Population dynamics and the influence of blight on American chestnut at its northern range limit: Lessons for conservation

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A B S T R A C T

Species of conservation concern may require special management consideration at their range limits where population vulnerability can be exaggerated by environmental stress. American chestnut, dramatically affected by chestnut blight in the early 1900s, has received extensive conservation attention especially in the central (U.S.) portion of its native range. However, relatively little is known about the population dynamics and the demographic effects of blight at the northern edge of its range, in Canada. Here we measure changes in tree size, reproduction, blight symptoms, and survival since a survey in 2001–02 and estimate the effect of chestnut blight on vital rates and population growth rates using a projection matrix model. Currently, chestnut trees in Canada range from <2 to 77.8 cm DBH. The incidence of reproductive trees (11%) decreased while frequency of blight (36%) and dieback (37%) increased since the 2001–02 survey. Mortality was 21.3% overall (41% for trees with blight) with few trees producing viable nuts or having established recruits (0.014 recruits per tree). Chestnut in Canada is in decline ($\lambda = 0.817$), but tends to differ in blight incidence, tree size, and reproduction compared to surveys in the central part of the range. Efforts to elevate recruitment may be necessary to mitigate extirpation in the northern population.

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1. Introduction

A major goal of biological conservation is to maintain or restore species to a demographic state with an acceptably low risk of extinction such that populations are stable or increasing toward a recovery threshold (Doak et al., 2015; Wolf et al., 2015). To be effective, conservation action therefore requires reliable information about population size, vital rates (growth, reproduction, survival), and viability over a defined period of time (Schemske et al., 1994; Morris and Doak, 2002). Without this knowledge, it is difficult to quantify the risk of extinction, identify the causes of endangerment, or set targets and criteria necessary to achieve recovery (Doak et al., 2015).

Demographic attributes and population viability of species at risk likely vary across their geographic range (Lawton, 1993; Aikens and Roach, 2014) due to variation in habitat density and quality. Many ecological models predict that range edges will be environmentally less suitable than central parts of the range (Brown, 1984; Brown et al., 1996; Holt et al., 2005). This gradient can lead to reduced population size and density, lower genetic diversity, and unique selective pressures and phenotypic values at the edge, although the consistency of central – margin range differences is still debated (Brown, 1984; Gyllenberg and Hanski, 1992; Lawton, 1993; Vucetich and Waite, 2003; Angert, 2006; Eckert et al., 2008; Dixon et al., 2013; Gerst et al., 2011; Aikens and Roach, 2014; Pironon et al., 2015). In turn, populations at the range edge may be more vulnerable to extirpation, which may influence the management strategies needed compared to the centre of the range. Such differential management is especially likely for species with large historical ranges that span political boundaries since populations at the periphery of the range may be subject to different conservation policies and criteria than those at the geographic centre.

American chestnut (*Castanea dentata* (Marsh.) Borkh.) exemplifies the challenges of managing species at risk across a broad geographic range. This species was a dominant and economically important tree species of deciduous forests in eastern North America; 96% of its historical range occurs in the United States while the most northerly 4% is found in southern Ontario, Canada (Boland et al., 2012). American chestnut's dominance (Youngs, 2000; Jacobs et al., 2013) came to an abrupt end with the introduction of a fungal pathogen (*Cryphonectria parasitica* (Murrill) Barr), which

causes chestnut blight. Since its appearance in 1904 in New York, blight quickly spread across the native range of chestnut, reducing populations to less than 1–10% of their original size (Boland et al., 2012; Dalgleish et al., 2016). While some trees persist as small sprouts from the rootstock of blight-infected trees (Paillet, 2002), relatively few individuals reach a mature, reproductive state or the large size known from the pre-blight era.

Current conservation status and action for American chestnut in Canada differs from the rest of its range. In the United States, chestnut has a national ranking of N4 (apparently secure), but ranges from critically imperiled (S1) to apparently secure (S4) and even unranked (SNR) among various eastern states (NatureServe, 2015). The current conservation focus in the U.S. is on restoring chestnut as a dominant species within eastern forests through creation of blight-resistant genotypes through several methods (backcross selection, transgenes) and mass plantings throughout the native range (Jacobs et al., 2013). Within Canada, chestnut is designated as imperiled at both national (N2) and provincial (Ontario; S2) levels. The significant decline and ongoing vulnerability to chestnut blight led to the species being designated as endangered under the Canadian Species at Risk Act (SARA). A recovery strategy has been developed (Boland et al., 2012) to guide conservation action through monitoring, management of blight through hypovirulence and breeding for resistance, and securing germplasm from blight-free trees.

The population of American chestnut within Canada exhibits a number of attributes that may further influence conservation action. This population of chestnut is relatively small. Tindall et al. (2004) recorded over 600 trees in their census, while Boland et al. (2012) estimated total population size to be 30–70% higher (i.e. N = 780–1020). These trees often occur in fragmented woodlots, are small (80% were <20 cm DBH) and rarely reproductive, and only 25% exhibit blight symptoms (cankers) (Tindall et al., 2004). It is unclear how demographic attributes have changed over time, and what impact the disease has on population vital rates and population dynamics at the northern limit.

As part of a larger effort to conserve populations of chestnut in Canada, we investigated population vital rates and growth rates using a demographic survey conducted 13 years after the first ever large-scale survey of the Canadian population (Tindall et al., 2004). We assessed three main questions: (1) How has tree size, incidence of blight, incidence of reproduction, and tree health changed over the last 13 years?; (2) To what extent are vital rates influenced by initial presence of chestnut blight?; and (3) What is the projected population growth rate and stable size distribution of American chestnut, and what stages of development are most influential in population recovery? Through these questions we test the null hypothesis that northern populations of American chestnut are stable in growth rate and size distribution.

2. Methods

2.1. Survey methods

To assess the current demographic state and population dynamics of American chestnut at its northern range edge, we conducted a survey of trees across southern Ontario, Canada, and compared our results to the 2001–02 (Tindall et al., 2004) survey. Our survey was conducted from May to September in 2014 and 2015 with the goal of resampling trees from the 2001–02 survey (marked via metal ID tags) and including previously unsurveyed individuals. The survey spanned 12 counties within the historical range of chestnut in southern Canada. We followed the sampling protocol from the 2001–02 survey, excluding soil and habitat mea-

surements (Tindall et al., 2004). In brief, we measured characteristics related to tree size, reproduction, and health.

Tree size was estimated as diameter at breast height (DBH) of all stems ≥2 cm DBH, total number of stems, and tree height (m, using a measuring stick or Hagg clinometer). Only values of DBH for the largest stem (hereafter, main stem) are reported here. Reproductive status (presence or absence) was assessed visually based on evidence of flowering (male or female), fruiting (burrs), or presence of viable seeds from the current or previous year. In addition, we searched a five-meter radius around the base of each tree for new recruits, avoiding double counting recruits in overlapping circles. The radius of five meters was chosen as encompassing an area large enough to include the tree canopy and with the highest likelihood of observing seed.

Tree health was measured as the incidence of blight symptoms, percentage dieback per stem, and tree survival. Presence of chestnut blight (*C. parasitica*) was noted when the orange fruiting bodies (pycnidia and/or perithecia) of the fungus were seen anywhere on the tree. Stem dieback was estimated as the percentage of a stem that had died from the top down for all stems ≥2 cm DBH (reported here for the main stem only). Trees were designated as dead when no living leaves or stems were observed.

2.2. Tree size, reproduction, and health status

To examine the current status of chestnut in southern Ontario, we assessed tree size distribution, magnitude of stem dieback, incidence of blight, and incidence of reproduction for trees in the 2014–15 survey and compared values to the 2001–02 survey (Tindall et al., 2004) using contingency analyses. We also documented mortality rates for trees assessed in both surveys.

To identify tree attributes linked to reproduction, infection, and mortality, we examined associations between these traits and height, DBH, and percentage dieback in 2014–15 using Wilcoxon rank-sum tests. Trees with a main stem recorded as <2 cm DBH were assigned a value of 1 cm for these analyses. Tree survival was compared with height, DBH, and percentage dieback measured in the 2001–02 survey.

2.3. Influence of chestnut blight on vital rates

To isolate the influence of blight on chestnut vital rates, we tested for statistical dependence between blight status (present, absent) in 2001–02 and tree survival (dead, alive) in 2014–15 using a contingency analysis. We also assessed the influence of blight status in 2001–02 on the change in tree DBH and change in percentage dieback over the 13-year census interval using Wilcoxon rank-sum tests. Change in DBH was calculated as the DBH of the main stem in 2014–15 minus that in 2001–02. Trees with a main stem recorded as <2 cm DBH were assigned a value of 1 cm. Similarly, change in dieback was calculated as the difference between percentage dieback of the main stem in 2014–15 and 2001–02. These analyses involved only those living trees measured in both surveys.

To assess the relationships between incidence of blight in 2001–02 and change in reproductive status over the past 13 years we used a contingency analysis. Changes in reproduction were represented by four categories: non-reproductive in 2001–02 and 2014–15, non-reproductive in 2001–02 and reproductive in 2014–15; reproductive in 2001–02 and 2014–15; and reproductive in 2001–02 but not in 2014–15. We excluded trees <2 cm DBH in 2001–02 since all of these trees were non-reproductive and therefore cannot be used to estimate the latter two categories.

2.4. Population growth rate, stable size distribution, and elasticity

To assess population growth rate, stable size distribution, and the effect of different demographic stages on population growth, we used a Lefkovitch matrix model with stage structure (Caswell, 2001). This approach uses demographic information contained in a transition matrix (A), which conveys the probability of individuals of different demographic stages surviving or changing demographic stage, and reproducing, over a given time interval (13 years in this case), and a vector (n), which describes the current distribution of individuals among demographic stages. Changes in the population over one time interval is represented as $n_{t+1} = An_t$. Using this model, we calculated the finite rate of increase of a stable population (λ, where a value of 1 = stable population size, <1 = population decline, >1 = population growth) as the dominant eigenvalue. We also estimated the stable distribution of trees among stages and elasticity of λ to each transition matrix element (Caswell, 2001).

The elements of the chestnut transition matrix are depicted in a life cycle graph (Fig. 1). Specifically, chestnut trees were classified into five demographic stages based on DBH and age. Stage 1 contained trees <2 cm DBH and less than 13 years old (i.e., new recruits not present in 2001–02). Trees older than 13 years were classified by size into stage 2 (<2 cm DBH), stage 3 (2 to <10 cm DBH), stage 4 (10 to <20 cm DBH), and stage 5 (≥20 cm DBH). A seed stage was not included since no information is available on the seed production per tree or germination rates. We assume that any viable seed produced germinates into a seedling within the same time step that it is produced.

Individual transition probabilities were based on observations for all trees censused in 2001–02 and 2014–15. Treating the Canadian range as a single population provides more robust estimates of the transition probabilities and reflects the regional perspective of current conservation management. Transition probabilities were calculated as the number of trees in a given stage that remain in the same stage (stasis) or change to a different stage (growth or retrogression), expressed as a proportion of all trees starting in that stage. Fecundity values (probability of seedling recruitment) were based on trees with both 2001–02 reproductive status assessed and their 2014–15 five-meter radius searched. Stage fecundity values were calculated as the probability of any reproductively mature tree producing a new recruit (total # of new recruits (t + 1)/total # of reproductive trees (t)) multiplied by the proportion of reproductively mature trees in any given stage (total # of reproductive trees in stage i (t)/total # of trees in stage i (t)). Using measures of both reproductive maturity and total new recruits produced over the transition interval provides a measure of fecundity that reflects the process from seed production to seedling establishment that is integrated across 13 years.

Since Tindall et al. (2004) could not identify new recruits (stage 1) in 2001–02, information on their fate over the 13-year interval was not available. Therefore, we assumed stage 1 trees had the same transition and fecundity probabilities as stage 2, since they were similar in size. Using the transition and fecundity probabilities calculated above, we constructed a transition matrix and calculated population growth rate (λ), stable stage distribution, and elasticity values for this chestnut population using R version 3.2.3 (R Core Team, 2015) and the 'popbio' package (Stubben and Milligan, 2007). Following Silvertown et al. (1996), we classified elasticity values as growth (G), stasis (L), retrogression (R), or fecundity (F) (Table A.1) and summed all values within each category. Though it is common to lump stasis and retrogression together (Jolls et al., 2015), we assessed these values separately since blight frequently causes retrogression through tree dieback and its impact on population growth is of interest.
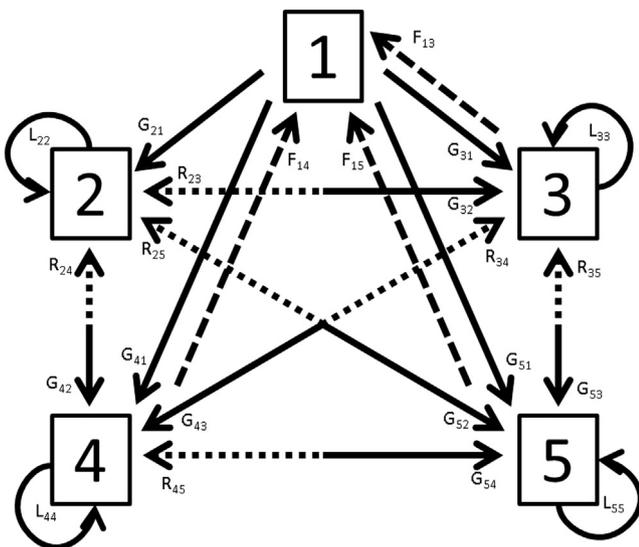
We estimated the variance associated with our estimate of λ by calculating the stochastic rate of increase (λ_s) from transition matrices based on trees sampled at random with replacement. Each stage was sampled a number of times equal to the total number of individuals in that stage. Since there were no individuals to sample in stage 1, we created stage 1 data with probabilities identical to stage 2 prior to bootstrap sampling. Using the bootstrap values, transition and fecundity probabilities were calculated in the same manner as above, a transition matrix constructed, and λ calculated. This analysis was repeated 5000 times to give an estimate of λ_s and 95% confidence limits based on the percentile method.

In our transition models, one time step (t to t + 1) is equivalent to 13 years, the approximate length of time between surveys. We used this longer time interval because population growth rate estimates based on shorter-term observations may fail to capture important changes in long-lived species (Parker et al., 1993; Davelos and Jarosz, 2004). At the same time, this interval limits our ability to discern transitions and reproductive rates at finer scales.

Fig. 1. Life cycle graph for a size-classified American chestnut population. Stage classes are represented by numbered squares (where 1 = <2 cm DBH less than 13 years old; for trees ≥ 13 years old: stage 2 = <2 cm; 3 = 2 to <10 cm; 4 = 10 to <20 cm; 5 = ≥20 cm DBH trees) and arrows represent possible transitions between stages. Solid arrows represent growth or stasis, long-dash arrows represent reproduction, and short-dash arrows represent retrogression. Arrow labels represent corresponding transition matrix elements of growth (*G*), stasis (*L*), retrogression (*R*), and fecundity (*F*).

3. Results

3.1. Survey summary

In total, 781 chestnut trees (dead and alive) were surveyed across southern Ontario in 2014–15 (Fig. 2), 595 of which were initially assessed in 2001–02. Chestnut trees were found in 12 counties across Ontario with >50% of trees occurring in the Haldimand-Norfolk area. The fate of 84 trees from the 2001–02 survey could not be assessed due to difficulties locating or accessing the trees in 2014–15. Another 19 trees were counted as presumed dead. These trees were surveyed in 2001–02 but we found no trace of them in 2014–15 despite having high confidence that we searched the correct location. Dead and presumed dead trees were lumped together for all analyses of mortality.
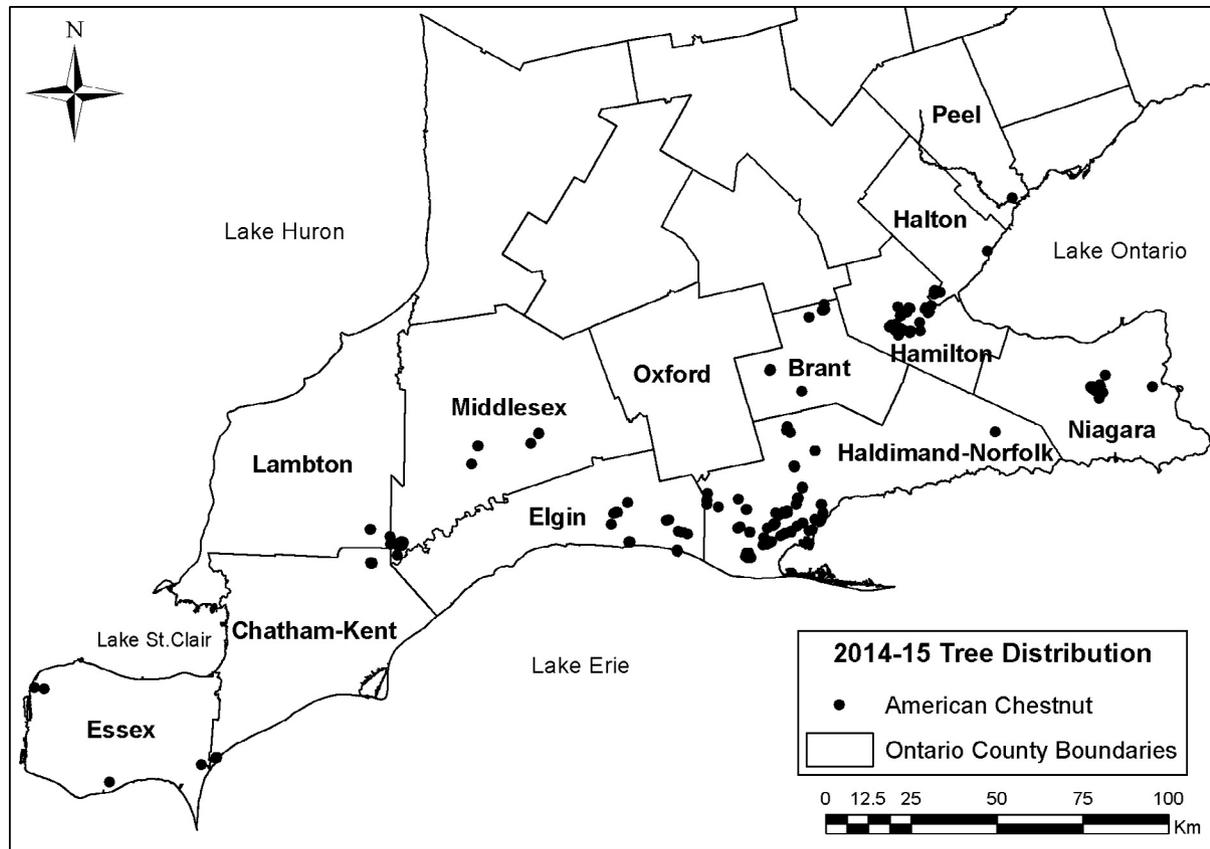
Fig. 2. Geographical distribution of living American chestnut trees across the native range in Canada, as surveyed in 2014–15. Actual density is obscured by overlapping points.

### 3.2. Tree size, reproduction, and health status

Tree size variation in 2014–15 was similar to that observed in 2001–02. In 2014–15, height ranged from 0.17 to 38.0 m (mean = 8.6 m, SE = 0.32, n = 663) and DBH ranged from <2 to 77.8 cm (mean = 12.97 cm, SE = 0.48, n = 651). Approximately 65% of trees were less than 10 m tall and 10 cm DBH; 12.6% of trees were ≥20 cm DBH. There was no significant difference in the distribution of trees among four DBH classes (<2 cm, 2 to <10 cm, 10 to <20 cm, ≥20 cm) between surveys (X^2 = 2.37, df = 3, p = 0.50).

Incidence of reproductive trees declined over the 13-year survey interval. Eleven percent (74 of 650) of trees in the 2014–15 survey were reproductive compared to 16.6% (86 of 517) in 2001–02 (X^2 = 6.27, df = 1, p < 0.05). Of trees assessed in both surveys, 87.0% maintained their original reproductive status (reproductive or non-reproductive), 5.7% (n = 17) of non-reproductive trees became reproductive, and 48.4% (n = 30) of reproductive trees became non-reproductive. An additional 11 trees that were reproductive in 2001–02 were dead by 2014–15. The percentage of reproductive trees in 2014–15 increased with tree DBH from 0% of trees <2 cm to 64% of trees ≥20 cm (Fig. 3A; X^2 = 263.74, df = 3, p < 0.001). Significantly, reproductive trees were 13.5 m taller (W = 4799, p < 0.0001) and 24.4 cm larger in DBH (W = 2499, p < 0.0001) than non-reproductive trees but there was no significant difference in mean percentage dieback (W = 15,398, p = 0.099; Fig. 4A). The five-meter radius search for new recruits was conducted around 498 trees, covering a total area of 3.91 hectares. No viable seed was observed and two trees had a total of seven new seedlings around their base giving a reproductive rate of 0.014 recruits per tree.

Incidence of dieback on main stems decreased over the 13-year survey interval from 90.6% (347 of 383 trees) in 2001–02 to 71.0% (319 of 449 trees) in 2014–15 (X^2 = 48.27, df = 1, p < 0.0001). The percentage of trees with dieback was similar among DBH size classes and ranged from 66.1% to 76.9% (Fig. 3B; X^2 = 5.81, df = 2, p = 0.055). The magnitude of percentage dieback per tree in 2014–15 averaged 36.6% (SE = 2.0, n = 449) compared to 31.9% (SE = 2.0, n = 383) in 2001–02. As in the 2001–02 survey, the magnitude of stem dieback in 2014–15 was bimodal in distribution with 44.4% of trees having <10% dieback, and 27.3% having >90% dieback (n = 450). While the surveys were similar in the shape of the distribution, dieback in 2014–15 had more values at either extreme (X^2 = 40.06, df = 9, p < 0.0001; Fig. A.1).

The incidence of blight increased significantly from 27.6% (139/503) in 2001–02 to 35.6% (230/646) of all living chestnut trees surveyed in 2014–15 (X^2 = 7.88, df = 1, p < 0.01). Of trees assessed in both surveys, 68.6% exhibited no change in blight status; 35.1% (n = 98) of blight-free trees acquired blight and 17.3% (n = 13) of trees with blight became blight-free (due to infected stems dying and rotting away). Percentage of trees with blight was lowest in small trees (<2 cm DBH; 13.4%) but higher (43–56%) and relatively uniform in larger size classes (Fig. 3C; X^2 = 68.49, df = 3, p < 0.001). Significantly, trees with blight were on average 4.8 cm larger in DBH (W = 31,064, p < 0.0001), 2.9 m taller (W = 32,906, p < 0.0001) and had 46.3% more dieback (W = 9890.5, p < 0.0001) than blight-free trees (Fig. 4B).

Of trees surveyed in 2001–02, 21.3% (127/595) had died by 2014–15, a mean rate of 1.64%/year over 13 years. Trees <2 cm DBH had approximately half the mortality rate found in ≥2 cm DBH size classes (12% vs. 23–28%; Fig. 3D; X^2 = 10.35, df = 3, p = 0.016). Significantly, trees that were dead in 2014–15 were
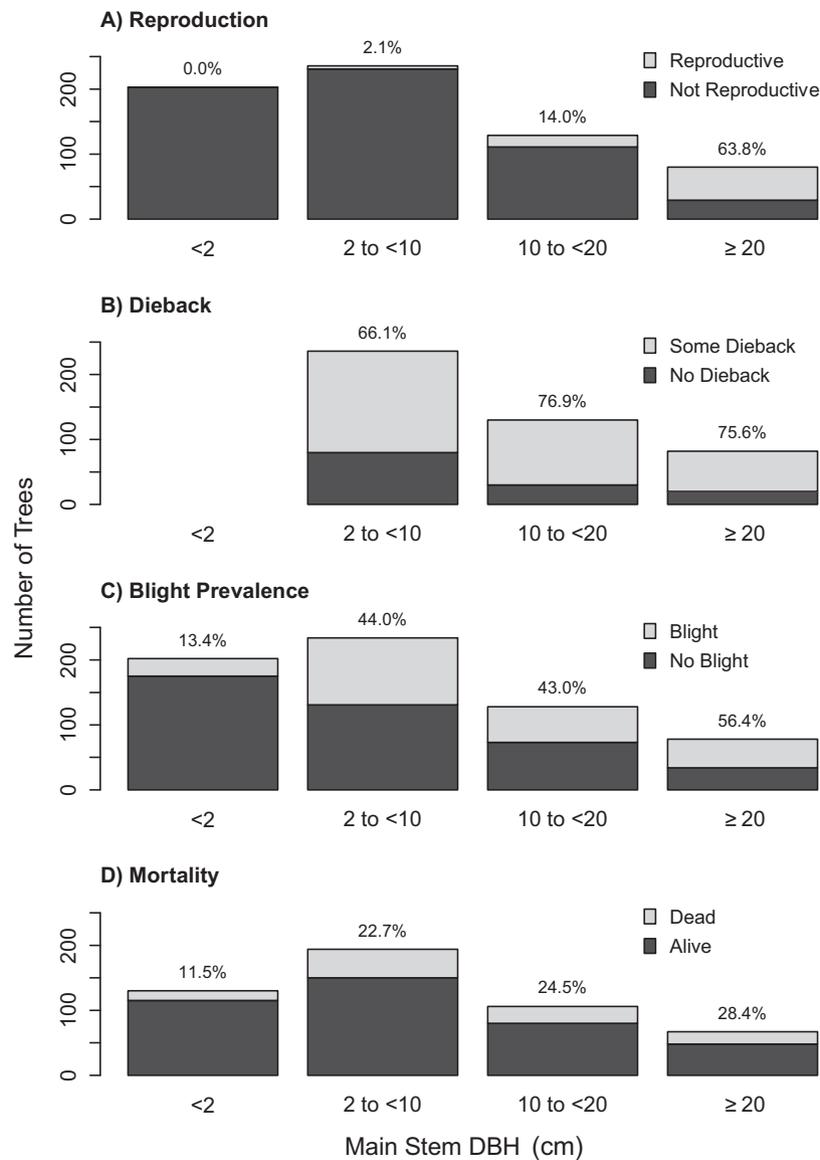
Fig. 3. Number of American chestnut trees in Canada exhibiting (A) reproduction, (B) dieback, (C) blight, and (D) mortality in the 2014–15 survey, expressed as a function of main stem DBH. Main stem DBH measurements are from the 2014–15 survey except for mortality for which DBH measurements are from 2001–02. Column labels represent percentage of trees with reproduction, dieback, blight, or mortality per DBH group. Dieback was not measured for stems <2 cm DBH.

on average 4.6 cm larger in DBH (W = 16,027, p < 0.001), 2.5 m taller (W = 14,434, p < 0.005) and had 18.9% more dieback (W = 8801, p < 0.005) in the 2001–02 survey than trees that survived (Fig. 4C).

3.3. Influence of chestnut blight on vital rates

Trees with blight in 2001–02 were significantly more likely to die by 2014–15 than trees without blight ($X^2 = 39.44$, df = 1, p < 0.0001). Of trees with blight in 2001–02, 40.5% were dead by 2014–15 whereas 13.2% of trees without blight had died. Presence of blight in 2001–02 was also significantly related to change in DBH between surveys (W = 15,210, p < 0.0001). Trees with blight in 2001–02 exhibited a mean reduction in DBH of 4.1 cm (SE = 1.04) while trees without blight increased by 2.6 cm (SE = 0.36). Changes in reproductive status were similar between trees with and without blight in 2001–02 ($X^2 = 5.2792$, df = 3, p = 0.15). Presence of blight in 2001–02 was significantly related to change in dieback between surveys (W = 4971.5, p = 0.034). Trees with blight in 2001–02 had a mean increase of 8.2%

(SE = 7.1) dieback while trees without blight increased by 31.7% (SE = 3.7).

3.4. Population viability analysis

Information on demographic stage and fate in both surveys was available for 495 trees (391 live and 104 dead) and used to construct a transition matrix (Table A.1). Over the 13-year interval, rates of stasis within stages ranged from approximately 43 to 54%; 15–18% of trees retrogressed and 12–38% grew to a larger stage. As previously noted, recruitment was low in this population leading to very low rates of reproduction within the transition matrix (Table A.1).

The finite rate of population increase (λ) was 0.817 for this population, while the approximate stochastic growth rate (λ_s) was 0.819 (95% CL = 0.783 < λ_s < 0.852). The population trajectory based on the trees in our survey is shown in Fig. A.2. The predicted stable stage distribution is similar to the size distribution of trees in both surveys (Table A.2) with the largest proportion of trees
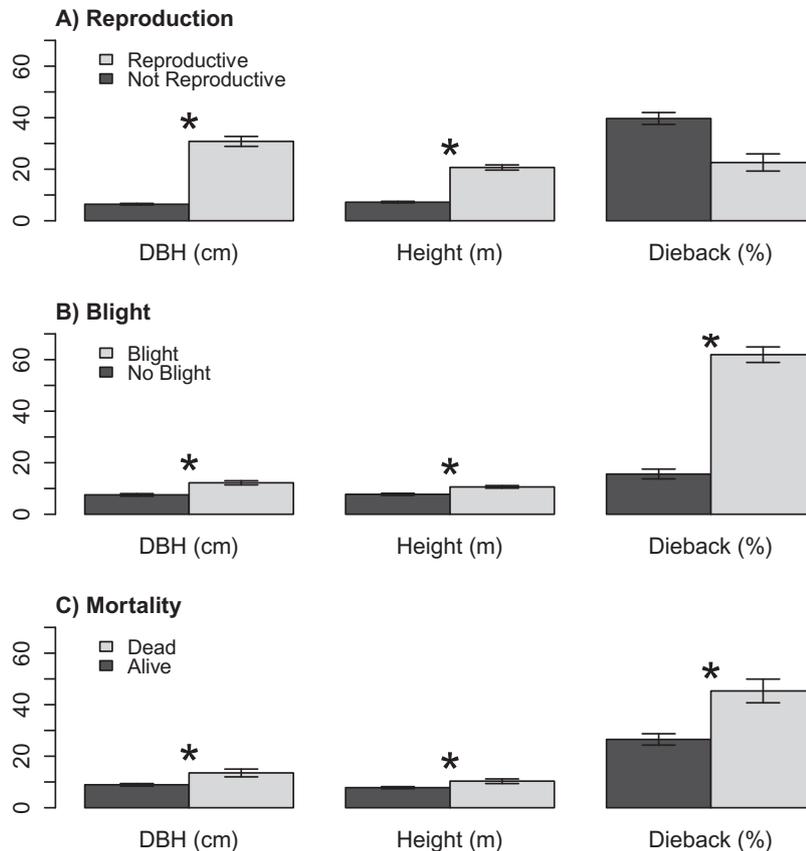
Fig. 4. Mean tree size (DBH, height) and health (dieback) of American chestnut trees in the native range in Canada as a function of incidence of reproduction, blight, and tree mortality. * indicates difference between means at p < 0.05. Y-axis units differ among reported variables (DBH = cm, height = m, dieback = %). Error bars represent standard errors.

residing in stages 2, 3, and 4. Elasticity values were highest for matrix elements representing stasis (Table A.2). The sum of the elasticity values for all stasis elements (L = 0.591) exceeded that for growth elements (G = 0.234), which exceeded that for retrogression (R = 0.147) and fecundity elements (F = 0.028). In other words, λ was most sensitive to changes in stasis rates within the population and least sensitive to changes in fecundity.

4. Discussion

The incidence of blight (35.6% of trees) observed in our study falls within values reported for U.S. *C. dentata* populations, which can be highly variable. Estimates of infection from previous surveys range from 100% of trees ≥2.5 cm DBH in a woodlot in Connecticut (Anagnostakis, 2001), to 38% (Griffin, 1989) and 15% (Burke, 2011a) of trees in forest plots in Virginia and W. Virginia, to multiple estimates ≤5% (Paillet, 1993; Fei et al., 2007; Schibig et al., 2005) including only 2% in a survey of 2156 trees in Kentucky (Fei et al., 2007). The cause of variation in blight frequency is unknown but likely is related to both developmental and environmental factors. Previous work suggests the incidence of infection can be positively correlated with high canopy cover and low litter depth (Tindall et al., 2004) and larger trees. In our study, larger trees were more likely to exhibit blight (Fig. 3C), although the actual proportion of infected trees ≥10 cm DBH (48.1%) was less than values reported in other studies (Brewer, 1995; Davelos and Jarosz, 2004 [infected populations only]; Schibig et al., 2005). Estimates may also differ due to factors affecting the expression of blight symptoms, which can vary with tree age, environment, and time since infection (McEwan et al., 2006). Regardless of cause,

the detection of blight in <50% of all chestnut in Canada was unexpectedly low given the severe impact that *C. parasitica* has had on the Canadian population since its introduction.

The incidence of blight increased over the 13-year interval, with 35.1% of blight-free trees in 2001–02 exhibiting blight in 2014–15. The infection rate of 2.7% of trees per year is lower than the 8%/year (49 of 300 trees over 2 years) found by Milo (2009) and approximately 11%/year reported by Stilwell et al. (2003). The rate of infection will depend on the epidemiological properties of the population, such as frequency and density of uninfected trees remaining and the likelihood that the fungal pathogen will encounter them. Nevertheless, for the time being, our results suggests the impact of chestnut blight continues to worsen in Ontario, nearly a century after the initial infection.

American chestnut in Canada has a greater proportion of large (DBH) trees than reported elsewhere. One third of trees (212/651) surveyed in 2014–15 were ≥10 cm DBH. In more central regions in the United States, Fei et al. (2007) found only 0.7% of 2156 trees to be >10 cm DBH and Schibig et al. (2005) reported 3.2% of 2068 trees ≥10.2 cm DBH. The Appalachian Trail Mega-Transect Chestnut Project censused 32,500 trees within 15 ft (4.6 m) of 900 miles (1448 km) of trail, out of which approximately 200 (0.6%) were ≥13 inches circumference at 4.5 ft in height (≥10.5 cm DBH; The American Chestnut Foundation, 2015). Eisen and Plotkin (2015) report almost all chestnut in the U.S. are <10 cm DBH in size and a wide-scale assessment of forest inventory data across the eastern U.S. by Dalgleish et al. (2016) estimates 84% of all chestnut within the U.S. are <2.5 cm DBH. The reason for an abundance of larger trees within the Canadian range is not known; Tindall et al. (2004) suggested it may be related to a

more open canopy and less competition for light however this remains to be tested experimentally.

Likely related to the relative abundance of large trees, we found more reproductively mature (flowering) individuals in Canada than has been reported in the United States. In our survey, 11% (74/650) of trees were reproductive, whereas Fei et al. (2007) found only a single flowering chestnut out of 2156 (0.05%) trees, Parker et al. (1993) found two trees flowering out of 1253 (0.2%), and Schibig et al. (2005) found 42 of 2068 (2%) trees flowering. This difference may have several explanations. It is possible that forests in the southern part of the range may be denser, leading to increased competition and slower growth of chestnut trees. Additionally, the virulence of C. parasitica may be higher or the tolerance to chestnut blight lower in U.S. chestnut populations, thus preventing trees from ever attaining reproductive maturity. None of these hypotheses have been tested directly. Regardless of cause, the larger and reproductive trees in the Canadian population are deserving of study and may play an important role in conservation management either as sources of blight- or cold-tolerant germplasm (Saielli et al., 2012) or seed for restoration programs (Alexander et al., 2005), especially given the ongoing struggle to locate flowering trees within the U.S. (Fei et al., 2007; The American Chestnut Foundation, 2015).

Compounding the low number of reproductive trees is a lack of recruitment. Only two trees with a total of 7 new recruits (0.014 recruit/tree in 13 years) were found in our survey. In the U.S., between 1982 and 1988, a population of 3266 chestnut produced 84 recruits (0.026 recruits/tree) (Parker et al., 1993). Paillet (1984) found no new recruits and Schibig et al. (2005) found 4 new recruits after surveying 2068 chestnut (0.002 recruits/tree). In contrast, outside of the native range, Davelos and Jarosz (2004) estimated the mean number of first-year seedlings in populations with blight ranged from 49 to 358. Why are our estimates of recruitment so low when the frequency of reproduction is relatively high? It is possible that our estimate of recruitment is an underestimate for three reasons. First, it is difficult to differentiate new seedlings from old, suppressed stems that are the same size (Paillet, 2002; Jacobs et al., 2013; Belair et al., 2014). Second, our fieldwork was conducted outside of prime seed production season and so assessments of viable seed were often made based on the previous year's burr remains, which were predominantly open, empty, and decayed. Finally, the five-meter radius searched for new recruits in our study may have been too small if seeds are more widely dispersed (Blythe et al., 2015). Alternatively, recruitment rates could be low due to ecological causes. For example, germination and establishment of seeds may be limited by the availability of mineral soil created by disturbance (McEwan et al., 2006) or by low light intensity in the understory (Belair et al., 2014). In addition, reproductive trees in our survey may be largely pollen-limited because they are often isolated within fragmented woodlots (mean distance between nearest neighbour reproductive individuals in 2014–15 = 4036 m; median distance = 736 m). Seed predators and herbivores have also been implicated in limiting chestnut dispersal and establishment through predation of seed and browsing of seedlings (Burke, 2011b; Jacobs et al., 2013).

Previous surveys of chestnut vital rates are typically based on a single census and so cannot separate the effects of blight from other factors influencing mortality and recruitment (Paillet, 2002). Our survey follows a set of trees, for which initial blight status is known, over a 13-year census interval. Using this information we estimate that trees with blight in the 2001–02 survey were three times more likely (40.5% vs 13.2%) to have died by 2014–15 than those without blight. In addition, trees with blight that survived to 2014–15 had a reduction in mean DBH whereas trees without blight increased in DBH. The decrease in mean DBH in the former group is likely the result of mortality or dieback

of the main stem in some individuals. Surprisingly, changes in the extent of dieback on the main stem increased more in trees without blight in 2001–02 compared to trees with blight. It appears this is due to the increase in dieback associated with initially healthy trees that acquired blight over the 13-year interval. The largest increase in dieback (+58%) occurred in trees that initially had no blight but acquired it over the 13-year interval, while trees that were already infected show little further increase (+10%). In conjunction with this, the distribution of dieback within chestnut in Ontario (Fig. A.1) suggests that once trees start to die, they progress quickly from low to high amounts of dieback.

Mortality of chestnut in Ontario (1.64% of individuals/year) is lower than in more southern regions and even falls below baseline rates of mortality for eastern deciduous forests. Within chestnut populations in the U.S., Burke (2011b) documented mean annual mortality rates in 6 control plots to range from 8.3 to 39.5%, and in another study found a range of 0.4–9.6%. Other estimates of annual chestnut mortality include 4.3% (Eisen and Plotkin, 2015), 5.6% (26 dead/154 trees/3 years; Schwadron, 1995), 5–11% (Davelos and Jarosz, 2004 [infected populations only]) and as high as 64% over 6 years (10.7%/year) during a severe drought (Parker et al., 1993). Moreover, Davelos and Jarosz (2004) report higher rates of chestnut mortality for new seedlings (38%/year) and low rates (<1%/year) in trees >1 cm DBH observed over a four-year period. In contrast, we found much higher rates of mortality in larger trees, most likely due to our longer census interval (13 years) and a general lack of seedlings.

Our estimate of population growth rate (λ = 0.817; λ_s = 0.819) offers some qualitative insights into the dynamics of chestnut populations and the impact of blight on the sustainability of chestnut at the northern edge of its range. Regardless of the exact number, it is clear that the chestnut population in Canada is in decline, predominantly due to mortality far exceeding recruitment. However, caution is warranted when making more specific forecasts (Crone et al., 2011; Bell et al., 2013) as a number of assumptions could influence the accuracy of our estimate. First, we assume that new recruits (stage 1 trees, <2 cm DBH and <13 years old) have equal transition probabilities (and thereby survival) as stage 2 trees (<2 cm DBH and ≥13 years old). This assumption is unlikely to be true, as new chestnut recruits generally have lower survival than similarly sized older trees (Davelos, 1999; Davelos and Jarosz, 2004), and may inflate our estimate of λ. Second, Lefkovitch models are deterministic and assume no change in vital rates or environmental conditions through time, which can cause significant forecasting errors (Crone et al., 2012). Since the expected stage distribution was similar to the actual distribution, this may not be a problem in the short term. However, we expect that the transition probabilities will change should the incidence of blight continue to rise, causing increased mortality in larger trees. This trend could lead to an increasingly steep decline in the chestnut population through time, at rates faster than predicted here. Lastly, our estimates are based on a single 13-year time interval. While using this time interval captures important changes in this long-lived species that shorter intervals would miss, it is possible that additional intervals would provide different results. Clearly, examination of population dynamics at different times and different spatial scales are needed to evaluate the reliability of our estimates.

Our study offers a number of insights for conservation management. During the 2014–15 survey, we located 118 previously undocumented trees in Ontario. Combined with earlier surveys, there are now approximately 1200 geo-referenced trees in the provincial database, which demonstrates the population size in Canada is larger than the upper estimate cited previously (N = 1020; Boland et al., 2012). That the total population size may be closer to 2000 trees is positive from a conservation per-

spective but this value is still a small fraction of the number of trees in Ontario prior to the introduction of blight (Boland et al., 2012). Less positive, our results demonstrate that the Canadian population of American chestnut is in decline. This runs contrary to some perceptions that populations are stable and simply reduced to small resprouting trees (Paillet, 2002; Eisen and Plotkin, 2015). On this basis and given its already small population size, in Ontario this species warrants the endangered status it has been given. Clearly, conservation action, either through active management of existing populations or restoration of populations through plantings, will be necessary to reverse this decline and ensure a sustainable population as required by Ontario's recovery strategy (Boland et al., 2012).

Elasticity values provide some insight as to what life stages are best to target in American chestnut for the most effective interventions. In our study, transitions associated with stasis (survival within a demographic size class) have the greatest relative impact on population growth rate, which is consistent with other tree species (Silvertown et al., 1996). This suggests that conservation actions should aim to increase survival in chestnut; however, as Silvertown et al. (1996) point out, this is an oversimplification especially for populations that are decreasing. Increased survival may prolong the decline more than changes to other matrix elements; however attention to recruitment is necessary to actually reverse the decline. Recruitment in our study was extremely low (0.014 recruits/tree/13 years) and may offer the most feasible management target for increasing λ, given that management of blight either through hypovirulence or cultural methods has not been effective to date. As an illustration, the number of new recruits per reproductive tree would have to be approximately $15\times$ higher than present to achieve a stable population ($\lambda = 1$) in Ontario. In situ and ex situ plantings offer alternative mechanisms for elevating recruitment and population size. The location and genetic composition of these restoration efforts must be considered with care to minimize further transmission and expression of chestnut blight within natural populations.

How does our study population at the northern limit of the species' range fit into the central-marginal model of demography and population dynamics? Since we did not include populations from the centre of the range in our study, any contrast between central and marginal regions is necessarily tentative. However, compared to published demographic data for the southern part of the range, the population in Canada has a relatively high frequency of large and reproductive trees, low recruitment and low mortality. This pattern suggests that the northern margin of the range is determined mostly by limited recruitment. Relatively low tree mortality (high survival) at the range edge is not expected under the typical central-marginal model (Brown, 1984; Lawton, 1993). Lesica (2014) observed a similar decline in recruitment, but not survival, at the range edge in a long-lived *Silene* and attributed the low mortality to diminished predation by voles at the margins of the range. This example reminds us that classical declines in tree survival toward the edge of the range may not always occur especially where vital rates are influenced by interactions with other species, whose geographic ranges are governed by different limiting factors. In the case of chestnut, the northern environment may represent the limits of ecological tolerance for the tree but simultaneously may diminish the spread or virulence of the pathogen compared to central populations. Populations of American chestnut are still expected to decline at the northern range edge, but the demographic attributes of these populations represent unique opportunities for conservation action that may not exist elsewhere.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.06.015.

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