griffiths, 1994; Ward, 1997; Feeley et al., 2001). Indeed, our current knowledge of the relative importance and potential linkages among any of these factors in influencing ash decline remains woefully inadequate, thereby limiting our ability to predict dieback patterns across the landscape.

Growing evidence suggests site nutrient deficiencies, putatively linked to anthropogenic changes in soil chemistry, may underlie the tree declines observed in North America and elsewhere (Blank et al., 1988; DeHayes et al., 1999; Horsley et al., 1999; Demchik and Sharpe, 2000). Although empirical assessments of the influence of site nutrition on white ash health remain lacking, several lines of evidence suggest this species may be sensitive to nutritional imbalances and these, in turn, may increase risk of decline. First, studies indicate white ash has high requirements for base cations (e.g., Ca^{2+}, Mg^{2+}) and is consistently associated with soils with higher pH and greater base cation availability (Boerner and

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Koslowsky, 1989; van Breemen et al., 1997; Finzi et al., 1998; Bigelow and Canham, 2002). Second, anthropogenic changes in precipitation chemistry and acidity over the latter half of the 20th century are associated with declines in soil pH and pronounced reductions in base cation concentrations ranging from 50% up to as high as order of magnitude (e.g., Likens et al., 1996; Drohan and Sharpe, 1997; Driscoll et al., 2001; Bailey et al., 2005). Finally, researchers have found tree declines are often associated with cation availability and stress: for sugar maple (*Acer saccharum*), another tree species with high cation requirements, interactions between nutrient imbalances and stress lead to regional declines (reviewed by Cronan and Grigal (1995)). Thus, tree species with high cation requirements, like sugar maple and white ash, may be bellwethers of regional nutrient imbalances and point to widespread changes in overall forest health.

Although nutrient imbalances alone may predispose trees to health decline symptoms, punctuated stress events appear to be important in triggering these weakened, yet otherwise healthy trees, into decline and mortality episodes (Manion, 1991; Horsley et al., 2000). Of the myriad short-term stressors potentially affecting tree health, drought and insect defoliations are the most commonly suspected stress agents inciting decline in white ash as well as other species (reviewed by Houston (1987), Millers et al. (1989), and Auclair et al. (1997)). Both drought and defoliation stress alter tree carbohydrate budgets by reducing carbohydrate storage through tissue loss or prolonged stomatal closure and accelerating carbohydrate use via increased assimilation and respiration (Tobiessen and Buchsbaum, 1976; Wargo, 1999). The net effect is a greatly reduced root starch and sugar content, which ultimately exerts strong control over tree vigor and predisposes individuals to infection by opportunistic pathogens (Wargo, 1981; Gregory and Wargo, 1986; Han et al., 1991; Kosola et al., 2001).

In this study, we examined the relationship among various biotic and abiotic factors linked to variability in white ash health. Our specific objectives were to: (i) identify the factors that contribute to white ash dieback and mortality, including foliar cation concentration and defoliation history and (ii) assess whether relationships between white ash health and any putative predisposing and stress factors differ between topographic positions. Earlier regional work determined the utility of topographic position as a robust predictor of cation concentrations and indicator of landscape positions associated with risk of decline in sugar maple (Horsley et al., 2000; Bailey et al., 2004; Long et al., 2009); we hypothesized topographic position is a key explanatory variable in white ash decline.

2. Methods

2.1. Study area

We surveyed forested areas within a 3000 km^2 area encompassing the Allegheny National Forest (ANF) in northwestern Pennsylvania to establish a white ash monitoring plot network in May–August 2009 (Fig. 1). Forests within the area are typically 80–100 year-old, second growth Allegheny hardwood stands dominated by black cherry (*Prunus serotina*) and red maple (*Acer rubrum*). The area has a humid temperate climate; annual precipitation averages 1077 mm, summer temperatures average 18.6 °C, and growing seasons last 100–130 days (Whitney, 1990). The strongly acidic soils are derived from relatively infertile sandstones and shale. Additionally, the unglaciated soils in the area have relatively low levels of exchangeable cations; the pH-sensitive high cation exchange capacity of the dominant kaolinite material, a course silicate clay, is further exacerbated by chronic acid precipitation inputs, particularly on upper slope positions (Bailey et al., 2004, 2005). Within the study area, Morin et al. (2006) found white ash mortality from unknown causes was responsible for an observed 60% decrease in ash live basal area in the 1990s.

2.2. Sampling

We superimposed a grid over the ANF ownership and, using existing stand information on ash basal area and landform classifications, we searched each 700 ha block to identify pairs of plots containing a range of 0.23–4.59 $m^2\ ha^{-1}$ of white ash, where one plot in the pair was established on a lower slope position (foot or bottom) and the other on an upper slope position (shoulder or plateau). At each plot, a focal ash tree was defined as plot center and the surrounding tree community was inventoried in a variable radius plot using a 10 factor prism. Within each pair of upper and lower slope positions, care was taken to choose the healthiest dominant or co-dominant focal trees in similar size and crown classes. Diameter at breast height (DBH) was measured for each tree and trees with two trunks were counted as separate trees if they divided below breast height (140 cm). We established 105 blocks with 20 being incomplete (e.g., they were missing a lower- or upper-site or site was harvested following establishment) and the median distance between plots in a pair was (805 m). Thus, we present data from 190 mature, second-growth plots. We noted the presence of seeps at each site as within the unglaciated portion of the Allegheny plateau weatherable minerals, including Ca and Mg, are confined to lower portions of the bedrock and are delivered to lower slope positions via water flow paths (Bailey et al., 2004).

In summer 2010, we assessed the health status of all ash trees using a variety of well-established canopy rating metrics. We rated crowns using the Forest Inventory and Analysis (FIA) metric of crown dieback defined as the percentage of the live crown area that exhibits signs of recent fine twig dieback, excluding snag branches and gaps in the canopy (USDA Forest Service, 2007). We also rated crowns using a categorical ash crown health condition rating developed specifically to assess ash decline and modeled after similar methods used to assess declines in other species (Ball and Simmons, 1980; Horsley et al., 1999; Smith, 2006). The categorical system is defined as follows: 1 = full, healthy canopy, 2 = some thinning canopy but no dieback, 3 = tree with dieback, defined as dead twigs or branches near the top of the tree, exposed to sunlight, 4 = tree with less than 50% of a full canopy, which could occur through a combination of dieback and thinning, and 5 = dead canopy (including trees with live epicormic or stump sprouts). Crown dieback and condition differ in that dieback assesses only recent stress events (e.g., fine twig dieback in live crown), whereas the crown condition captures longer-term stress (i.e., fine twig dieback, dead limbs, and thinning). For ease of interpretation, we present these analyses on crown condition as the difference between 5 and the crown rating, (i.e., Crown Condition = 5 − Crown Rating Value), such that a dead tree is rated "0" and a healthy tree is rated "4". Finally, using our inventory data, we calculated the relative abundance (%) of standing dead white ash within each plot. Thus, our three estimates capture the progression of decline over short- (dieback), medium- (crown condition), and long-term (mortality) time frames.

We assessed site nutritional quality with ash tree foliar chemistry and herbaceous indicator species. Foliar chemistry was used as a bioassay of site nutritional quality because of its ability to integrate horizontal and vertical differences in soil nutrition within stands (Bailey et al., 2004). In each plot, a mid-crown sample of healthy, sun-exposed leaves was sampled from the focal tree during the last 2 weeks of August in 2009 and 2010. Foliage samples were oven dried at 70 °C and sent for analyses at the University of Maine Analytical Lab. Dried foliage samples were analyzed for various macro and micro nutrients, most importantly Ca and Mg. For data analyses, foliar chemistry was expressed as mg kg^{-1} dry

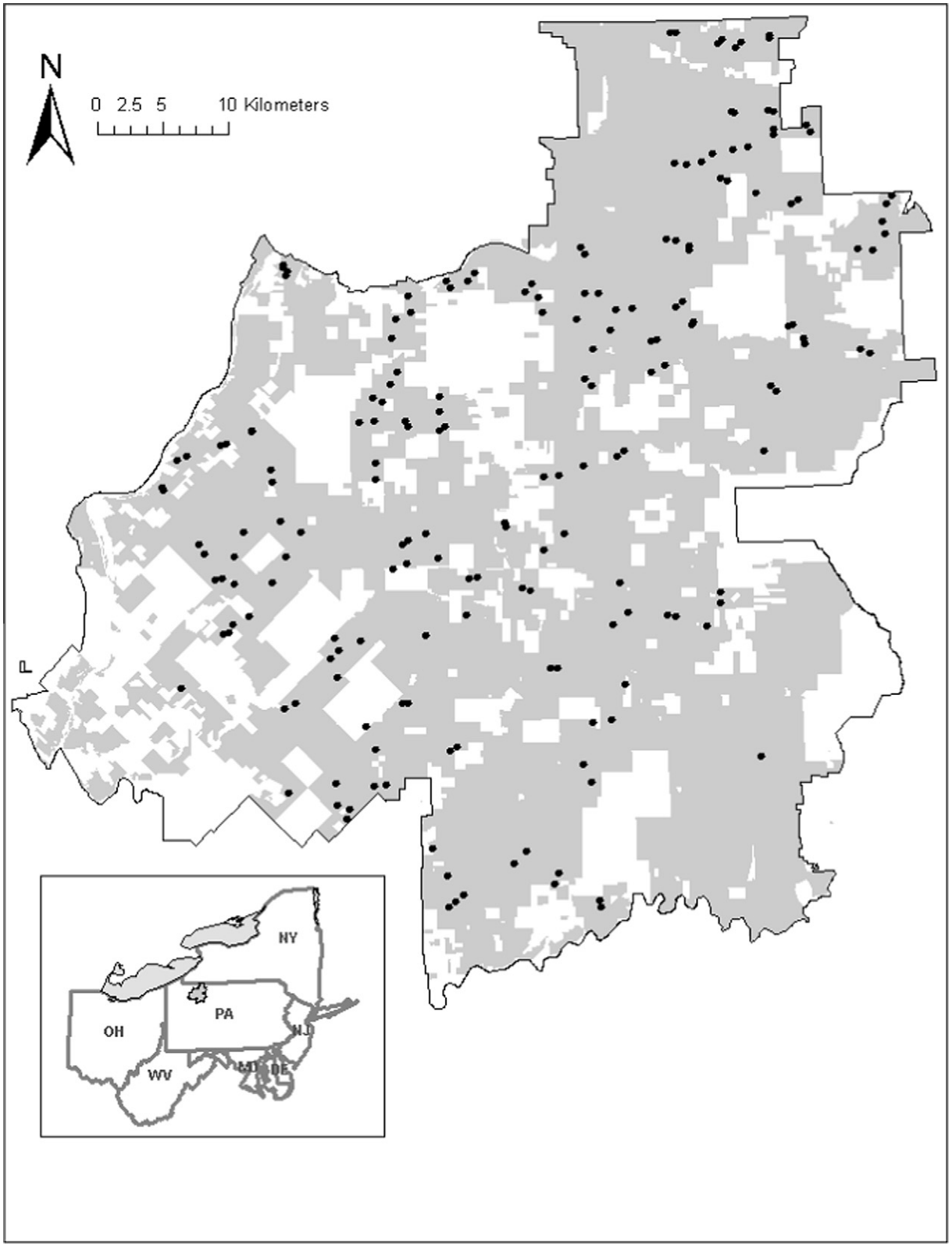

Fig. 1. Approximate locations of the ash health monitoring plots throughout the Allegheny National Forest proclamation boundary. Areas in grey represent National Forest lands while areas in white denote private inholdings within the proclamation boundary.

mass. At each plot we conducted herbaceous plant surveys to detect the presence of 34 herbaceous species known to be reliable indicators of high base cation nutrition in the region (Horsley et al., 2008).

We obtained defoliation history at each site from existing GIS records. Defoliation records were based on aerial surveys (1984–1998) and include gypsy moth (*Lymantria dispar*), cherry scallop-shell moth (*Hydria prunivorata*), and elm spanworm (*Ennomos*

subsignarius). Of these, only the polyphagous elm spanworm is known to defoliate ash while the other insects feed on ash opportunistically, if at all (Fedde, 1964; Drooz, 1985). Elm spanworm outbreaks began in 1991, peaked in 1993, and collapsed by 1994. These records indicate that 45% of our sites suffered elm spanworm defoliation during this period with only one of these having >1 defoliation event. Based on these records, plots were categorized as defoliated or not defoliated. There have been no major defoliation events in our study area since 1997 (Morin et al., 2006).

2.3. Analyses

To investigate the combination of factors that influence white ash health, we utilized a modeling strategy guided by information from existing regional data regarding the relationship between site nutrition and tree health. We tested for differences in ash canopy health variables using mixed model analysis of covariance (Proc Glimmix; SAS Institute Inc., 2011). Although the three ash health responses, mean canopy dieback, mean canopy condition, and percent mortality, were discrete at the individual tree level, means calculated at the plot level were treated as continuous variables in the analyses. Topographic position was modeled as a fixed factor, plot(block) was modeled as a random factor, and tree diameter, elm spanworm defoliation (none, 1+), and cation index (i.e., foliar Ca + Mg in mg kg^{-1} of dry mass; Horsley et al., 2008) were treated as covariates.

Model simplification was performed by removing non-significant interactions ($P \geqslant 0.10$) one by one among the two-way interactions. Main effects were retained in the model even if they were non-significant (Neter et al., 1996). We further explored two-way interactions by examining the association between significant continuous predictors and the response variable within the context of the overall mixed effect model using the R^2_β statistic developed for mixed models (Edwards et al., 2008). This statistic is the direct extension of the univariate R^2 statistic to linear mixed models. Analyses on average canopy dieback and average ash condition were right-skewed and were best modeled using a gamma distribution with a log-link function (Bolker, 2008). To model mortality we utilized a zero-inflated negative binomial model (ZINB) using Proc Countreg; SAS Institute Inc., 2011). A ZINB model is a mixture model consisting of two parts: a binomial model, with or without covariates, used to model the excess zeros, and a count process, including expected zeros, modeled by a negative binomial generalized linear model. The choice of the ZINB model was justified by the existence of excess zeros compared to a Poisson distribution, which made a zero-inflated model necessary and excessive variation in the count process, which made a negative binomial model more appropriate than a Poisson model (Zurr et al., 2009). As the Countreg procedure works only on discrete data, mortality was rounded to the nearest 10%. Finally, we contrasted our two phytometer-based estimates of site nutrition (ash foliar chemistry and herbaceous indicator plant frequency) between topographic positions using a paired analysis of variance.

3. Results

Overall, we assessed 538 white ash trees throughout the entire study region (Fig. 1). Ash relative dominance across all stands, which is biased toward areas where ash was present, averaged 19.54 ± 1.1% of the basal area and 10.70 ± 1.1% of the stems. Ash tree density and basal area on the paired plots did not differ significantly between topographic positions (Density : $\overline{X}_{Lower} = 41.99 \pm 4.57$ stems ha^{-1} versus $\overline{X}_{Upper} = 46.11 \pm 3.96$, $P = 0.49$; Basal Area: $\overline{X}_{lower} = 5.63 \pm 0.48$ m^2 ha^{-1} versus $\overline{X}_{Upper} = 6.62 \pm 0.52$, $P = 0.17$).

Phytometer-based site nutrition measures suggested base cation availability differed between topographic positions. Sites on lower slope positions contained greater concentrations of foliar Ca and Mg than paired upper slope positions (Table 1; $P < 0.0001$ for both cations). Additionally, the incidence of herbaceous species known to track base cation availability was positively related to foliar cation index ($F = 63.16$, $P < 0.0001$, $r^2 = 0.25$) and was an order of magnitude greater on lower slope positions relative to upper slope positions ($\overline{X}_{Lower} = 155 \pm 0.19$ species per site versus $\overline{X}_{Upper} = 0.20 \pm 0.06, P < 0.0001$).

Table 1
Means (±1 SE) and ranges of foliar nutrition data from white ash trees in lower and upper slope positions of the Allegheny National Forest. Values are in mg kg^{-1}.

Foliar nutrients (mg kg^{-1})	Lower slope		Upper slope	
	Mean ± SE	Range	Mean ± SE	Range
Calcium	8216 ± 347	2000–17,100	5418 ± 282	1360–14,440
Magnesium	2289 ± 72	820–4040	1544 ± 76	610–5080
Cation index (Ca + Mg)	10,506 ± 388	2950–21,140	6963 ± 319	2030–16,860
Nitrogen	22,879 ± 236	18,400–29,900	23,095 ± 273	15,700–30,400
Phosphorus	1400 ± 34	950–3480	1535 ± 42	920–2790
Potassium	11,028 ± 244	6330–17,500	10,404 ± 217	5190–14,600
Aluminum	19 ± 1	0.7–64	27 ± 1	5–80
Manganese	78 ± 3	24–198	128 ± 9	33–554

Levels of white ash crown dieback were significantly greater on upper slope positions (Table 2 and Fig. 2A) and were inversely related to foliar cation concentrations, but only on upper slope positions (significant Topographic Position × Cation Index interaction; Table 2 and Fig. 3A). Crown dieback was not significantly related to defoliation or mean ash diameter (Table 2). White ash crown conditions were poorer on upper slope positions relative to lower slope positions (Table 2 and Fig. 2B). Crown conditions improved with both increasing foliar cation concentrations and mean ash diameter (Table 2 and Fig. 3B). Trees in upper slope positions with past defoliation stress or on sites with low foliar cation concentrations tended to have the poorest crown condition (Topographic Position × Defoliation and Topographic Position × Cation Index: $0.1 > P > 0.05$, Table 2).

Only 23 sites had any standing dead ash. The likelihood of a plot exhibiting ash mortality was greater in plots with lower foliar cation concentration ($P = 0.04$) and marginally greater on upper slope positions ($P = 0.08$; Table 3 and Fig. 2C). The relative abundance of standing dead ash was greater on sites with smaller diameter ash trees ($P = 0.0004$) and marginally greater on sites with a history of elm spanworm defoliation stress ($P = 0.07$).

Table 2
Mixed model analysis of variance results of the effect of predictor variables on crown dieback and crown condition of white ash trees. Significant relationships between covariates and response variables are shown as positive (↑) or negative (↓) associations.

Predictors	Crown dieback			Crown condition		
	F-value	*P*-value		*F*-value	*P*-value	
Topographic position	$F_{1,182} = 25.66$	<0.0001		$F_{1,181} = 18.45$	<0.0001	
Defoliation	$F_{1,182} = 1.50$	0.2229		$F_{1,181} = 3.91$	0.0495	(↓)
Cation index	$F_{1,182} = 8.84$	0.0033	(↓)	$F_{1,181} = 6.41$	0.0122	(↑)
Mean diameter	$F_{1,182} = 1.59$	0.2092		$F_{1,181} = 4.50$	0.0353	(↑)
Topo * defoliation	–	–		$F_{1,181} = 2.81$	0.0955	
Topo * cation index	$F_{1,182} = 5.91$	0.0160		$F_{1,181} = 3.00$	0.0851	

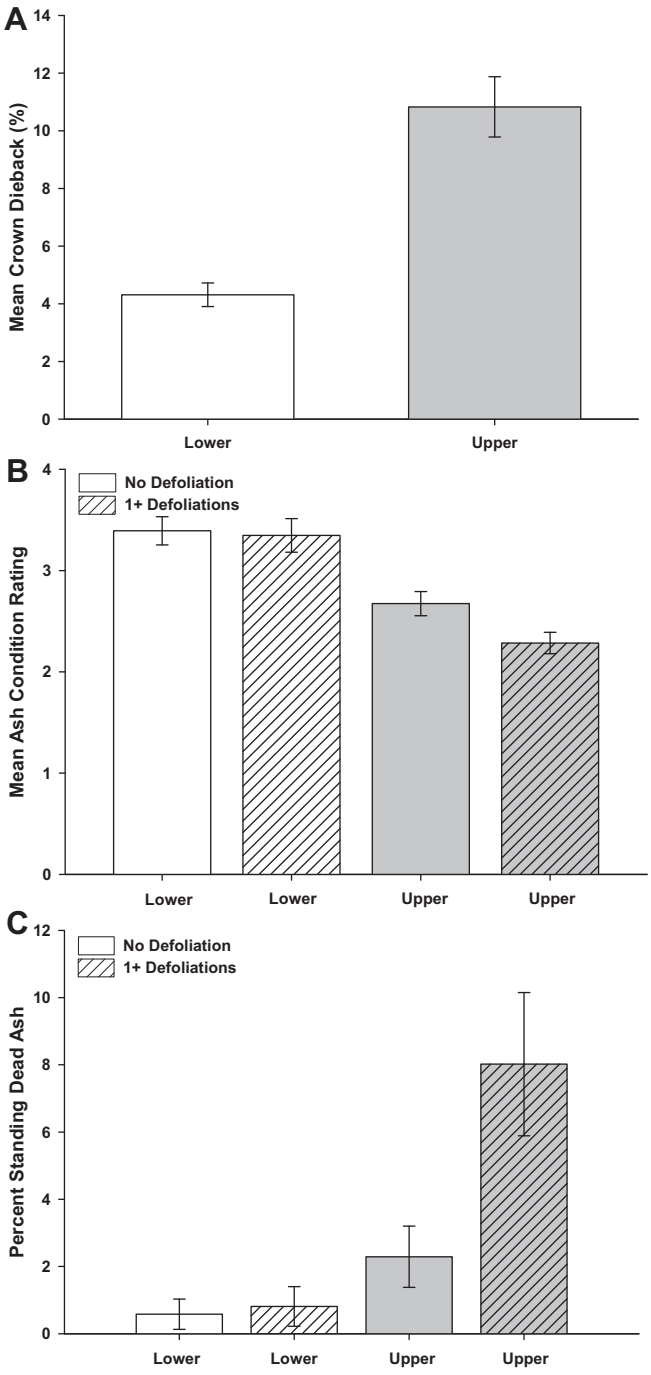

Fig. 2. Mean white ash crown health measures for each statistically significant topographic position and defoliation history effect (Table 2). Response variables are: (A) crown dieback (percentage of crown with fine twig dieback), (B) crown condition (where 0 is dead canopy, 4 is a healthy canopy, and 1–3 are stages of decline), and (C) stand mortality. Means (±1 SE) depicted for each predictor variable.

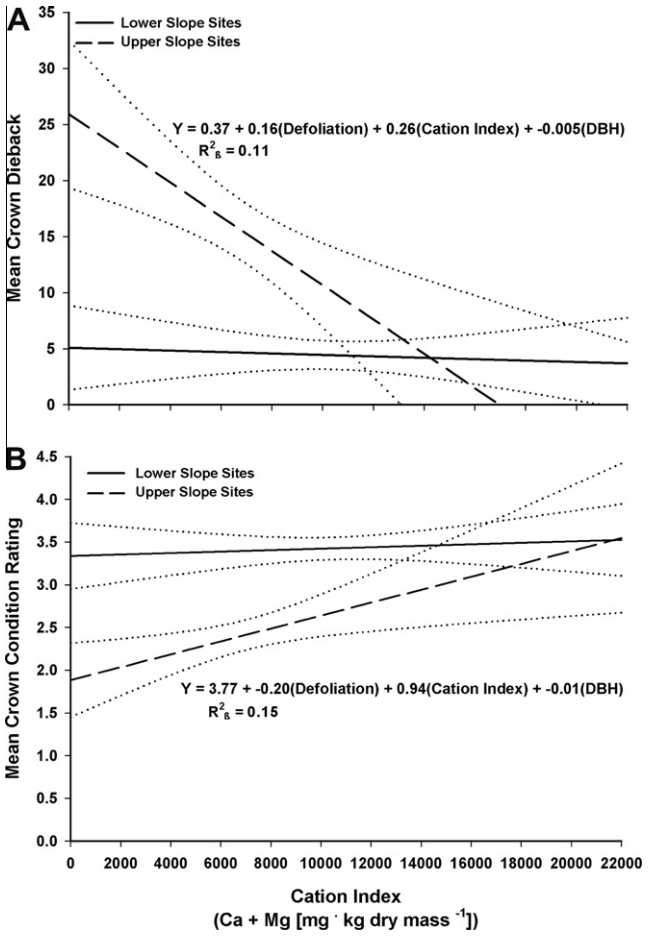

Fig. 3. Relationship between foliar cation concentration index (Ca + Mg) and (A) white ash crown dieback (percentage of crown with fine twig dieback) or (B) crown condition (where 0 is dead canopy, 4 is a healthy canopy, and 1–3 are stages of decline) in both lower (- - -) and upper (—) topographic positions with 95% confidence intervals. Equation of the linear mixed model for the significant upper slope relationship shown along with model fit (R^2_β).

Table 3
Parameter values for zero inflated negative binomial (ZINB) model evaluating the effect of various predictor variables on white ash mortality. Count process coefficients model the effect of a predictor on the relative abundance of standing dead trees for plots where mortality is present with parameter values (β) denoting whether the relationship is positive or negative. Zero inflation coefficients model the likelihood that a stand has zero mortality with parameter values (β) denoting that the lower slope positions and sites with greater cation concentrations both have a greater (positive estimate) of having zero-mortality sites. The intercept terms represent the model performance if all predictor variables are evaluated at zero.

Predictors	Parameter value (β)	SE	*t*-Value	*P*-value
Count process model				
Intercept	6.08	0.82	7.41	<0.0001
Defoliation	0.33	0.18	1.83	0.0672
Mean diameter	−0.06	0.02	−3.53	0.0004
Zero-inflation model				
Intercept	−1.84	1.43	−1.28	0.2001
Topographic position	1.09	0.63	1.74	0.0822
Cation index	1.94	0.92	2.09	0.0362

4. Discussion

4.1. Landscape position, cation concentration and stress

The present work expands on prior results documenting regional declines in white ash (e.g., Morin et al., 2006) by linking the severity of these declines to topographic position, cation concentration, and defoliation stress. Throughout the 3000 km^2 study area, topographic position and defoliation stress acted synergistically in influencing white ash health. White ash populations on upper slope positions consistently had greater dieback, poorer crown conditions, and greater abundance of standing dead trees than paired plots on lower slope positions and past elm spanworm defoliation stress further amplified the differences in health and mortality seen between slope positions.

Our results also showed that Ca and Mg availability are key factors mediating crown dieback and condition. Although van Breemen et al. (1997) and Finzi et al. (1998) documented that mature ash trees were associated with high pH soils rich in calcium and magnesium, to our knowledge this is the first study to document that the health and vigor of white ash are influenced by soil cation availability. Our results complement previous findings of declines in mature sugar maple health and growth corresponding with Ca and Mg deficient upper slope positions that experience defoliation stress (Horsley et al., 2000; Drohan et al., 2002; Hallett et al., 2006; Long et al., 2009). Their work, alongside our own, suggest the deteriorating condition found in populations of these two species regionally fit Manion's (1991) conceptual model of tree decline where declines are characterized by (i) underlying, long-term factors (e.g., topographic position, cation deficiencies) that predispose canopy-dominant trees to (ii) increased vulnerability to punctuated stress events (e.g., defoliation), and may ultimately result in death.

Despite the relatively short distance between paired stands, cation concentrations were lower and defoliation more prevalent on upper slope sites, thereby clouding our ability to disentangle the effects of any specific causal factor. In fact, research from within the region as well as elsewhere has found upper slope positions are often nutrient deficient and also suffer disproportionately greater defoliation incidence and severity relative to lower slope positions (Houston and Valentine, 1977; Bailey et al., 2004). Indeed, Horsley and others (2000) posited that on unglaciated sites, such as ours, landscape position serves as a surrogate for site quality and stress factors that delineate risky sites for species with high base cation requirements. Our analyses suggest that despite the potential covariance among these factors, both factors exert independent and interactive effects on ash health.

4.2. Long term stress signatures

Interestingly, surveyed white ash populations still displayed a lasting legacy of past defoliations. Although 17 years have elapsed since the last major defoliation, ash crown condition and mortality, measures that integrate longer-term signatures of stress, were both related to past defoliations. Conversely, crown dieback, a metric designed to assess recent stress events (USDA Forest Service, 2007) did not reflect any signature of past defoliations. This legacy of past defoliations is somewhat surprising given results from sugar maple documenting a relatively short (<5 years) lag in crown recovery following the abatement of stress (Gross, 1991; Allen et al., 1992; Payette et al., 1996) and the fact that our metric of mortality likely underestimates the magnitude of defoliation stress by ignoring already downed trees and unidentified snags in the estimate (Royo, pers. obs.). Additionally, evaluations of sugar maple crown health and mortality conducted at our study sites found sugar maple crown conditions and mortality were identical across sites varying in nutrition and defoliation history (Royo, unpub. data) which suggests white ash possesses a much longer lag in response to stress.

4.3. Additional factors linked to ash dieback

Researchers have hypothesized white ash dieback may be influenced by a variety of factors beyond slope position, cation concentration, and defoliation (reviewed by Hibben and Silverborg (1978), Houston (1987), and MacFarlane and Meyer (2005)). For example, Woodcock et al. (1993) conjectured white ash was drought sensitive and vulnerable to shifts in moisture availability (see also, Tobiessen and Buchsbaum, 1976), whereas others have cautioned the relationship between ash dieback and drought is indistinct (Castello et al., 1985). Although we cannot assess the influence of soil moisture on ash condition beyond our qualitative measure of the presence or absence of seeps, preliminary analyses did not identify this variable as a significant predictor. Perhaps more telling is the fact that growing season (May–August) moisture availability between 2000 and 2010, as measured by the Palmer drought severity index (PDSI), reveal average moisture conditions were slightly wet (PDSI = 1.18) for the decade with only a moderate drought event (PDSI = −2.05) in 2001 (Palmer, 1965; National Climatic Data Center, 2012). Nevertheless, given the wet conditions and the presence of seeps on lower slope positions, we cannot discount the potential role of periodic drought as potential stress factor.

Tree senescence is also suspected to play a role in diminishing *Fraxinus* health (e.g., Ward, 1997). Indeed, Palik et al. (2011) found black ash (*Fraxinus nigra*) dieback and mortality increased with mean stand diameter and suggested that for this short-lived species, dieback was associated with cohort senescence. In contrast, we found crown condition improved and relative abundance of standing dead trees decreased with increasing mean stand diameter suggesting that for white ash, dieback and mortality occurs more frequently on smaller, suppressed, and potentially younger trees (see Han et al., 1991 for similar findings). Thus, for the typically longer-lived white ash (average age of mortality = 260 years; Loehle, 1988) mortality in individuals sampled in these ~100-year-old second growth stands is likely not related to senescence.

Finally, ash yellows (AshY phytoplasma), has been linked to decline episodes throughout much of the range of white ash (Sinclair et al., 1990; Sinclair and Griffiths, 1994). None of the trees we surveyed displayed the occasionally symptomatic deformity associated with AshY infection known as witches' brooms (i.e., clusters of spindly, upright twigs near the root collar; Sinclair and Griffiths, 1994). While we cannot rule out the possibility of AshY phytoplasma infection at our sites without the appropriate tests (e.g., PCR analyses), white ash crown dieback is often independent of AshY infection and positive detection of the AshY phytoplasma is often quite low even within trees exhibiting crown dieback (Luley et al., 1992; Feeley et al., 2001).

4.4. Management implications

Knowledge of landscape patterns of ash health may be helpful in the early detection of the emerald ash borer (*Agrilus planipennis*) (EAB). Accidentally introduced from Asia, this beetle produces larvae that can cause >99% mortality of mature ash trees by creating extensive feeding galleries beneath the bark (Herms et al., 2009). EAB is present in Pennsylvania but has not yet been detected within our study area.

It is clear that the initial health of ash trees affects the movement of EAB as well as the subsequent infestation process. EAB adults are known to be attracted to stressed ash trees (McCullough et al., 2009) due to the volatile compounds they emit (Rodriguez-Saona et al., 2006). As the infestation progresses, EAB larvae in initially healthy trees develop more slowly than larvae in initially stressed trees (Tluczek et al., 2008) resulting in faster mortality in ash trees with initially unhealthy canopies (Knight et al., in press). Although it is unknown how landscape-scale patterns of ash health will impact spatial patterns of EAB infestation, it seems likely that EAB will initially be attracted to those areas of the landscape with a high concentration of stressed ash trees. Knowing what landscape positions are likely to contain stressed ash trees (e.g., upper slope areas with a history of defoliation) may lead to better risk models, detection strategies, and mitigation measures. Managers may choose to prioritize silvicultural efforts in the highest risk stands prior to EAB in order to mitigate ash mortality impacts on forest diversity and function and optimize ash timber revenue. Furthermore, knowing which landscape positions (e.g., lower slope, cation-rich areas) are most suitable to ash may be important for any potential future restoration of ash.

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