

Are biotic disturbance agents challenging basic tenets of growth and yield and sustainable forest management?

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We examined the performance of older even-aged plantations to check the validity of three of the most fundamental tenets of forest site productivity: the height–age site index, Eichhorn’s rule and the thinning response hypothesis. We assessed the condition of >14 000 trees in 60 randomly selected plantations to determine whether the stands were following site productivity expectations and growth and yield projections. We evaluated the health status of all the trees by height class (<2, 2–4 and >4 m tall). We found strong evidence that older, managed plantations are subject to damage agents that are targeting dominant trees. We found natural ingress was not filling voids created by loss of planted trees. Our findings were clearly in conflict with the assumptions of low and stable levels of loss of dominant trees in aging plantations. The tendency of forest growth models to emphasize stability and predictability needs to be reconsidered. The assumptions driving the traditional forest growth models were developed largely in the absence of biotic and abiotic damage agents and certainly prior to the knowledge of climate change. The combined influence of these two drivers must be better accounted for in growth models through more intensive stand and forest level monitoring.

Introduction

Individual tree performance and the prediction of stand-level growth need to account for the risk of damage agents and their effects, given the expectation of increased disturbance in forests as the climate warms (Dale *et al.*, 2001; Bolte *et al.*, 2009). It is essential that forest managers strive to develop practices that reduce the risk of long-term productivity losses to provide the greatest mitigation efforts against anthropogenic climate change (Nabuurs *et al.*, 2007). Promoting resilient and adaptable forests may require taking a systems view of forest management in contrast to the traditional approaches (Messier *et al.*, 2013). Managed forests in British Columbia (BC), Canada, will play a critical role as it is here that we have the opportunity to influence outcomes through adaptive management (Campbell *et al.*, 2009).

The prediction of site productivity in even-aged stands in BC and elsewhere has been based on the assessment of dominant stand height, Eichhorn’s rule and the thinning response hypothesis (Skovsgaard and Vanclay, 2008). These foundational tenets of stand yield rely on the knowledge that height growth correlates well with stand volume growth and that stand volume growth is independent of thinning practices for a wide range of densities (Langsaeter, 1941). Hence, total volume production of a given tree species at a given stand height across a range of densities should be nearly identical with slight variations to account for site conditions (Gehrhardt, 1909; Assmann, 1970 as referenced in Pretzsch, 2009, 435–6). These tenets of growth prediction in even-aged stands and the various indicators used to aid yield predictions

were developed long before we began to view forests as dynamic social-ecological systems with interactions and feedbacks between climate, management and disturbance agents (Dale *et al.*, 2001; Seidl *et al.*, 2012; Messier *et al.*, 2013).

Growth models used to project forest yield in even-aged stands draw on these foundational tenets of forest site productivity (Stage, 1973; Mitchell, 1975; Garcia, 2005; Skovsgaard and Vanclay, 2008; Pretzsch, 2009). Growth models have largely been based on data from small, uniform structured, research and inventory plots that have maintained their integrity, that is, plots experiencing no or limited disturbances (e.g. Bruce, 1977). It was not uncommon for individual trees, plots or entire replicate units to be dropped from growth and yield experiments if outside factors, such as pests, herbivory or windstorms increased variation (Pretzsch, 2005). Traditional growth models implicitly accept that controlled research plots provide reliable information to guide management at much larger scales supporting the notion that managed forests have predictable yields and are generally free of unplanned disturbances (Puettmann *et al.*, 2009). The impact of unexpected disturbance on stand development cannot be predicted from research plots or growth models that assume fully stocked, regular stands.

No single factor, not site index, species composition nor growth rates has a greater influence on modelled stand productivity than unexpected loss of crop trees (Flewelling and Monserud, 2002). Clearly, an understanding of tree loss, through either mortality or damage rendering the tree unacceptable, is central to predicting stand-scale yield. Mortality in natural forests is believed to follow

a U-shaped pattern, with high initial rates among young seedlings and saplings, followed by an extended stable period with a low risk of mortality, and lastly, a period of increased senescence mortality caused by old age and an accumulation of pests and pathogens (Lines *et al.*, 2010).

The foundational tenets of estimating forest site productivity and projecting growth of managed stands rely on uniform conditions, predictable mortality rates driven primarily by competition and a constant climate. This norm or reference condition on which yields are projected may be an artificial or idealized condition that no longer exists. The environmental conditions of the forests in BC have already changed due to global warming, and the extent of those changes has exceeded earlier projections (Wang *et al.*, 2012). The low mortality and damage rates assumed throughout the mid-rotation period are a widely held belief in managed stand yield projections, but this is in conflict with the emerging knowledge of forest disturbance and climate impacts (Dale *et al.*, 2001; Logan *et al.*, 2003; Soja *et al.*, 2006; van Mantgem *et al.*, 2009; Sturrock *et al.*, 2011; Hennon *et al.*, 2012). We have already observed apparent changes to biotic disturbance agents linked to climate change in natural and managed stands in BC (Carroll *et al.*, 2004; Woods *et al.*, 2005; MacLauchlan *et al.*, 2006; Woods *et al.*, 2010; Woods, 2011). Given climate change projections for BC (Spittlehouse *et al.*, 2008), we expect to witness more examples in the future.

The last mandatory assessment made of even-aged plantations in the province of BC occurs typically 10 to 15 years post-harvest (Woods and Bergerud, 2008). To achieve acceptable stocking, harvested sites must be reforested with a minimum number of well-spaced trees of minimum height, which are ecologically appropriate to the site and free from brush competition (BC Ministry of Forests, 2000). On public forest land in much of Canada, after minimum stocking levels are achieved, it is assumed that these managed stands will remain on a predictable growth and yield trajectory with low modelled loss rates for dominant crop trees (Feng *et al.*, 2006).

Our study involves an examination of even-aged plantations ten or more years after their last mandatory assessment with the

general purpose of determining whether these stands are continuing to conform to the basic tenets of forest site productivity and thus following modelled timber productivity projections. More specifically, we examine whether disturbances in these stands are challenging traditional forest management theories and the models which were derived from them and how this may be affected under climate change. Our ultimate objective is to examine the extent to which managed forests are following their projected growth and yield trajectory and thus meeting their climate change mitigation potential.

Methods

Study area

Our study was conducted in the Okanagan timber supply area located in south-central British Columbia. The study area stretched from the Seymour River and Shuswap Lake in the north to the Canada–US border in the south and from the Monashee Mountains in the east to the Okanagan Mountains in the west. The study area covered ~2.25 million hectares of gross land base, of which 782 693 hectares contributed to the long-term timber harvesting land base of the study area (BC Ministry of Forest, 2012).

Stand selection and data

In order to make inferences about managed stands in the operable land base of the timber supply area, we identified the entire target population of stands that had met free-growing stocking obligations between 1987 and 2001 and were greater than 15 ha in size. Our sample population included 1732 stands within the long-term timber harvesting land base meeting these criteria. We then randomly selected 60 stands from this population (sampling intensity of 3.5%). The mean age of our sample was 27 years, and the time that had elapsed since the last mandatory assessment ranged from five to 17 years with a mean of 11 years.

At the last mandatory assessment, lodgepole pine (*Pinus contorta* Douglas & Loud. var *latifolia* Engelm ex S. Wats.) plantations dominated. The remainder were interior spruce (cross of white spruce (*Picea glauca* (Moench) Voss) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), western larch (*Larix occidentalis* Nutt.), western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla*

Table 1 Tree counts by species, height class and condition for 60 randomly selected managed stands in the Okanagan timber supply area of southern British Columbia, Canada

Species	Count		Height class			Condition				
	Total	% of Total	<2	2–4	>4	Live	Damaged	% Damaged	Dead	% Dead
Cottonwood	157	1.1	8	59	90	157	0	0.0	0	0.0
Trembling aspen	250	1.7	16	42	192	245	6	2.4	5	2.0
Subalpine fir	3000	21.0	564	1442	994	2973	250	8.3	27	0.9
Western redcedar	990	6.9	289	460	241	976	196	19.8	14	1.4
Paper birch	608	4.3	34	119	455	594	13	2.1	14	2.3
Douglas-fir	838	5.9	71	223	544	770	165	19.7	68	8.1
Western hemlock	641	4.5	122	301	218	610	149	23.2	31	4.8
Western larch	74	0.5	8	16	50	66	13	17.6	8	10.8
Lodgepole pine	5577	39.0	451	1579	3547	5357	1177	21.1	220	3.9
Western white pine	108	0.8	16	51	41	78	68	63.0	30	27.8
Interior spruce	2057	14.4	433	829	795	2027	291	14.1	30	1.5
Total trees	14 300	100.0	2012	5121	7167	13 853	2328	16.3	447	3.1

(Raf.) Sarg.), subalpine-fir (*Abies lasiocarpa* (Hook.) Nutt.) or western white pine (*Pinus monticola* Douglas ex D. Don) leading. All plantations were considered even-aged in the provincial silviculture database. Natural ingress of conifer species is common and typically augments planted density particularly in moist sites ecologically suitable to western hemlock and subalpine fir. Several hardwood species also regenerate naturally in plantations in the study area including cottonwood (*Populus trichocarpa* Torr. & A. Gray), trembling aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera* Marsh.). Although lodgepole pine remained the dominant managed species at the time of our assessment, only 30% of stands contained more than 50% lodgepole pine, compared with almost 50% at the prior survey. Half of the plantations had received silvicultural treatments in addition to being planted, ranging from early brushing treatments to juvenile spacing. The remainder had simply been planted and surveyed.

The previous survey maps and survey data were obtained for each of the sample stands to ensure our current survey covered the correct areas. We then established up to fifteen 3.99-m-radius (50 m²) circular plots on a systematic grid in each stand following the methods of the prior silviculture survey though no attempt was made to re-establish the prior plot locations. In each plot, all trees taller than 1.3 m were tallied by species and health status and were placed into one of three height classes (<2, 2–4 and >4 m tall) (Table 1). The health status of each individual was assessed using the current provincial damage criteria (BC Ministry of Forests, 2008), and trees deemed unhealthy based on these criteria were recorded as unacceptable. All dead trees were considered unacceptable. If a tree was affected by more than one damage agent, the damage agent considered the most severe and most likely to cause mortality was recorded. Lastly, we estimated site index, the predicted height of trees at 50 years age at breast height of 1.3 m, for each stand based on one sample tree per plot up to a maximum of 15 sample trees per stand.

From this data, we calculated three indices of stand density in stems per hectare: total, well-spaced and free-growing. Total density was all live trees tallied. Well-spaced density was a subset of total density, which takes into account species acceptability for management objectives, tree health and their spatial distribution. Unacceptable trees, either due to their species or health status, do not contribute to well-spaced density. To ensure a regular distribution between acceptable trees, we used a minimum inter-tree-distance of 2 m to define well-spaced in our assessment, the same as that used in the previous survey. Free-growing trees are a further subset of well-spaced trees that must be >1.3 or 2 m tall (species dependent) and free from competition by other tree or shrub species (BC Ministry of Forests, 2000). This cohort of trees is generally considered as the future crop trees as they are considered established, well-spaced and free of competition. In our survey, only trees that showed obvious signs of suppression were considered not free-growing from a brush competition perspective.

We assumed that trees designated as free-growing in the previous survey (on average 11 years earlier) had been of acceptable species, form, health and a defined minimum distance apart from each other. The previous survey included leading species, site index and prior estimates of free-growing, well-spaced and total tree densities.

Another important matrix for estimating the yield of managed stands is the overall spatial distribution of the stand. The spatial distribution of trees within each sampled stand was estimated based on the ratio of total over well-spaced density. The estimated spatial distributions were then compared with theoretical spatial distributions for regular (or planted), random (or natural) and clumped distributions as modelled in the spatially explicit growth and yield model TASS (tree and stand simulator, Mitchell, 1975) and its derivative TIPSYP (Table Interpolation Program for Stand Yield) (Di Lucca, 1999).

Analysis

To test whether the incidence of unacceptable trees varied by tree height class, we undertook an analysis where every sample plot (882) was

Table 2 Counts of unacceptably damaged trees by individual damage agents from 882 survey plots distributed across 60 randomly selected managed stands in the Okanagan timber supply area of southern British Columbia, Canada

Damage agents	Number of trees affected
Vegetation competition	684
Deformities	332
Diseases	
Western gall rust	<i>Endocronartium harknessii</i> 270
Atropellis canker	<i>Atropellis pinophila</i> 259
Armillaria root disease	<i>Armillaria ostoyae</i> 176
White pine blister rust	<i>Cronartium ribicola</i> 61
Comandra blister rust	<i>Cronartium comandra</i> 51
Stalactiform blister rust	<i>Cronartium colesporoides</i> 16
Lodgepole pine dwarf mistletoe	<i>Arceuthobium americanum</i> 16
Laminated root disease	<i>Phellinus weirii</i> 12
Elytroderma needle blight	<i>Elytroderma deformans</i> 5
Dothistroma needle blight	<i>Dothistroma septosporum</i> 3
Blackstain root disease	<i>Ophiostoma wageneri</i> 1
Unknown canker	1
Insects	
Warren root collar weevil	<i>Hylobius warreni</i> 30
Mountain pine beetle	<i>Dendroctonus ponderosae</i> 23
Spruce weevil	<i>Pissodes strobus</i> 19
Lodgepole pine terminal weevil	<i>Pissodes terminalis</i> 11
Pitch nodule moth	<i>Petrova sp.</i> 4
Yosemite bark weevil	<i>Pissodes schwartzii</i> 4
Red turpentine beetle	<i>Dendroctonus valens</i> 3
Sequoia pitch moth	<i>Vespa mima sequoiae</i> 1
Mammals	
Black bear	<i>Ursus americanus</i> 60
Snowshoe hare	<i>Lepus americanus</i> 35
Beaver	<i>Castor canadensis</i> 10
Unknown mammal	6
Douglas squirrel	<i>Tamiasciurus douglasii</i> 4
Voies	<i>Myodes sp.</i> 2
Cattle	<i>Bos primigenius</i> 2
Porcupine	<i>Erethizon dorsatum</i> 1
Abiotic damage	
Drought	74
Flooding	65
Silviculture treatment	5

considered an experimental unit. We then tested whether the height class distribution based on the tree counts was similar among the various damage types using a nominal logistic regression model (SAS Institute Inc., 1990). Our plots were uniformly distributed over the stand and so should not have been strongly affected by any spatial dependencies in the spread of damage agents.

Stand density indices were analysed using a repeated-measures analysis with stands as the main-plot random effect (59 degrees of freedom)

Table 3 Tree counts by height class, damage agent group and live/dead status from 882 survey plots distributed across 60 randomly selected managed stands, mean age 27 years, in the Okanagan timber supply area of southern British Columbia, Canada

	<2 m		2 m–4 m		>4 m		Total		Live and dead
	Live	Dead	Live	Dead	Live	Dead	Live	Dead	
Vegetation competition	212	13	347	14	95	3	654	30	684
Deformities	28	0	119	0	185	0	332	0	332
Western gall rust	11	6	35	14	190	14	236	34	270
Atropellis canker	1	0	14	0	244	0	259	0	259
Armillaria root disease	1	21	5	73	9	67	15	161	176
Other diseases	5	8	40	19	69	25	114	52	166
Abiotic damage	38	4	40	7	45	12	123	23	146
Mammal damage	15	15	6	8	57	19	78	42	120
Insects damage	2	3	11	3	60	16	73	22	95
Dead unknown		20		38		24	0	82	82
Total affected	313	90	617	176	954	180	1884	446	2330
Total trees	1922	90	4945	176	6987	180	13 854	446	14 300

and time of sampling, the prior survey or our current survey as the repeated measures factor, a fixed effect, and the Stand by Time interaction, a random effect (58 degrees of freedom). The analysis of variance was conducted using the mixed procedure within SAS (SAS Institute Inc., 1990). Residuals and influence statistics were examined to see whether the model adequately fits the data. Values for free-growing, well-spaced and total density from the previous survey were compared with simple means of the current survey on a stand basis.

We used TIPSy version 4.2 to project the density of well-spaced trees in 1000 to 2000 stems ha⁻¹ lodgepole pine plantations (regular distribution) over a rotation period of 90 years. We used a minimum inter-tree distance of 2 m, a minimum height of 1 m, a site index of 20 m and operational adjustment factors (OAFs) of 5 and 15%, the default OAFs used with TIPSy in BC for timber supply analysis (BC Ministry of Forests, 2012).

Results

Health status of plantations

In our survey, we examined 14 300 trees representing 11 different tree species (Table 1). Lodgepole pine, interior spruce, Douglas-fir and western redcedar are the commonly planted species with the remaining species being dominantly natural ingress. Lodgepole pine was the most frequently planted species and represented 39% of all tallied trees (Table 1). Subalpine fir natural regeneration was abundant and represented 21% of the tallied trees (Table 1). Western larch, western white pine, cottonwood and aspen were minor components in the sampled stands (Table 1). Among the managed species (lodgepole pine, interior spruce, Douglas-fir, western redcedar and western hemlock), the proportion of trees damaged, and deemed unacceptable, was relatively similar and varied from 14.1 to 23.2%; the proportion of trees dead among these species varied from 1.5 to 8.1% (Table 1).

We recorded a total of 33 different damaging agents that rendered trees unacceptable as well-spaced or free-growing stems for stocking purposes (Table 2). Just over 16% of all trees were either dead or afflicted by biotic or abiotic damage agents rendering the stems unacceptable (Table 2). Only 5% of stands in the Okanagan timber supply area were completely free of unacceptable

damage. Forty per cent of the stands we assessed contained Armillaria root disease. The root pathogen was most prevalent in plantations from the Interior Cedar-Hemlock (ICH) zone (Pojar et al., 1987) where 83% of stands contained infected trees. A small percentage of plantations (<7%) had been impacted by the mountain pine beetle epidemic that attacks and kills lodgepole pine trees and has caused extensive mortality in mature pine stands throughout the study area for the past few years (Westfall and Ebata, 2007).

Unacceptable trees as a proportion of total were found in relatively even incidences among the three height classes at rates of 20.0, 15.5 and 15.8% for trees <2, 2–4 and >4 m tall, respectively (Table 3). However, there were significant differences in the proportion of unacceptable trees by specific damage agent among height classes (Tables 4 and 5). The majority of damage agents affected the taller trees. Vegetation competition was the only damage agent where damage was significantly less on larger trees (Tables 4 and 5). Only trees damaged by abiotic causes had height class distributions that were not significantly different from a uniform distribution among the three height classes (Table 4).

More specifically, with the possible exception of vegetative competition, damage agents tended to be frequently associated with trees >4 m tall (Table 5 and Figure 1). Figure 1 illustrates the strong divergence of the probability of damage for the tallest trees, those most likely to be critical members of the well-spaced and free-growing cohort that contribute most to overall stand yield. Tallest trees had the highest probability of being impacted by deformities, mammal damage, western gall rust, insect damage and atropellis canker.

Plantation densities

Five to 17 years after meeting the last mandatory assessment made of managed stands in the province of BC, total, well-spaced and free-growing densities were significantly lower in the Okanagan timber supply area than those in the previous survey (Table 6). Well-spaced densities decreased by 290 to 854 stems ha⁻¹ in stands averaging 27 years of age. Total stems

Table 4 Pair-wise comparisons of each damage agent or damage agent grouping between height classes

Damage agent	Test	DF	Estimate	Standard error	Chi-square	P value (unadjusted)
Abiotic damage	<2 vs >4	1	-0.2877	0.2585	1.2381	0.2658
	<2 vs 2-4	1	0.091	0.2703	0.1133	0.7365
	2-4 vs >4	1	-0.1967	0.252	0.6091	0.4351
Armillaria root disease	<2 vs >4	1	-1.2182	0.2874	17.9626	<0.0001
	<2 vs 2-4	1	1.2862	0.2853	20.3309	<0.0001
	2-4 vs >4	1	0.0681	0.191	0.127	0.7216
Atropellis canker	<2 vs >4	1	-5.4972	1.0251	28.7581	<0.0001
	<2 vs 2-4	1	2.6391	1.0589	6.2114	0.0127
	2-4 vs >4	1	-2.8581	0.2811	103.3508	<0.0001
Dead unknown	<2 vs >4	1	-0.1823	0.3475	0.2753	0.5998
	<2 vs 2-4	1	0.6419	0.3171	4.0977	0.0429
	2-4 vs >4	1	0.4595	0.2993	2.3578	0.1247
Deformities	<2 vs >4	1	-1.8882	0.2077	82.6286	<0.0001
	<2 vs 2-4	1	1.4469	0.2152	45.2254	<0.0001
	2-4 vs >4	1	-0.4412	0.1204	13.4365	0.0002
Insect damage	<2 vs >4	1	-2.7213	0.6609	16.9528	<0.0001
	<2 vs 2-4	1	1.0296	0.7458	1.9059	0.1674
	2-4 vs >4	1	-1.6917	0.4163	16.5092	<0.0001
Mammal damage	<2 vs >4	1	-0.9163	0.3154	8.4405	0.0037
	<2 vs 2-4	1	-0.7621	0.4725	2.6012	0.1068
	2-4 vs >4	1	-1.6784	0.4251	15.5925	<0.0001
Healthy	<2 vs >4	1	-1.3257	0.0469	799.7333	<0.0001
	<2 vs 2-4	1	0.9886	0.0488	410.1602	<0.0001
	2-4 vs >4	1	-0.3372	0.0333	102.6579	<0.0001
Other diseases	<2 vs >4	1	-1.6094	0.3023	28.3379	<0.0001
	<2 vs 2-4	1	1.4955	0.3054	23.985	<0.0001
	2-4 vs >4	1	-0.1139	0.1797	0.4019	0.5261
Vegetation competition	<2 vs >4	1	0.8311	0.206	16.2704	<0.0001
	<2 vs 2-4	1	0.4728	0.1446	10.6895	0.0011
	2-4 vs >4	1	1.3039	0.1939	45.2135	<.0001
Western gall rust	<2 vs >4	1	-2.4849	0.3375	54.2001	<0.0001
	<2 vs 2-4	1	1.0586	0.3764	7.9116	0.0049
	2-4 vs >4	1	-1.4263	0.2127	44.9594	<0.0001

A significant difference ($P < 0.05$) between height classes indicates the distribution of damage was not even. Data are from 882 survey plots located in the managed stands of the Okanagan timber supply area.

still remained high (3123 stems ha^{-1}) but had decreased by 42% since the previous survey (Table 6). More importantly, we estimated that 30% of the stands in the timber supply area had free-growing densities that are now below the minimum stocking threshold of 700 free-growing stems ha^{-1} used at the prior survey (Figure 2). In contrast, we estimated that 27% of stands now have the same or higher free-growing densities than at the previous survey. Overall free-growing densities were considerably lower in the majority of stands compared with the earlier survey estimates (Figure 2).

In terms of ecological classification zone, 75% of the free-growing stands in the higher elevation Engelmann Spruce Subalpine Fir zone experienced an increase in free-growing density (likely due to ingress of subalpine fir) since the last survey compared with 33.3% in the Montaine Spruce zone and only 12.5% in the ICH zone.

Spatial distribution of trees in plantations

The plantations we surveyed did not maintain the assumed regular distribution used in model projections to predict yield from these managed forests (data not shown). Plantations between 15 and 35 years of age in the Okanagan timber supply area had random-to-clumped distributions. The loss of the planted or regular distribution was driven primarily by the incidence of damaging agents in the tallest trees and the effect that had on the well-spaced density (Figure 3 and Table 6).

Model projections for managed plantations

Modelled yields in TIPSy are sensitive to the initial density of well-spaced trees in lower density stands (Martin et al., 2005, Figure 2). Martin et al. (2005) found an initial density of ~2000 well-

Table 5 The predicted probabilities (and 95% confidence intervals) of damage agent or damage agent grouping by height class for trees across 882 survey plots located in randomly selected managed stands of the Okanagan timber supply area of southern British Columbia, Canada

Damage agent	Height class (m)	Predicted probability	Lower 95% limit	Upper 95% limit
Abiotic damage	<2	29.17%	19.76%	38.57%
	2–4	31.94%	22.30%	41.59%
	>4	38.89%	28.80%	48.97%
Armillaria root disease	<2	12.50%	6.71%	18.29%
	2–4	45.24%	36.53%	53.95%
	>4	42.26%	33.62%	50.91%
Atropellis canker	<2	0.39%	0.00%	1.16%
	2–4	5.41%	2.59%	8.22%
	>4	94.21%	91.30%	97.12%
Dead unknown	<2	24.39%	13.72%	35.06%
	2–4	46.34%	33.95%	58.73%
	>4	29.27%	17.97%	40.57%
Deformities	<2	8.43%	5.37%	11.50%
	2–4	35.84%	30.56%	41.13%
	>4	55.72%	50.25%	61.20%
Insect damage	<2	5.26%	0.00%	11.69%
	2–4	14.74%	4.53%	24.94%
	>4	80.00%	68.49%	91.52%
Mammal damage	<2	25.21%	13.82%	36.60%
	2–4	11.77%	3.31%	20.22%
	>4	63.03%	50.36%	75.69%
Healthy	<2	13.42%	12.40%	14.44%
	2–4	36.06%	34.62%	37.50%
	>4	50.52%	49.02%	52.02%
Other diseases	<2	9.56%	4.64%	14.48%
	2–4	42.65%	34.38%	50.92%
	>4	47.79%	39.44%	56.15%
Vegetation competition	<2	32.90%	26.90%	38.89%
	2–4	52.78%	46.41%	59.15%
	>4	14.33%	9.86%	18.80%
Western gall rust	<2	6.30%	2.42%	10.17%
	2–4	18.15%	12.00%	24.30%
	>4	75.56%	68.70%	82.41%

spaced stems ha⁻¹ maximized merchantable volume and that yields began to drop off rapidly when well-spaced densities fell below 800–1000 stems ha⁻¹ (or 4–5 trees per 3.99-m plot). The current modelled growth and yield trajectory for managed stands in the Okanagan timber supply area is based on an initial planting density of 1300 stems ha⁻¹ in a regular spatial distribution where, effectively, all planted trees are considered well-spaced (BC Ministry of Forests, 2012).

TIPSY projects a well-spaced density of just under 1000 stems ha⁻¹ at age 15 for a 1300 stems ha⁻¹ initial planting density plantation (Figure 4), and the previous silviculture survey found a somewhat higher density of 1144 well-spaced stems ha⁻¹ at that age, likely reflecting higher initial planting densities in the past. TIPSY further projected that well-spaced density declines by 45 stems ha⁻¹, to 940 by age 30 compared with our finding of a 290 stems ha⁻¹ decline to 854 in plantations averaging

27 years age (Figure 4 and Table 6). The rate of decline observed in the field data for 15-to-30-year-old stands was considerably steeper than that of model projections (Figure 4, Okanagan field data line).

Well-spaced trees in TIPSY simulations declined to just over 830 stems ha⁻¹ at age 90 years in the 1300 stems ha⁻¹ regular distribution plantation simulation (Figure 4). Final, well-spaced densities were somewhat independent of initial establishment density in the model simulations (Figure 4). For example, TIPSY projects well-spaced densities ranging from 700 to 900 stems ha⁻¹ at age 90 for initial plantation densities varying from 1000 to 2000 stems ha⁻¹ (Figure 4). These modelled projections for well-spaced densities at rotation may be far higher than reality given the trend in our field data to date (Figure 4).

Discussion

We re-surveyed a sample of older plantations in the southern interior of BC that had previously met stocking obligations, on average 11 years earlier, to examine assumptions around the survival and condition of well-spaced trees and yield predictions. The well-spaced and free-growing trees are considered the crop trees in these plantations and those most likely to contribute to future yield. We found strong evidence that these older, managed plantations are subject to damage agents that are targeting dominant trees, rapidly decreasing well-spaced and free-growing densities, causing a more clumped spatial distribution and threatening yield projections.

Although the stands had lost a significant number of well-spaced crop trees, there were still a considerable number of total stems on the sites. Why did these trees not fill in the gaps created when the crop trees were killed or damaged? There are two primary reasons. First, to be considered as well-spaced, trees had to be healthy, of an acceptable species and of good form. Second, very few managed stands had what could be described as a regular or planted distribution and between assessments the spatial distribution of trees became more clumped. This change in spatial distribution meant that gaps were being formed by the loss of crop trees that were not being filled (Figure 3a). The loss of the regular spatial distribution has significant negative yield implications, particularly in low density stands. Based on TIPSY simulations, a 1300 stems ha⁻¹ plantation with a regular distribution yields 11 to 25% more volume at 90 years than 1300 stems ha⁻¹ stands starting with a random or clumped distribution, respectively.

Our results mirror those of Heineman et al. (2010) who found that plantations in the southern interior of BC were suffering significant losses to forest health agents. Our results also add to the growing body of evidence that suggests managed and unmanaged forests are under increasing levels of risk provincially (Woods et al., 2010; Woods, 2011; Woods et al., 2011), nationally (Michaelian et al., 2010), continentally (van Mantgem et al., 2009; Alfaro et al., 2010) and globally (Soja et al., 2006; Allen et al., 2010).

Competition-induced mortality or suppression is generally considered as the leading cause of tree death in traditional growth and yield models (Enquist and Niklas, 2001; Lutz and Halpern, 2006; Pretzsch, 2009). Suppression-caused mortality typically leads to more uniform spacing of members of a population

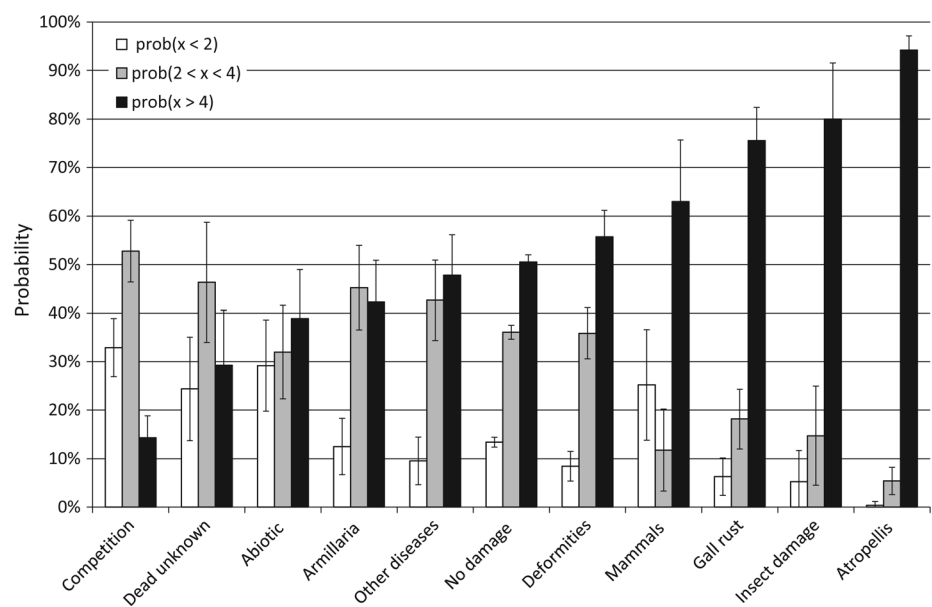


Figure 1 The probability of damage by height class (<2, 2–4 and >4 m) ranked from left to right by increasing probability for the tallest trees (black bars). For example, trees damaged by atropellis have a 94.2% probability of being >4 m tall, a 5.4% probability of being between 2 and 4 m tall and a 0.4% chance of being less than 2 m tall. Values can be found in Table 5.

Table 6 Means and estimates of the mean differences, including *P* values for free-growing, well-spaced and total density, between the prior silviculture survey and our re-survey for 60 randomly selected managed stands in the Okanagan timber supply area of southern British Columbia, Canada

Contrasts	Contrast means		Difference	SE of difference	<i>P</i> value
	Prior survey	Re-survey ^a			
Free-growing (stems ha ⁻¹)	987.5	816.6	–171.4	34.5	<0.0001
Well-spaced (stems ha ⁻¹)	1144	854.1	–290.3	31.1	<0.0001
Total trees (stems ha ⁻¹)	5384	3123	–2261	368	<0.0001

a = total trees reported in the re-survey include all trees above a minimum height of 1.3 m.

(Pielou, 1960) including trees in stands (Lutz and Halpern, 2006). We found substantially lower levels of competition-induced mortality compared with pests such as Armillaria root disease, the leading cause of tree death we observed. Further, the larger tree size classes were most affected by damage and mortality. Neither of these findings conforms to the notion of smaller trees being most likely to die in plantations (Enquist and Niklas, 2001). The stands we assessed were at a stage of development where mortality rates should have been low and stable at the bottom of the U-shaped curve (Lines et al., 2010). Most of the trees that had died across stands in the study area did not follow the characteristics normally associated with trees predisposed to death

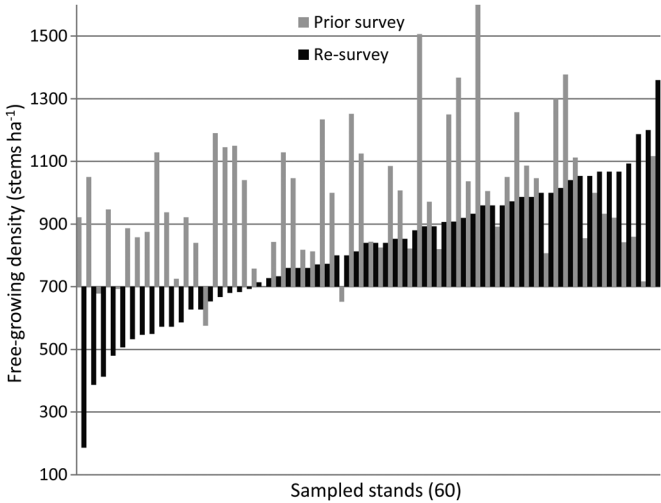


Figure 2 Free-growing density of the 60 randomly selected managed stands in the Okanagan timber supply area of southern British Columbia, Canada, assessed at the prior silviculture survey (grey) and a subsequent re-survey (black), sorted by the free-growing density at the time of the re-survey, portrayed in reference to the minimum stocking standard of 700 stems ha⁻¹ used in BC.

(Waring, 1987). They were not shaded or obviously stressed by drought. Instead, trees were killed by biotic agents, and these non-competition-induced mortality causes are generally not accounted for in most even-aged plantation growth and yield model projections (Kirilenko and Sedjo, 2007). We found damage agents to be common in managed forests of BC as have other recent studies (Heinemann et al., 2010; Mather et al., 2010; Woods et al., 2010; Woods, 2011; Woods et al., 2011).

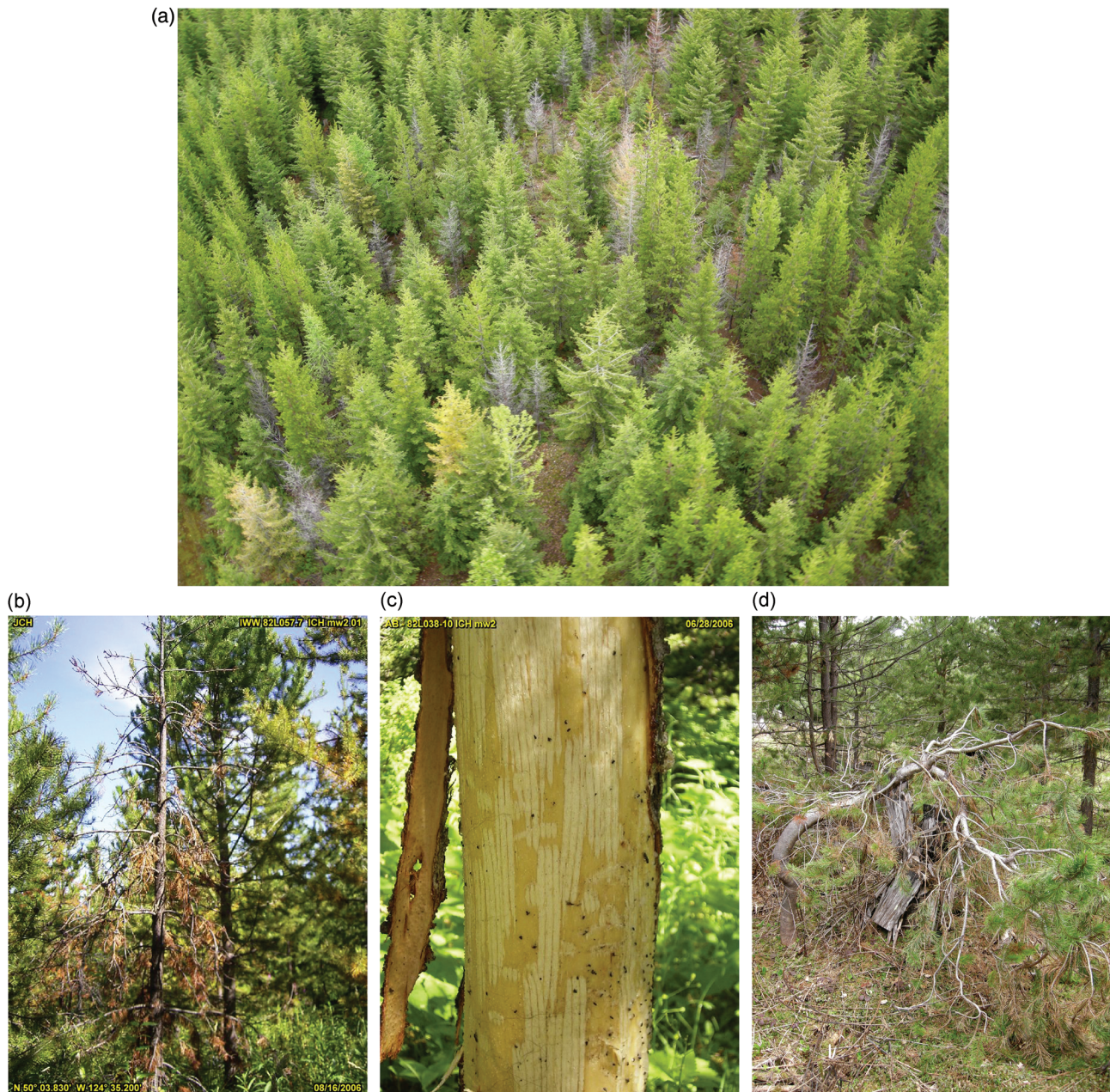


Figure 3 Examples of damage agents effecting dominant trees and the spatial distribution of those trees in managed stands of the Okanagan timber supply area of southern British Columbia, Canada, including: *Armillaria* root disease in a Douglas-fir plantation (a); a lodgepole pine tree killed by Warrens root collar weevil (b)*; bark stripping of a lodgepole pine tree caused by black bear (c)*; and an unacceptably deformed lodgepole pine tree (d). Latin names for damage agents found in Table 2. *Photo credit: J. Hodge.

Not all damage agents kill trees but they may ultimately deem individual trees unacceptable as merchantable timber (BC Ministry of Forests, 2008). The basic assumption after stocking obligations are met at the free-growing assessment is that the future incidence of these sub-lethal damage agents will be low just as mortality rates are predicted to be stable and low. This is demonstrated in the TASS derived growth and yield application TIPSy (Di Lucca, 1999) simulations of 1000 to 2000 stems ha^{-1} pine plantations (Figure 4). The extent of future crop tree loss (dead and damaged

trees) that we observed over the 11-year period between stand assessments was as great as that projected by TIPSy over an entire 90-year rotation, and over five times the loss forecasted to occur over the 10-to-15-year period we assessed. Our findings are clearly in conflict with the assumptions of low and stable levels of loss of dominant trees in aging plantations.

Traditional forestry growth models and yield tables for even-aged plantations generally rely heavily on one or more of three deeply rooted concepts in forestry and forest science:

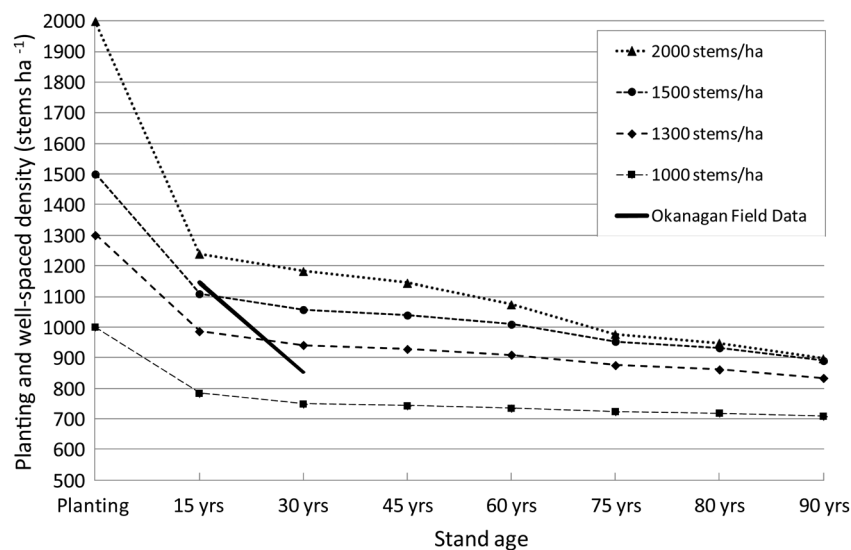


Figure 4 Projected changes in well-spaced density over a 90-year rotation for typical lodgepole pine plantations, based on initial planting densities covering a range from 1000 to 2000 stems per hectare (typical planting densities in BC) in the Okanagan timber supply area based on the growth and yield application TIPSy (version 4.2), compared with actual changes in well-spaced density based on field data from 60 randomly selected managed stands (Okanagan field data shown in solid black line).

predictable dominant stand height (assessed by the height–age site index), the thinning response hypothesis and Eichhorn’s rule (Skovsgaard and Vanclay, 2008). These fundamental tenets of growth prediction were developed prior to the knowledge of climate change and its impacts on forests and forest health. Climate science is unequivocal in its projections of change and a lack of stability (IPCC, 2007), and many of those changes have been forecast to be detrimental to forests (Dale et al., 2001). Unexpected disturbances, including those associated with climate change impacts, challenge all three tenets of forest site productivity and the growth models built upon them. At the same time, very few forest production models include these effects, which severely limits the reliability of the model results (Kirilenko and Sedjo, 2007). Our results illustrate an apparent deviation from the projected stand-level growth and yield trajectory for managed stands in our study area largely before many of the forecast impacts of climate change have materialized. It is quite conceivable that the gap between projected and realized yield will widen if models developed on the premise of stability and predictability are not updated to reflect the increasing levels of biotic and abiotic disturbance.

Our study did not directly address the use of site index to aid stand yield prediction, yet our results do raise concerns about assigning a yield curve to a stand based on an early assessment of dominant stand height. This popular metric, which uses tree height as a bioindicator, requires stability in the dominant tree class. We observed high losses in the dominant tree class by various disturbance agents with the greatest extent of damage in the tallest trees. Changes in dominant tree dynamics and the influence that those changes have on site index curves have been reported (Raulier et al., 2003). Mortality rates in top height trees have similarly been reported and have been found to vary by species and shade tolerance (Mailly et al., 2009). Despite these findings, the extent to which such dynamics are incorporated in growth

and yield models remains minimal. Site index is an example of the deeply entrenched focus of traditional growth and yield on stability and homogeneous stands (Puettmann et al., 2009). The early assessment of dominant stand height as a reliable prediction of future stand productivity is challenged if the interactions among climate, management and disturbance result in unacceptably high losses of the dominant trees as observed in our study.

The thinning response hypothesis implies that yield is constant across a wide range of densities and that efficiencies can be achieved by concentrating the growth potential of a site on as few stems per hectare as possible without creating voids. Langsaeter’s relation states that there is a minimum managed stand density above which projected harvest yields are stable and below which timber volume sharply declines (Langsaeter, 1941 as cited in Pretzsch, 2009). Based on the projections by TIPSy, this inflection point, or threshold level, where yield begins to diminish, is around a well-spaced density of 1000 stems ha^{-1} with steep losses evident below 800 stems ha^{-1} (Martin et al., 2005). We found that well-spaced densities had declined at a much more rapid rate in plantations averaging 27 years (by 290 stems ha^{-1} to 854) than that projected by TIPSy, suggesting plantations in the Okanagan timber supply area were, on average, dangerously close to suffering significant yield losses unless other trees could fill the void of missing well-spaced trees. We found no evidence of filling of voids by naturals in stands averaging 27 years of age suggesting a potential compounding of yield loss due to low density and a more clumped spatial distribution.

Clearly, the closer one manages to the threshold minimum density, the lower the per hectare costs incurred for activities such as planting and stand tending, and this assumption has been a driving force behind stocking standards for Canadian and global even-aged plantation management. Flewelling and Monserud (2002) recognized that unforeseen mortality resulting from disturbance agents can push managed stand densities below the

ideal minimum, particularly if planting densities and stocking standards were created in the absence of knowledge of pest impacts. A fundamental guiding rule for all forests managers is to maintain site occupancy and avoid dropping below the inflection point of Langsaeter's relation. In our study area, it is becoming increasingly difficult to determine which crop trees will survive to rotation. Our results show how the density of trees that were expected to reach rotation declined significantly over an 11-year period. Employing the thinning hypothesis to optimize the yield by reducing density and focusing growth on select trees involves great risk when the incidence of forest health agents is overlooked or their impacts are poorly understood.

Eichhorn's rule states that the total volume production of a given tree species at a given stand height should be very similar for all site classes, regardless of age (Skovsgaard and Vanclay, 2008). This implies that when the dominant tree height is known, and future dominant height remains predictable, then stand yield can be easily estimated now and then projected into the future. This fundamental tenet is based on the belief that forest disturbances that attack larger crop trees, particularly during early- to mid-rotation, are rare exceptions. We found the opposite, and for some of the most prevalent damaging agents including atropellis canker and western gall rust, we found the tallest trees had an increased probability of being damaged. Final harvest volumes will be negatively influenced by damage agents that target the largest trees, and model projections that ignore these impacts will not be realized (Kirilenko and Sedjo, 2007).

The current forest management approach followed in much of Canada (Feng et al., 2006) relies on growth and yield models rather than systematic rotation length monitoring of stand condition. In BC, once managed stands reach a free-growing condition, typically by age 10–15, they are assumed to be on a stable predictable growth trajectory with little risk of loss to the dominant crop trees. There are >7.2 million ha of managed stands in BC's provincial forest base (Province of British Columbia, 2010). Their health and productivity have important implications for everything from community stability in forest-dependent communities to global carbon accounting (Kurz et al., 2008; Metsaranta et al., 2011; Pan et al., 2011) and BC's role in climate change mitigation as a forest dominated land-base. We can no longer rely on stability and predictability in our managed forests (Millar et al., 2007). Clearly, more intensive monitoring and the development of model interfaces to readily input monitoring data into growth and yield models to ensure flexibility and adaptability need to be pursued. Our results also suggest that more trees, and probably a greater variety of species, need to be planted in order to compensate for the losses to biotic and abiotic damage agents.

It is imperative that we constantly improve our approach to the science and practice of forest management. The current tendency of forest growth models to emphasize stability and predictability needs to be reconsidered. We need a more flexible approach to modelling forest growth that recognizes changing forest dynamics.

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Conflict of interest statement

None declared.

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