Species-specific determinants of mortality and recruitment in the forest-steppe ecotone of northeast China

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ABSTRACT

Tree mortality is a notable phenomenon in the forest-steppe ecotone of China. However, the association between mortality and factors such as a changing climate is uncertain. In the summer of 2014 tree mortality was investigated in 20 × 400 m² plots to determine the species-specific determinants of mortality and their influence on subsequent species recruitment. Nine soil physical-chemical properties were examined in addition to slope position, mean DBH and total number of trees. Generalized linear models analyzed relationships between these variables and mortality and recruitment. Mortality was positively associated with increasing average diameter and negatively to high soil pH and total nitrogen content. Recruitment models indicate that *Populus davidiana* recruitment was positively affected by available phosphorus and mortality, and negatively related to mean DBH. Slope position was the most important contributing variable to *Betula platyphylla* recruitment. With *Quercus mongolica* recruitment, soil variables played an important role. These results suggest that tree mortality is affected by soil properties, topography and tree size in China's forest-steppe ecotone, and may improve our understanding of species mortality and contribute to improved forest management.

Key words: tree mortality, forest-steppe ecotone, recruitment, broad-leaved forests

RÉSUMÉ

La mortalité des arbres est un phénomène marquant dans l'écotone de la steppe boisée de la Chine. Cependant, il n'est pas facile d'associer la concordance entre la mortalité et à divers facteurs comme les changements climatiques est incertaine. Au cours de l'été 2014, nous avons examiné la mortalité des arbres a été étudiée dans des parcelles de 20 x 400 m afin de déterminer les causes spécifiques de mortalité pour chaque espèce et leur influence sur le développement subséquent des espèces. Les analyses ont porté sur neuf propriétés physico-chimiques du sol ont été analysées, en plus de l'emplacement selon la position sur la pente, le diamètre moyen et le nombre total d'arbres. On s'est servi de modèles linéaires généralisés généraux ont servi à l'analyse pour analyser les relations entre ces variables et la mortalité et le recrutement. L'analyse a montré une corrélation positive avec la croissance en La mortalité était positivement associée à l'accroissement du diamètre moyen et négativement reliée à l'augmentation du pH du sol et du contenu en azote total. Les modèles de recrutement indiquent que le recrutement du *Populus davidiana* était lié au était positivement affecté par le phosphore disponible et à la mortalité, et négativement relié et diminuait avec le diamètre moyen. L'emplacement selon la position sur la pente représentait la variable la plus importante pour le recrutement du *Betula platyphylla*. Dans le cas du recrutement du *Quercus mongolica*, ce sont les variables du sol qui ont eu le plus d'influence ont joué un rôle déterminant. Ces résultats indiquent la mortalité des arbres dépend des propriétés du sol, de la topographie et de la taille des arbres dans le cas de l'écotone de la steppe boisée de la Chine; ils et qu'ils pourraient améliorer notre compréhension de la mortalité des de chaque espèce et contribuer à améliorer bonifier l'aménagement forestier.

Mots clés : mortalité des arbres, écotone de la steppe boisée, recrutement, forêt feuillue

Introduction

Tree mortality in broad-leaved forests of China's forest-steppe ecotone is becoming an issue due to pressure from climate change (Liu *et al.* 2010, Dulamsuren *et al.* 2011, Kharuk *et al.* 2013). Under the stress of drought (Liu *et al.* 2013), species mortality and subsequent recruitment are more sensitive to environmental conditions (Laurance *et al.* 2001, Phillips *et al.* 2009). Environment-related tree mortality has been reported from several countries (Ferry *et al.* 2010, de Toledo *et al.* 2011, Redmond *et al.* 2015), however, there are no studies of species-specific determinants of mortality and recruitment at the plot-level in the forest-steppe ecotone in China.

Empirical studies have shown that unexpected tree mortality is a complicated natural event provoked by environmental factors such as inter- and intra-specific competition, pathogen and insect outbreaks, mechanical failure, and variable edaphic controls associated with differences in physiographic characteristics of landscapes (Koepke *et al.* 2010, de Toledo *et al.* 2011, Zeppe *et al.* 2011, Crosby *et al.* 2015). Demchik and Sharpe (2000) observed high species mortality in sample plots with low calcium-to-aluminum ratios in A and B soil horizons. Dorman *et al.* (2015) found that rapid infiltration of water, particularly in sandy soils, can cause the water to pool at deeper levels, making the water inaccessible

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Fig. 1. Location map showing the study area and plots (▲).

Fig. 2. Monthly meteorological data of the area during 1959–2012

to roots. Tree mortality rates increased in soils with low bulk densities and high N-NO_3^- to N-NH_4^+ ratios (Corcobado *et al.* 2013). Low soil bulk density may help reduce the potential for soil compaction and adherence of roots (Cubera *et al.* 2009). In addition, high N-NO_3^- to N-NH_4^+ ratios may be an indication of soil degradation (Wilson and Tilman 1991). On the other hand, Ferry *et al.* (2010) found that low mortality rates were typically found at the bottom of slopes, as bottomlands tend to provide more favorable growing conditions in terms of available water and temperature.

Other studies demonstrate an association between species mortality and forest structure such as stand density, stand age,

mean DBH (diameter at breast height), and spatial patterns in plant communities (Simard *et al.* 2012). However, there does not appear to be a consistent suite of factors that could reliably predict patterns of mortality. High mortality rates were positively related to age and negatively related to density in planted stands of *Pinus halepensis* Miller (Dorman *et al.* 2015). This result does not support the commonly-held view that the probability of drought survival increases at lower stand densities, despite the assumption that levels of inter- and intra-specific competition and available resources are all improved with fewer trees in the stand. The effect of soil conditions on mortality may also be age-specific. In the state of Sarawak Malaysia, Hattori *et al.* (2013) found no significant relationship between seedling mortality and soil factors, including nutrient stocks (nitrogen, phosphorus, potassium, calcium, and magnesium) and water content. Previous research clearly showed site-specific factors

influencing mortality and recruitment. These kinds of study, however, mostly focused on a single tree species. We hypothesize that a determinant of mortality and recruitment should be different for species with different ecological features (e.g., pioneer or climax species) in a mixed forest at the same time. To test this, local-scale heterogeneity in soil and topographical factors should also be included for a multi-variable statistical analysis.

In forest-steppe ecotones, massive recruitment has often occurred following unexpected tree mortality, leading to the replacement of the dominant species and turnover of the community (Kelly and Goulden 2008). For example, in the

central Pyrenees of northeastern Spain, during an episode of drought-induced species mortality, abundant recruitment of *Quercus* spp. occurred which may lead eventually to the replacement of the currently dominant species *Pinus sylvestris* L. (Galiano *et al.* 2010). Although studies have analyzed mortality and subsequent species recruitment in several regions of the world, many factors potentially associated with species mortality still have yet to be examined in the forest-steppe ecotone of China. More observational experiments are needed to understand the bio-physical elements that control widespread tree mortality (Allen *et al.* 2010). Soil chemical properties (water content, pH and nutrient stocks) are extremely important factors in the forest-steppe ecotone, and which affect community composition, nutrient cycling and distribution of vegetation (Chytrý *et al.* 2008). Slope position may also influence species mortality as an important indirect factor, since microclimate and light conditions change with different slope positions (Ferry *et al.* 2010).

The goal of this study is to determine if soil chemical properties, slope position and two forest structural factors (mean DBH and total number of trees) are related to species mortality and recruitment, and to quantify these effects at the plot-level. Three main questions were addressed in our study:

- 1) How is mortality and recruitment affected by diameter?
- 2) Since drought induced mortality is widespread in the forest-steppe ecotone, does soil water content play a role in plot-level tree mortality?
- 3) Can variations in mortality and community recruitment be explained by the factors selected?

Material and Methods

Site description

The study was carried out in a broad-leaved forest dominated by *Betula platyphylla* Sukaczew, *Populus davidiana* L. and *Quercus mongolica* Fisch. ex Ledeb. in the Saihanwula Forest Ecosystem National Research Station (118° 18' – 118° 55' E; 43° 59' – 44° 27' N) located in the forest-steppe ecotone of the eastern region of Inner Mongolia, China (Fig. 1).

The climate is characterized by an annual mean temperature of 2°C and an annual accumulated precipitation of 358 mm (Weather Bureau of Bairin Right Banner, 2016), with a wet season from May to September. The highest rainfall (120 mm) and temperatures (23°C) occur in July (Fig. 2). Soil characteristics vary along an altitude gradient: grey forest soil, brown loam and dark chestnut soil are distributed at elevations of 1500–1900 m, 800–1400 m and 500–1200 m respectively. Soils are slightly acidic or near-neutral, and the topography has a mean elevation of 1000 m, gradually lowering from northeast to southwest (Zeng *et al.* 2014).

Field sampling

In May to September 2014, 20 square plots (400 m² each) were selected along a slope gradient based on the following criteria to avoid environmental heterogeneity: (i) no recent management or disturbance on the plots; (ii) the plots had the same aspect; and, (iii) plots were at least 50 m apart.

Tree mortality and recruitment data

For each plot, all trees (DBH > 1 cm) were identified and DBH, height, state (alive or dead) and location in the plot were recorded. Latitude and longitude of plots were measured using a GPS. Diameter was measured to the nearest 1 mm 1.3

m height above the ground (DBH). Mortality was recorded as the number of dead trees relative to the total number of trees (Galiano *et al.* 2010).

Five subplots (4 m² each) were sampled in each plot for surveying recruitment. Species, quantity, mean height, basal stem diameter and coverage of every seedling were recorded for each of 105 subplots. The position of a plot on the slope was classified into five categories: bottom, footslope, backslope, shoulder and summit, with three to four plots within each category. Field survey work was conducted based on the “Forestry Standards: Observation Methodology for Long-term Forest Ecosystem Research” of People’s Republic of China (Wang *et al.* 2011a, Wang *et al.* 2011b, Yu *et al.* 2013).

Soil sampling

Three soil samples were collected from each of four soil layers (0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm) at the centre of each plot, and mixed to form one composite sample for each plot. Each sample was then separated into two sub-samples, one used to measure soil water content (SWC), the other to determine physical and chemical characteristics such as primary nutrients (nitrogen (N), phosphorus (P) and potassium (K), soil organic matter (OM) and pH.

Sub-samples for SWC determination were weighed fresh before drying at 105°C for 24 hours. Gravimetric soil moisture was calculated as the percentage of water in the sample mass by weight. Sub-samples for physical and chemical properties were air-dried for 3–5 days, fine roots and stones removed, and the samples sieved (2 mm mesh) and stored in envelopes for analyzing pH, available N (AN), available P (AP) and available K (AK). A portion of the 2 mm-mesh samples were sieved further using a 0.25 mm mesh for analyzing OM, total N (TN), total P (TP) and total K (TK).

Soil pH was measured using a pH meter (320P-01N, Thermo Orion, USA). The chemical oxidation of potassium dichromate (K₂Cr₂O₇) process was used to determinate OM. A 5-ml solution of concentrated sulfuric acid, 5 ml of K₂Cr₂O₇ and soil samples were heated to 180°C, boiled for five minutes, and titrated with ferrous ammonium sulfate solution until the color changed to turbid blue. TN was measured by Kjeldahl nitrogen analyzer (KDY-9830, China). A spectrophotometer was used to determine TP and AP and a flame photometer (FP640, China) to determine TK and AK. All methods for determining soil properties were conducted according to Bao (1999).

Statistical analyses

Models were fitted to determine if measured or derived factors could explain the spatial variation in species mortality and recruitment. Species mortality was derived from dividing the number of dead trees in each diameter class by the total number of trees in that class. Nine soil variables (SWC, pH, OM, TN, TP, TK, AN, AP, AK), two forest stand variables (mean DBH and total number of trees) and one topography variable (slope position) were introduced into the mortality and recruitment models as explanatory variables. Species mortality was introduced into the three species recruitment models as one of the explanatory variables. Some of these variables did not comply with normal distribution after standard transformations; therefore, generalized linear models were used to analyze the relationship between selected factors and species mortality or recruitment (Galiano *et al.* 2010).

Fig. 3. Number of living and dead trees in different DBH classes

A stepwise selection method was used for model fitting, and began with all original explanatory and eliminating one variable at a time based on Akaike information criterion (Akaike 1974). At each step, the model was improved by adding back an explanatory variable which had been removed at a previous step. The final models here represent the most sparing fit achieved. The marginal R^2 describes the proportion of variance explained by the fixed factors alone, and the conditional R^2 the proportion of variance explained by both fixed and random factors (Araujo Calçada *et al.* 2015). Parameter β is the unknown model parameter and was estimated by a maximum likelihood method. Spearman correlation coefficients were used to measure the correlation between pairs of variables. All calculations and statistical analyses used the R software (R Development Core Team 2013).

Results

Species-specific determinants of mortality and recruitment

P. davidiana had the highest mortality, followed by *B. platyphylla* and *Q. mongolica* (Fig. 3). The number of live trees of *P. davidiana*, *Q. mongolica* and all species combined peaked in the smallest diameter class (3–6 cm; Fig. 3). *P. davidiana*

showed the highest mortality (69.2%) between DBH 15–18 cm (Fig. 3a). In contrast, *Q. mongolica* had lower mortality, with no dead trees in diameters 9–12 cm and >18 cm (Fig. 3c). The lowest mortality of *P. davidiana* (15.2%) was in the smallest diameter class (< 3 cm); a parabolic mortality trend was displayed across diameter classes for this species (Fig. 3a). Mortality of *B. platyphylla* showed no clear trend across DBH classes and was generally low across the range of diameters. Mortality of this species peaked (19.1%) below 3 cm DBH and was lowest (4.8%) in the highest class (>18 cm; Fig. 3b). Overall, mortality was lowest for *Q. mongolica*, and actually zero for DBH classes 9–12 cm and >18 cm (Fig. 3c).

The bottom of the slope had the largest number of live trees (Fig. 4). Mortality tended to be the highest (24.5%) on the slope shoulders (Fig. 4); however, this was largely due to high mortality of *P. davidiana* in this position. The other species had peak mortality on the lower slope (bottom and footslope). There were no clear trends in mortality across the slope gradient. The highest number of *Q. mongolica* seedlings appeared on the footslope, whereas the most *P. davidiana* seedlings appeared on the shoulder (Fig. 5). The number of *B. platyphylla* seedlings tended to become higher along the slope gradient with the exception of the shoulder (Fig. 5).

Fig. 4. Number of living and dead trees along the slope. Error bars show standard errors. 1 (bottom), 2 (footslope), 3 (backslope), 4 (shoulder) and 5 (summit).

Fig. 5. Number of seedlings along the slope. Error bars show standard errors. 1 (bottom), 2 (footslope), 3 (backslope), 4 (shoulder) and 5 (summit).

Multiple factor influences on mortality

Stepwise model selection was used to fit a mortality model, and SWC, OM, TP, TK, AK, total number of trees and slope position were removed as explanatory variables (Table 1). Both pH and TN (total nitrogen) were negatively associated with mortality; the relationship was significant ($\beta < 0$, $p < 0.001$). Mortality was positively associated with mean DBH ($\beta > 0$, $p < 0.001$); mortality was significantly higher in the larger diameter classes and lower in the smaller classes (Fig. 3d).

There was also a significantly positive relationship between AP (available phosphorous) and mortality ($\beta > 0$, $p = 0.003$). Available N was also retained in this model and positively correlated with mortality, although this relationship was weaker ($\beta > 0$, $p = 0.05$) than the other predictors (Table 1).

Determinants of spatial variation of recruitment

Based on the results of stepwise model selection, SWC, TN, TP, AK and slope position were removed from the recruitment model of *P. davidiana* (Table 2). Apparently recruitment was not controlled by a linear response to the gradient of slope position (Fig. 5). The most significant relationships detected in the model recruitment were positive associations with available P and mortality ($\beta > 0$, $p = 0.0001$), and a negative association with mean DBH ($\beta < 0$, $p = 0.0001$). The next most important variable selected indicated a strong negative relationship

between the total number of trees and *P. davidiana* recruitment ($\beta < 0$, $p = 0.004$). Other significant explanatory variables included positive relationships to OM (organic matter) content, and negative relationships with TK (total potassium) and AN. There was a positive and marginally significant relationship between pH and *P. davidiana* recruitment ($\beta > 0$, $p = 0.079$), therefore pH was not removed from the model.

Six explanatory variables (TN, TP, TK, AN, AP and total number of trees) were removed from the model of *B. platyphylla* recruitment. Slope position was retained in this model

Table 1. The generalized linear model for tree mortality

Response variables	Explanatory variables	β	Std. Error	p-value
Tree mortality	pH	-0.3484	0.0744	<0.001***
	Total nitrogen	-0.1914	0.0301	<0.001***
	Available nitrogen	0.0006	0.0003	0.050
	Available phosphorus	0.0238	0.0078	0.003**
	Mean DBH	0.0293	0.0076	<0.001***

Degrees of freedom=79; AIC=-86.421; Marginal $R^2=0.53$; conditional $R^2=0.53$.

Table 2. Generalized linear models for recruitment in different species

Response variables	Explanatory variables	β	Std. Error	p-value
<i>P. davidiana</i>	pH	6.0729	3.4074	0.079
	Organic matter	0.8479	0.3789	0.028*
	Total potassium	-0.5438	0.2136	0.013*
	Available nitrogen	-0.0262	0.0117	0.028*
	Available phosphorus	1.5842	0.3171	<0.001***
	Mortality	47.6431	4.1254	<0.001***
	Mean DBH	-1.3386	0.3726	<0.001***
	Total number of trees	-0.0662	0.0222	0.004**

Marginal $R^2=0.79$; conditional $R^2=0.79$.

<i>Betula platyphylla</i>	Soil water content	-0.6675	0.2913	0.025*
	pH	4.6038	3.1756	0.151
	Organic matter	-1.3573	0.4158	0.002**
	Available potassium	-0.0161	0.0114	0.163
	Mortality	-8.1641	3.8769	0.039*
	Mean DBH	0.7501	0.2873	0.011*
	Slope position	1.4146	0.3609	<0.001***

Marginal $R^2=0.40$; conditional $R^2=0.40$.

<i>Q. mongolica</i>	Soil water content	0.7782	0.4221	0.069
	Total phosphorus	-41.6668	11.1147	<0.001***
	Total potassium	0.8676	0.2819	0.003**
	Available nitrogen	-0.0439	0.0145	0.003**
	Available phosphorus	-1.6277	0.4061	<0.001***
	Available potassium	0.0566	0.0133	<0.001***
	Total number of trees	0.0524	0.0270	0.056
	Slope position	0.9354	0.5543	0.096

Marginal $R^2=0.54$; conditional $R^2=0.54$.

Degrees of freedom=79; AIC_{*P. davidiana*}=504.34; AIC_{*Betula platyphylla*}=500.39; AIC_{*Q. mongolica*}=549.35.

as the highest contributing variable ($p < 0.001$) and was positively associated with recruitment ($\beta > 0$). Recruitment tended to increase with slope increase; the highest number of seedlings was on the summit and lowest at the bottom (Fig. 5). *B. platyphylla* recruitment was significantly and negatively correlated with OM ($p = 0.002$). Significant relationships were also found between *B. platyphylla* recruitment and SWC ($p = 0.025$), mortality ($p = 0.039$) and mean DBH ($p = 0.011$). The association with mortality and SWC was negative ($\beta < 0$), whereas mean DBH was positively correlated with recruitment ($\beta > 0$). Both pH and AK were not significant variables in this model ($p = 0.151$; $p = 0.163$).

Five explanatory variables (pH, OM, TN, mean DBH and mortality) were eliminated from the model of *Q. mongolica* recruitment, the only recruitment model that did not include these explanatory variables. In this model, soil variables played an important role, in particular TP, AP and AK ($p < 0.001$), of which both TP and AP were negatively associated with seedling recruitment ($\beta < 0$) and AK was negatively associated ($\beta < 0$). Other notably contributing variables were TK and AN, which were positively and negatively correlated with recruitment respectively ($\beta > 0$, $p = 0.003$; $\beta < 0$, $p = 0.003$). Less important explanatory variables that were significant included SWC, total number of trees and slope position, all positively related with *Q. mongolica* recruitment ($\beta > 0$).

Discussion

How is tree mortality and recruitment affected by diameter?

Higher mortality occurred in larger DBH classes for *P. davidiana* and *Q. mongolica*. However, the mortality rate of *B. platyphylla* did not show a clear difference across diameter classes. This result is in agreement with observations of Osumi and Sakurai (2002), as *B. platyphylla* mortality tended to decrease with increasing diameter. This may be explained by the low shade tolerance of *Betula* spp. (Baleshta *et al.* 2015), which typically require canopy disturbance to promote growth of *Betula* spp. seedlings in the understory. The survival of *B. platyphylla* in diameter classes greater than 3 cm likely reflects greater access to light, indicating that canopy openings have released these seedlings in the understory. Other studies have reported the similar trend of increasing size along with decreasing density of overstory *Betula* spp. (Simard and Zimonick 2005).

The first and second highest mortality of *B. platyphylla* occurred in 12–15 cm and 15–18 cm diameter classes but mortality subsequently decreased in the 18 cm DBH class. The trend of mortality to diameter was a threshold response of improved survival at diameters ≥ 3 cm rather than a linear increase in mortality with diameter. These nonlinear results are not consistent with some previous studies (Brumelis *et al.*

2009, Luo and Chen 2011) which suggested that mortality increased with tree size linearly which has been attributed to increasing competition for below-ground soil resources and above-ground light (Canham *et al.* 2004). Galiano *et al.* (2010) concur with our findings; after increasing and reaching a peak threshold, mortality did not further increase in the largest DBH classes. de Toledo *et al.* (2011) considered that patterns of size-dependent mortality may be influenced by the range of tree size. Similar conclusions were shown by Chao *et al.* (2008) and Laurance *et al.* (2009).

In addition, our data indicated a substantial difference in mortality or recruitment associated with slope position: the

slope shoulder had the greatest mortality and highest recruitment for *P. davidiana*, and the lowest recruitment for *B. platyphylla* and *Q. mongolica*. Royo and Knight (2012) also found that white ash on upper slopes had higher dieback than paired plots on the lower slope. Vanak *et al.* (2012) suggested that trees on the mid-slope were more likely to suffer mortality than those on the slope crest. Our results are in agreement with these reports, as the frequently deficient nutrient conditions on upper slopes may lead to elevated mortality and favorable light conditions on crests possibly decreases mortality. Recruitment of *Q. mongolica* and *B. platyphylla* seedlings decreased on the slope shoulder, possibly from competition between seedlings (Takahashi *et al.* 2010).

Does soil water play a role in plot-level mortality?

Unexpectedly, soil water did not improve the model's power for explaining mortality. This is in disagreement with Fensham *et al.* (2007) and Phillips *et al.* (2010) who proposed that tree death increased when soil moisture became less. In contrast to their results, Galiano *et al.* (2010) removed the topographic wetness index related to soil water content from their model of recruitment, possibly due to the relatively narrow range of sites they sampled which encompassed only slightly varying topographic conditions. Since only one-season measurement was undertaken at our site, which is definitely not enough to give a wide range of soil water changes, we would not suggest that SWC (as we measured it) did not play an important role in tree mortality. Our local result may be explained by the limited research/experiment scale. Responses of mortality to drought events, differentiated sensitivities and resilience of vegetation were reported to vary between local and regional scales (Yin *et al.* 2013). The relationship between water stress and tree mortality at the local scale is more complicated than at a regional scale. The combined influences of micro-environment, wood density and xylem hydraulic failure in individual trees would be more sensitive indicators of water stress and provide additional insights into mortality trends observed in our study (Barigah *et al.* 2013). Perhaps water stress in our sites had not reached the severe conditions and its insignificant influence on mortality could be hidden by other factors.

Mortality in our study decreased as the TN increased. To some extent, nitrogen addition caused increased growth in some trees, but nitrogen saturation also likely damaged some trees (Wallace *et al.* 2007). Available P was positively associated with mortality, and the increase of AP should improve stand productivity, leading to more intense or severe competition among trees and therefore higher mortality (Ferry *et al.* 2010). Demchik and Sharpe (2000) found that high mortality plots showed a lower pH, a result in agreement with our data. Overall, it seems likely that the determinant of mortality is related to the spatial scale of the study, probably shifting depending on whether the data are local or regional. In our case, our local-scale data indicate that pH, TN, AP and mean DBH are the most important factors affecting mortality.

Can variations in mortality and community recruitment be explained by the factors selected?

Our results indicate that the factors selected do provide a better explanation of the variations of community recruitment (Table 2; $R^2 = 0.79, 0.40$ and 0.54 for three species respec-

tively). Soil variables explained a large part of community recruitment, especially for *Q. mongolica*. A seven-year study demonstrated significant positive effects of total soil nitrogen and water content on relative recruitment (Hattori *et al.* 2013). However, Li *et al.* (2015) found that plant density of recruited saplings decreased with nitrogen concentration. The same variable may affect community recruitment by distinct direction and magnitude in different ambient conditions (climate, soil, and dominant tree species). The influence of heterogeneous soil properties on recruitment dynamics needs to be comprehensively analyzed by considering competition, plant-soil feedback and soil-climate interactions (Peters *et al.* 2010, Brandt *et al.* 2013).

Death of over-story trees may alter understory recruitment by changing light intensity and soil moisture conditions, leading to changes in species composition and density of seedlings (Castro *et al.* 2004). Therefore, mortality rate was introduced into the models of recruitment as an explanatory variable, and was positively associated with recruitment of *P. davidiana* and negatively with *B. platyphylla*. This *P. davidiana* observation may be explained by the over-story mortality creating favorable light conditions for the shade-intolerant *P. davidiana* seedlings (Sankey 2008). In contrast, *B. platyphylla* recruitment decreased with increased mortality, although it is also a shade-intolerant species. Three possible reasons for the unexpected result are: 1) the range of gap or opening formed from dead trees could be a crucial factor to seedling establishment. Gärtner *et al.* (2011) suggested that a partial canopy is able to protect seedlings from impacts of climate extremes; 2) at the stand level (several hectares), species recruitment was negatively influenced by shrub cover. Béland and Chicoine (2013) reported that yellow birch regeneration was mainly affected by shrub competition; dead trees also provide ideal conditions for establishment of shrubs, which may lead to competition among shrubs, and seedlings of *P. davidiana* and *B. platyphylla*; and, 3) some fungal pathogens were possibly concentrated in plots with high tree mortality. O'Hanlon-Manners *et al.* (2004) found that the recruitment of white birch was inhibited by emerging fungal pathogens.

In conclusion, the dynamic variations in tree mortality and recruitment in forest stands may be explained by considering multiple factors, including species, size, slope location, and a suite of soil characteristics. These results may contribute to improved forest management by forest practitioners.

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