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The 3/4 power law in forest management: how to grow dead trees

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Abstract

Structural complexity of managed forests is proving to be vitally important for the conservation of wildlife and ecological processes. We test for the factors most important in determining the availability of snags (dead standing trees) in fire-origin boreal forests of northwestern Ontario. The strongest correlate of snag basal area (m^2/ha) was the amount of live tree basal area, which accounted for 68% of variation in the production of snags. The relationship between live and dead tree basal area followed a 3/4 power law with a slope of 0.74 for the forest community and differing slopes for forest stands and forest age. A relationship between tree mortality and metabolic rate is consistent with rate of self-thinning theory. This invariance indicates that total community biomass is likely to be insensitive to species diversity. Mixed hardwood forest types produced the greatest basal area of snags, followed by poplar, mixed conifer, jack pine and spruce stands. The percentage of stems that were dead was greatest in young forests (18% of stems in 0–60-year-old forests), decreased to a low percentage of 12% in 61–80-year-old forests, and thereafter increased with age of forests from 15 to 16% in 81–100, >100-year-old forests, respectively. In contrast, the number of small diameter (10–22 cm dbh) snags (stems/ha) was greatest in 61–100-year-old forests, whereas medium diameter (22–30 cm dbh) snags and large diameter (>30 cm dbh) snags were greatest in old-growth (>100 years) forests. The management implications are that increased live tree density due to environmental conditions, or possibly intensive forest management practices following clear cutting, may secondarily result in greater snag production and the structural complexity that favors wildlife biodiversity. Forest management guidelines that incorporate allometric relationships are needed to ensure maintenance of biodiversity and habitat heterogeneity following timber harvesting.

Keywords: Biodiversity; Boreal forests; Metabolic rate; Self-thinning; Snags; Structural complexity; Tree mortality

1. Introduction

Classical ecological theory has largely ignored ecosystem structure while emphasizing composition. Yet, the individual and collective architecture of the components is a major factor in biological diversity and ecosystem processes (Harmon et al., 1990; Maser et al., 1988; Hunter, 1993; Spies and Franklin, 1996). The lessons of modern disturbance ecology have important management applications. Natural resource management practices are purportedly modeled on natural disturbances (Attiwill, 1994; Galindo-Leal and Bunnell, 1995; Bergeron and Harvey, 1997). Clear-cutting as a forest harvesting practice leaves little structural complexity that includes living and dead wood. Loss of both horizontal and vertical structural complexity of timber harvest relative to fire disturbance occurs because of the uniformity and

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frequency, and the loss of organic material through timber removal and disposal of woody debris. New forest practices incorporate the retention of structural legacies as part of forest management (Kohm and Franklin, 1996; Franklin, 1997; Watt and Caceres, 1999). For example, retention of large trees, snags (dead standing trees), and logs as well as patches of forest on harvested sites is a major part of Forest Plans for private and public managed forests in North America, South America, Australia and Europe, including Scandinavia (Bergeron et al., 1999).

The self-thinning rule describes a density-dependent upper boundary of stand biomass for even-aged pure stands in a given environment by relating mean plant weight (or total stand biomass per unit area) to stand density on log scales with a constant slope (White and Harper, 1970; Westoby, 1984; Whittington, 1984; Bi et al., 2000). Such invariant scaling relations across forested landscapes implies that standing biomass per area is insensitive to species number, latitude, or elevation, even though tree density increases from northern to southern latitudes (Enquist and Niklas, 2001). As predicted by allometry theory, the number of individuals per sample area scales as the -2 power of stem diameter or as the $-3/4$ power of body mass both within and across communities (Niklas, 1994). Also, a self-thinning relationship suggests that the biomass of trees that die is constant at maximum live tree stand biomass. Thus, the percentage of stems dying decreases as stand biomass increases but the biomass changes over time remains constant (log–log slope). However, a power relationship indicates that stands accumulate biomass faster earlier in their life and older forests show an upper limit for the relationship between density of dead trees and live biomass (i.e., constant rate of mortality of individuals).

Here we ask, what are the implications of macro-scale processes, such as the self-thinning relationship, to the production of snags? Invariant relationships may assist ecological management if unmanaged and managed forests follow similar patterns. We investigated an area of boreal forest in northwestern Ontario to determine the factors important to production of snags and to their size distribution. Factors considered include the amount of living trees (biomass), age, height and forest type (e.g., hardwood or softwood dominated). The forest area we investigated has a 50 years history of forest management ranging from more intensive harvesting in southern areas (starting in the 1950s) to recent (1980s) harvesting of northern areas. We describe the biological legacy of snags in present forests as a result of past forest management practices to understand the processes involved in producing snags and the forest characteristics that relate to snag density, basal area and size-class frequency.

2. Methods

2.1. Study area

The study area was in northwestern Ontario, part of the boreal forest region (50°N, 91°W). Covering 24×10^3 km^2, this area is part of a large physiographic region of postglacial lakes (Rowe, 1972). Located at the southern limit of the boreal forest, the area is characterized by a mixed-wood composition dominated by balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and paper birch (*Betula papyrifera*) with white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*) and jack pine (*Pinus banksiana*) as codominants (Rowe, 1972). Human disturbances (e.g., logging) have transformed the original forest cover in the southern portions of the study area. In the northern portion, human settlement and logging of the forest are at a minimum.

2.2. Sampling design

Stand level patterns of dead/live tree biomass were investigated over the entire forest mosaic. Data were collected at 49,562 field sites that were systematically sampled (2 km grid; 1 cluster/4 km^2) among four Forest Management Units: Black Sturgeon, Brightsand, English River and Caribou. We used a systematic sampling design to cover the range of forest types in each Management Unit. We defined seven forest types based on stand composition: mixed conifer, upland spruce, lowland spruce, jack pine, poplar, hardwood and mixed hardwood. These stand types compose the major cover of the study area in the boreal region.

Stand level forest structure (dbh, age, height) and composition (dead/live, species) were tallied at each sampling station during ground surveys from mid-July to mid-August, 1996–1999. Cluster locations were

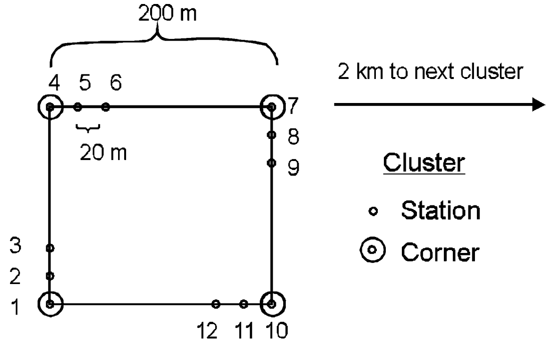

Fig. 1. Sampling design. Clusters were systematically placed at 2 km intervals across the forested landscape. Within clusters, four corners were located in a square pattern (200 m sides) and 12 stations (sampling units) placed 20 m along side transects from corners.

systematically located at 2 km distances to ensure independence (Fig. 1). Measurements were taken at 12 stations (sampling units) within each 4 ha cluster site. Stations were located 20 m apart (except at corners), whereas corners were placed 200 m apart within a square pattern (Fig. 1). Stations were considered the appropriate level (cluster, corner, station) to sample as 83.6% of the variance in basal area occurred at this level (relative to 6.5% at the level of cluster and 9.7% at the level of corner; nested analysis of variance). Diameter increment data were collected for the dominant tree species at each corner. To determine the tree layer basal area, we recorded basal area for each tree species (dead and alive) with a metric factor 2 prism (Grosenbaugh, 1952) at all stations. A "snag" was defined as a self-supporting, standing dead tree >10.0 cm dbh (with or without bark) and >3 m tall. Snag and live tree dbh was measured to the nearest 1 cm using a diameter tape at 1.5 m above ground level. We also determined the height and age of two representative stems per stand with a clinometer and an increment borer, respectively. Measurements of snag stem density (stems/ha) and snag area (m^2/ha) were estimated from fixed area plot tally sheets that recorded species and dbh information within a stand sampling site.

2.3. Statistical analyses

We tests the relative contribution of various factors to the production of snag density (trees/ha) and basal area (m^2/ha). First, a general linear model (PROC GLM: SAS, 1990) was used to measure the effects of live tree basal area, forest type, Forest Management Unit, tree height, and forest age on snag basal area. The explanatory variables were categorized according to density of snags: forest type (jack pine = 1; mixed hardwood = 2; poplar = 3; mixed conifer = 4; spruce upland = 5; spruce lowland = 6); height (< 5 m = 1; 5–10 m = 2; 10–15 m = 3; 15–20 m = 4; > 20 m = 5); Forest Management Unit (English River = 1; Black Sturgeon = 2; Brightsand = 3; Caribou = 4); and ages (0–60 = 1; 60–80 = 2; 80–100 = 3; $> 100 = 4$). The complete set of explanatory variables was examined in all combinations to determine the best model as a compromise between parsimony and bias according to Aikaike information criteria (AIC_c, Burnham and Anderson, 1998). This reduced model was then examined for interactions among explanatory variables.

Next, based on the presence of interactions, we describe the pattern of snag density and basal area across forest types and age.

Last, the relationship (i.e., slope) between live and dead tree basal area was investigated using general linear models. For each forest type ($n = 6$), a model predicting the response of dead tree basal area to the explanatory variables that included forest age (continuous variable) as covariate and live tree basal area × age as an interaction was tested. Also, a predictive model of snag basal area for all data was tested using live tree basal area, forest age, forest type, and their interactions. Slopes and intercepts derived from these general models were used to investigate a possible power law relationship between dead and live trees.

Basal area data were $\log_e$ transformed to meet assumptions of normality. Values reported as mean± 1S.E. are untransformed.

3. Results

3.1. Determinants of snag abundance

Variation in snag abundance was most strongly correlated ($r^2 = 0.68$) with live tree basal area, and secondarily with forest type, forest age, Forest Management Unit, and height of trees (Table 1).

Table 1
General linear model to predict snag basal area according to five explanatory variables: live tree basal area, forest type, Forest Management Unit, tree height, and forest age on snag basal area[a]

Explanatory variable	d.f.	Sum of squares	*F*	*P*
Live basal area	1	3484.73	21846.33	0.0000
Forest type	5	194.64	232.18	0.0001
Age (years)	3	31.64	62.90	0.0001
FMU[b]	3	11.70	23.27	0.001
Tree height (m)	4	11.12	16.58	0.006
Reduced model				
Live basal area	1	4693.04	26649.01	0.0000
Forest type	5	260.81	296.19	0.0001
Age (years)	3	5.74	10.86	0.0001
Forest type × age	15	32.06	12.14	0.0001

[a] The explanatory variables were categorized according to density of snags: forest type (jack pine = 1; mixed hardwood = 2; poplar = 3; mixed conifer = 4; spruce upland = 5; spruce lowland = 6); height ($< 5\,\text{m} = 1$; $5-10\,\text{m} = 2$; $10-15\,\text{m} = 3$; $15-20\,\text{m} = 4$; $> 20\,\text{m} = 5$); Forest Management Unit (English River = 1; Black Sturgeon = 2; Brightsand = 3; Caribou = 4) and ages ($0-60 = 1$; $60-80 = 2$; $80-100 = 3$; $> 100 = 4$). The best model was selected according to AIC_c.

[b] Forest management unit.

Forests with greater live tree basal area and older forests were associated with more snags. The relationship between live and dead tree basal area followed a 3/4 power law with a slope of 0.74. The most parsimonious model included live tree basal area, forest type, and forest age. Not including the tree height was also justified due to a significant positive correlation with forest age ($r^2 = 0.132$, $P = 0.001$), a variable that contributed more to the explained variation. Not including Forest Management Units was also justified, as they were not considered a focus of the current investigations. An interaction was observed between forest type and age; thus, subsequent analyses separated the effect of forest type and age.

3.2. Density of size classes of snags

Distribution of size classes of snags varied with forest age and forest type (Table 2). Overall, greatest number of snag stems (18% of total live and dead trees) occurred in young forests (0–60 years) and thereafter increased from 12% in 61–80-year-old forests, to 15% in 81–100-year-old forests, to 16% in >100-year-old forests. The density of large diameter (>30 cm dbh) snags increased with age of forest from 0.25 stems/ha in 61–80-year-old forests, to 0.33 in 81–100-year-old forests, to 0.38 in >100-year-old forests with the exception of young forests (0–61 years) that had a large number of large diameter snags (0.34 stems/ha; Table 2). The greater density of medium diameter (22–30 cm dbh) snags also occurred in the oldest forests (>100 years), whereas the greater density of small diameter (10–20 cm dbh) snags occurred in 61–80-year-old forests (Fig. 2).

Different forest types produced different distributions of snag sizes (dbh) with age (Table 2). The density of large diameter snags (>30 cm dbh) produced by different forest types followed the same pattern as overall snag density; mixed hardwood produced the most (0.65 stems/ha), followed by poplar (0.48), mixed conifer (0.45), upland spruce (0.16), jack pine (0.06) and lowland spruce (0.02). The exception to this pattern was upland spruce forests that

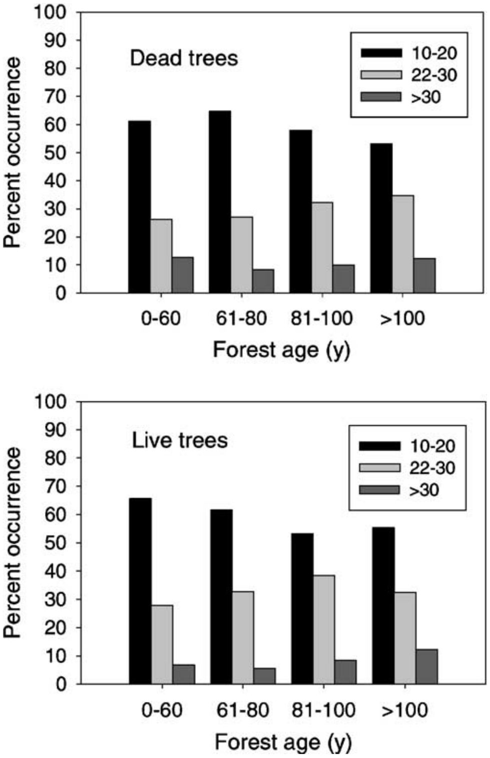

Fig. 2. Distribution of dead and live tree size (dbh) with age of forests (all forest types combined).

Table 2
Distribution of size classes (dbh) of live and dead trees with different forest types and age. Data gathered from managed boreal forest in northwestern Ontario

Forest type	Age	Diameter classes (snags/ha)						Number plots	% dead stems
		10–20		22–30		>30			
		Dead	Live	Dead	Live	Dead	Live		
Mixed conifer	0–60	2.02	11.34	0.98	5.66	0.53	1.26	915	16.2
	61–80	2.44	17.22	0.99	8.92	0.34	1.41	1255	12.1
	81–100	2.28	11.42	1.41	11.18	0.37	2.32	454	14.0
	>100	2.56	8.32	2.32	8.98	0.70	3.64	391	21.0
	All	2.30	13.42	1.22	8.28	0.45	1.79	3015	14.5
Mixed hardwood	0–60	2.58	8.88	1.07	5.80	0.58	1.99	1139	20.3
	61–80	2.38	8.92	1.37	10.48	0.45	3.12	623	15.7
	81–100	2.90	6.72	1.75	9.48	0.92	4.48	301	21.2
	>100	2.28	4.90	1.98	7.16	1.03	5.56	266	23.4
	All	2.54	8.16	1.34	7.68	0.65	3.02	2329	19.4
Poplar	0–60	1.91	7.40	0.68	5.26	0.40	1.49	800	15.7
	61–80	2.28	7.06	1.49	15.46	0.32	4.54	400	13.1
	81–100	3.14	13.04	1.30	15.98	0.60	1.20	494	14.9
	>100	2.44	4.32	1.89	12.88	1.01	8.04	169	17.5
	All	2.06	6.76	1.11	9.18	0.48	3.58	1436	15.7
Jack pine	0–60	0.57	10.62	0.16	2.70	0.04	0.26	1311	5.7
	61–80	3.06	16.90	0.64	13.00	0.06	1.06	1054	12.1
	81–100	3.14	13.04	1.30	15.98	0.06	1.20	494	14.9
	>100	2.84	6.88	2.60	15.30	0.22	3.18	199	22.3
	All	2.00	12.92	0.67	9.22	0.06	0.88	3058	11.8
Spruce lowland	0–60	0.68	8.28	0.18	1.81	0.02	0.15	895	8.0
	61–80	0.93	13.86	0.24	3.68	0.01	0.21	1294	6.3
	81–100	0.92	11.92	0.36	3.30	0.02	0.24	824	7.8
	>100	1.07	12.56	0.42	4.30	0.02	0.18	2234	8.1
	All	0.94	12.06	0.33	3.56	0.02	0.19	5247	7.5
Spruce upland	0–60	1.28	12.58	0.62	3.66	0.19	0.41	1672	11.2
	61–80	1.53	19.38	0.61	5.94	0.15	0.49	2587	8.2
	81–100	1.59	17.38	0.76	7.32	0.16	0.53	992	9.1
	>100	1.81	14.90	0.88	6.86	0.12	0.46	1164	11.2
	All	1.52	16.48	0.69	5.72	0.16	0.47	6415	9.5
Total	0–60	1.65	9.72	0.70	4.10	0.34	0.99	8574	18.2
	61–80	1.97	15.12	0.82	7.02	0.25	1.38	8318	12.4
	81–100	1.94	11.96	1.08	8.62	0.33	1.88	3777	15.0
	>100	1.64	10.76	1.07	6.32	0.38	2.36	5239	15.9
	All	1.72	12.01	0.87	6.46	0.32	1.52	25908	14.6

produced the greatest density of large diameter stems in young (0–60 years) forests (0.19 stems/ha) relative to jack pine (0.04) and lowland spruce forests (0.02).

The distribution of 22–30 cm dbh snags with different forests and ages followed a different pattern than observed for large dbh (>30 cm) trees (Table 2). Old (>100 years) jack pine forests produced the most snags (2.60 stems/ha), followed by mixed conifer (2.32), mixed hardwood (1.98), poplar (1.89), upland spruce (0.88) and lowland spruce (0.42). Jack pine forests produced the greatest number of small snags (10–20 cm dbh) in mature forests (>61 years), and the greatest number of medium sized snags (22–30 cm dbh) in old forests (>100 years; Fig. 3).

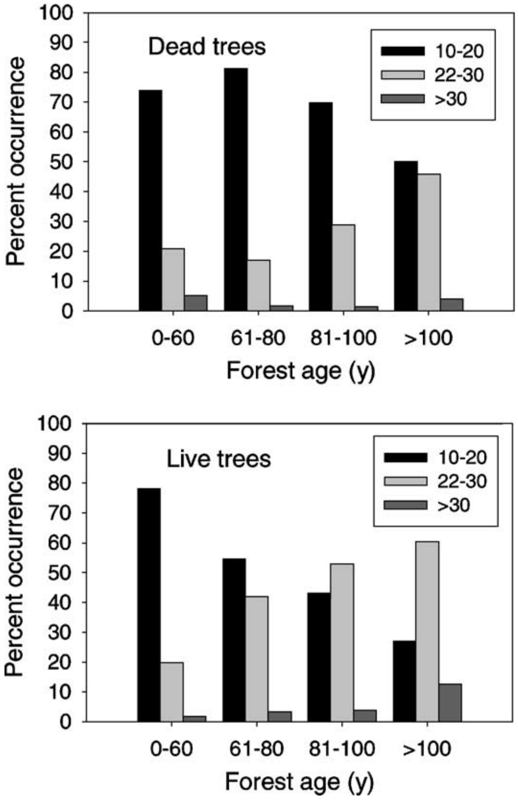

Fig. 3. Distribution of dead and live tree size (dbh) with age of jack pine forests.

3.3. Power relationships

The relationship between dead and live basal areas varied with forest type (Table 3). Age of forests did not significantly affect the dead and live basal area relationship for any of the forest types, although both lowland and upland spruce had a significant interaction affect (Table 3). An interaction (age × living) indicates significant differences in the rate of production of snags with live tree growth (i.e., lower production). Hardwood forests (mixed hardwood and aspen) produced more snag biomass as indicated by larger slopes although y-intercepts were lower indicating that low snag production occurred in slow growing or young forests (Fig. 4). In contrast, spruce forests had smaller slopes and larger y-intercepts indicating lower snag production overall but better snag production in poor growth and young forests. Mixed hardwood produced the most snags (19% of standing trees; Table 2) and lowland spruce forests the least (8%). Whereas, the 3/4 power law relationship held for all data combined, regression coefficients (i.e., slope) of live and dead basal area for individual forest types were generally greater, ranging from 0.79 to 0.93 (with the exception of lowland spruce forests with a slope of 0.67).

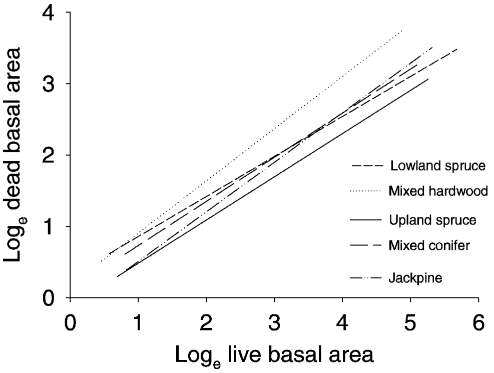

Fig. 4. Regression of dead versus live trees with forest type.

Table 3
Results of general linear models to describe the relationship between dead and living tree basal area for different forest types that included age of forest and age × living (forest age × living tree basal area) interaction

Forest type	Intercept, mean ± S.E.	Slope, mean ± S.E.	Age[a]	Age × living[a]	n	F	P	r^2
Mixed conifer	−0.602 ± 0.0491	+0.852 ± 0.0170	0.44	0.40	1851	5775	0.0000	0.757
Mixed hardwood	−0.727 ± 0.0588	+0.874 ± 0.0215	0.97	0.84	1386	4023	0.0000	0.744
Jack pine	−0.350 ± 0.0560	+0.849 ± 0.0210	0.19	0.17	1552	4609	0.0000	0.748
Poplar	−0.457 ± 0.0899	+0.926 ± 0.0411	0.40	0.24	771	1607	0.0001	0.676
Spruce lowland	−0.0382 ± 0.0620	+0.667 ± 0.0320	0.20	0.001	1808	4010	0.0000	0.689
Spruce upland	−0.230 ± 0.0408	+0.792 ± 0.0236	0.32	0.02	3147	6459	0.0000	0.673
Overall	−0.107 ± 0.0475	+0.743 ± 0.0475	0.0001	0.02	13045	28022	0.0000	0.682

[a] Probability.

4. Discussion

Our results indicate that greater live tree basal area results in greater dead tree basal area and implies that mortality is relatively constant across age of forest. Hence, the relationship between stem growth and death relates to the physiological process of growth (i.e., metabolic efficiency). Metabolic rate is expected to change with the 3/4 power law (Schmidt-Nielsen, 1984; Damuth, 1998), which would explain the 3/4 power relationship between log (dead) and log (live) in our regressions. The log–log regressions following the 3/4 power law underlie a nonlinear pattern. Mortality of individual trees decreases as stands accumulate biomass. However, if stands follow a self-thinning curve, the biomass lost to mortality is constant as biomass accumulates and, therefore, the decline in forest growth does not contribute to increased tree mortality. Among 'juveniles', death from light starvation is the result of extensive canopy overlap. Light attenuation and the number of overlapping canopies above shorter individuals determine the probability of dying. Thus, for all individuals, there is a constant probability of death each time step independent of plant size (i.e., constant hazard rate; Johnson et al., 1995; Ryan et al., 1997; Enquist and Niklas, 2001). These scaling relationships appear to be more statistically robust as the spatial sampling area increases to the community.

In forests, the self-thinning rule defines an upper limit for the relationship between density and biomass that many even-aged stands follow through time (Westoby, 1984; Bi et al., 2000) such that older stands have fewer, larger individuals. Our results indicate a relationship between density of dead trees and living biomass suggesting a pattern of mortality that occurs if a managed stand were moving along a self-thinning trajectory. What we found is that with a unit increase in biomass, the number of stems dying decreases, but the biomass of the trees that die is constant. Because stands accumulate biomass faster earlier in their life, stands following a self-thinning trajectory should show lower mortality when trees are older and growing slowly. Therefore, a constant rate of mortality of individuals could relate to lower productivity in older forests. Enquist et al. (1998) empirical demonstrate that total plant resource use (indirectly estimated as whole-plant xylem transport) scales both within and among species as the 3/4 power of body mass, which is the same exponent as for metabolic requirements. Using this as an intra-specific value, Enquist et al. (1998) predict a thinning exponent of $-4/3$ if resource levels are constant. What this means is that usable energy is being deployed in a variety of growth-form, life history, and wood-density strategies that each amount to varying ways of attaining the same optimal use of energy (West et al., 1999; Whittaker, 1999). Within this seeming evolutionary constraint, there are inter-specific differences in energy allocation over the lifespan that take the form of differing rates of volume growth, differing lifespan and varying reproductive strategies.

Do our results conform to predicted allometric patterns? Inter-specific basal metabolic rate (resting energy use) allometries of animals (Brown et al., 1993) and plants (Enquist et al., 1998) often scale with an exponent of 0.75 (3/4). However, a single regression with a slope of 0.75 does not adequately predict the basal metabolic rate of organisms (e.g., Heusner, 1991). Similarly, our study described different regression lines for dead/live trees indicating the need for other explanations of dead tree biomass variance based on underlying mechanisms such as age and forest type. As forests aged, the regression exponents generally decreased whereas the intercepts generally increased. For different forest types, snag basal area was described by a number of regression lines with different slopes (0.67–0.93) and different intercepts (-0.73–0.04). The overall relationship observed across multiple forest types arises from a series of tighter relationships within communities with grade shifts across communities. Hence, the ratio (dead/live) was relatively constant, a finding reported elsewhere (Spetich and Guldin, 1999; Spetich et al., 1999: log–log slope $= 0.73$).

How do tree mortality patterns relate to ecosystem conservation? Emulating natural disturbance patterns is an overall goal of forest management (Franklin, 1993). Our research did not compare natural disturbance patterns with forest harvesting disturbance patterns; however, the proportion of human disturbance on these forests from 1960 to 1999 was low (16% due to harvesting and 3% due to fire; Ferguson unpublished). Hence, forest management goals should be to maintain a constant production of tree mortality as observed, here, from a semi-natural boreal forest.

Many organisms require snags, including approximately 1/3 of bird species, 1/3 of mammal species (Bunnell and Kremaster, 1990), lichens (Goward and Arsenault, 1997), fungi and invertebrates (Berg et al., 1994). Many species of birds and mammals depend on cavity trees (dead or dying trees with holes in the trunk or main branches) for nesting, rearing young, roosting, feeding, storing food, escaping predators and hibernating (Davis et al., 1983; Harmon et al., 1986; Tubbs et al., 1987; Bull et al., 1997; OMNR, 1999). The availability of tree cavities is thought to be a limiting factor for some populations of several hole-using species (Meredith, 1984; Newton, 1994; Pell and Tideman, 1997). Hence, knowledge of the dynamics of snags as a possible limiting resource will provide the identification of critical components of the environment to individual fitness and facilitate conservation. The length of time that dead trees remain standing, and consequently have the potential to serve as feeding and cavity nesting sites, is largely a function of wood durability (Harmon, 1982; Dickson et al., 1995). Also, the amount of coarse woody debris in a forest depends on processes that affect its accumulation from tree mortality and breakage, as well as processes that affect its loss, such as decomposition, burning, and harvesting. Snag features important for wildlife conservation are linked to disturbance regimes and decomposition rates, which vary with forest stands.

Kozlowski and Weiner (1997) show that interspecific allometries are by-products of biomass distributions of intra-specific production and mortality parameters such that within-species variance reflects selective processes to optimize biomass production and mortality. This model has applicability to managed forests, as different forest stands are adapted to different disturbance regimes, such as fire cycles, and therefore forests are expected to evolve adaptations, including allometries between live and dead production, specific to environmental selection pressures including mortality patterns. Our results from a managed boreal forest suggest that different forest stands show specific allometric relationships between dead and live tree production and that the overall relationship observed across multiple forest types conformed to the 3/4 power law. Despite wide variation in species diversity, abundance, and biomass, managed boreal forest communities were characterized by similar size-frequency distributions of live and dead trees reflecting nearly equivalent standing biomass relationships. Future research is needed to describe differences in tree mortality due to stand-level disturbance (fire or harvesting) over time (e.g., young <60-year-old forests produced the most snags in this region).

This constant ratio of dead/live biomass has management implications. Assuming that site productivity can be improved with management then forest management activities that focus on stand growth (e.g., fertilization, thinning, weeding) may secondarily create structural complexity (i.e., greater snag density and volume). The assumption is that more and larger live trees will, through natural processes of mortality, become large dead trees. Confirmation of this hypothesis requires long-term studies investigating different mortality processes over time (DeBell and Franklin, 1987; Franklin and DeBell, 1988; Hofgaard, 1993) between managed and unmanaged forests in a split-plot experimental design. However, greater production of snags occurred with more productive forests (e.g., hardwood forests relative to lowland spruce forests). Forest management guidelines that incorporate allometric relationships are needed to ensure maintenance of biodiversity and habitat heterogeneity following timber harvesting.

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