# Multi-decade biomass dynamics in an old-growth hemlock-northern hardwood forest, Michigan, USA

I use multi-decade observations of permanent plots in undisturbed mesic forests in northern MI, USA to estimate trends in aboveground living biomass and inputs to the pool of coarse woody debris (CWD). Data from seven plot censuses over 47 years (1962-2009), combined with one-time measurement of CWD pools, help assess landscape biomass/carbon status. I assess whether trends are consistent with traditional notions of late-successional forests as equilibrial ecosystems: specifically, I ask whether biomass pools and CWD inputs show consistent long-term trends and relationships, and whether living and dead biomass pools and trends can be related to forest composition and history. Aboveground living biomass densities, estimated using standard allometric relationships, range from 360-450 Mg/ha among sampled stands and types; these values are among the highest recorded for northeastern North American forests. Biomass densities showed significant decade-scale variation, but no consistent trends over the full study period (one stand, originating following an 1830 fire, showed an aggrading trend during the first 25 years of the study). Even though total above-ground biomass pools have are neither increasing nor decreasing, they have been increasingly dominated, over the full study period, by very large (>70 cm dbh) stems and by the most shade-tolerant species (*Acer saccharum* and *Tsuga canadensis*). CWD pools measured in 2007 averaged 151 m$^3$/ha, with highest values in *Acer*-dominated stands. Snag densities averaged 27/ha, but varied nearly ten-fold with canopy composition (highest in *Tsuga*-dominated stands, lowest in *Acer*-dominated); snags constituted 10-50% of CWD biomass. Annualized CWD inputs from tree mortality over the full study period averaged 1.9-3.2 Mg/ha/yr, depending on stand and species composition. CWD input rates tended to increase over the course of the study. Input rates may be expected to increase over longer-

term observations because, a) living biomass is increasingly dominated by very large trees whose dead trunks have longer residence time in the CWD pool, and b) infrequent major disturbances, thought to be important in the dynamics of these forests, have not occurred during the study period but would be expected to produce major, episodic pulses in CWD input. Few fragments of old-growth cool-temperate forests remain, but such forests can constitute a very large carbon pool on a per-area basis. The carbon sink/source status of these forests remains unclear. While aboveground living biomass at this study site shows no strong aggrading or declining trend over the last half-century, this remains a modest span in the innate time-scale of late-successional forest. The effects of rare disturbances, long-term shifts in composition and size structure, and changes in soil carbon and CWD pools may all influence long-term carbon status.

2  *Multi-decade biomass dynamics in an old-growth hemlock-northern hardwood forest*

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8  *Introduction:*

9  Old-growth temperate forests include stands with the highest known densities of living biomass

10  (Keith, Mackey & Lindenmayer, 2009) and large pools of persistent dead biomass add

11  substantially to total carbon reservoirs. In typical old-growth forests, large individual trees

12  contribute disproportionately to total biomass in the highest-biomass stands (Brown, Schroeder &

13  Birdsey, 1997; Keith et al., 2009; Keeton et al., 2011).  However,  these generalizations are based

14  on a relatively few studies with biomass estimates from direct measurement of trees -- fewer than

15  a dozen from northeastern North America (see below) --  and nearly all of these are based on one-

16  time measurements. Consequently, although several recent authors have suggested that old-

17  growth forests can act as carbon sinks as well as important carbon reservoirs (Keeton et al., 2010,

18  2011), the temporal dynamics of living or dead biomass components have been inferred from

19  modeling of forest growth or from space-for-time substitution.  Models of old-growth systems

20  often assume, explicitly or implicitly, that community and ecosystem processes are in steady

21  state, but the long-term data-sets necessary to assess such assumptions are rare.  A few long-term

22  studies and some simulation models suggest that, in fact, composition may not be steady-state

23  even in old-growth stands (Pacala, Canham & Ribbens, 1996; Woods, 2004, 2007).

24  Consequently, it is important to assess whether ecosystem properties like biomass density also

25  show significant general or predictable trends in old-growth forests.

26  I use data from permanent plots with multiple remeasurements over 47 years to calculate

27  aboveground biomass dynamics in old-growth hemlock-northern hardwood forests in northern

28  Michigan, U.S..  Combined with a one-time measurement of the standing CWD pool, these data

29    allow assessment of behavior of both living and dead biomass and carbon pools in a cool-

30    temperate old-growth forest.

31    Coarse woody debris in (CWD) in hemlock-northern hardwood forests plays an important role in

32    mediating nutrient and carbon cycling   (Liu et al., 2006; Gough et al., 2007), in providing

33    substrate for plant germination and seedling growth (Marx & Walters, 2008; Bolton & D'Amato,

34    2011), and in structuring habitat for many other species  (Harmon et al., 1986; D'Amato, Orwig

35    & Foster, 2009).  Past estimates of  CWD density for old-growth hemlock-northern hardwood

36    forests are generally based on one-time inventories, but variation in rates of CWD input could

37    have far-reaching consequences beyond effects on carbon sequestration.  In old-growth forests,

38    where large logs can persist on the forest floor for decades, historical variation in biomass and

39    CWD dynamics could leave long-persistent signatures.  One-time measurements may, then, be

40    influenced by historical legacies of rare disturbances and not reflect stable conditions.  Mesic

41    forests of the upper Great Lakes region appear to be structured predominantly by wind

42    disturbances of varying intensity and frequency (Brewer & Merritt, 1978; Canham & Loucks,

43    1984; Woods, 2004).  If  biomass and CWD inputs are strongly influenced by rare, severe wind

44    events, they  may be significantly altered by changing frequency and severity of such events due

45    to predicted climate changes.

46    Specifically, I ask:

47    - Do living biomass pools show consistent trends at decadal time scales?

48    - How do inputs of CWD through tree mortality vary over time at decadal scales?

49    - Are historical CWD input rates, consistent with current CWD constituting a steady-state pool?

50    - Are living and dead biomass pools and trends related to forest composition and history in

51    consistent ways?

52    ***Methods:***

53    *Study-sites and field sampling:*

54    Analyses are based on repeated measurements of nineteen 0.2 acre (0.081 ha) circular permanent

55    plots established in 1962 by Eric Bourdo (Ford Forestry Center, Michigan Technological

56 University) within an approximately 5000 ha tract of old-growth forest near Big Bay, MI and

57 within 3 km of the Lake Superior shoreline (approximately 46°52'N 87°54'W). This tract has

58 been owned by the Huron Mt. Club for over 120 years – since before any logging activity in the

59 immediate vicinity -- and has been free from any active management since acquisition.

60 The Bourdo plots are distributed over a range of habitats and community compositions (Fig. 1).

61 Substrate ranges from acidic, rocky soils developed on thin glacial drift over pre-Cambrian

62 granites to coarse sandy soils, to soils on fine-textured alluvial deposits with relatively high

63 cation availability. Canopy composition ranges from strong hardwood (*Acer saccharum*

64 Marshall, *Tilia americana* L.) dominance on high-cation soils to varying mixes of *A. saccharum*

65 and *Tsuga canadensis* (L.) Carrière on other soils (Woods 2000). Three plots are in a *Tsuga*-

66 dominated stand originating following a fire about 1830 (prior to significant European-American

67 presence in the area); all other sampled stands are multi-aged with individual stems exceeding

68 300 yr old and little evidence of strong cohort structuring (K.D. Woods, unpublished increment

69 core data). All live trees greater than 5 inches in diameter at breast height were measured and

70 marked in 1962 and Bourdo and colleagues remeasured live trees in 1967.

71 In 1989, I remeasured the Bourdo plots, mapping all stems > 5 cm dbh for the entire plot and > 2

72 cm for a central sub-plot of 8 m radius. Painted stem-numbers were still visible, allowing

73 tracking of individual trees from earlier measurements. Subsequently, plots have been

74 remeasured every five years through 2009, documenting growth, mortality, and recruitment. In

75 all measurements, dead trees were recorded as dead standing, tipped up, or broken (with height

76 of break).

77 In 2007 I censused CWD on the Bourdo plots. For any piece of down wood partially within the

78 plot and > 10 cm diameter at any point, we measured end diameters and mapped both ends of the

79 piece, recording polar coordinates with a LaserCraft Contour XLRic. Bent or branched CWD

80 segments were subdivided into relatively straight, unbranched segments for mapping. For CWD

81 segments resting on slopes or not resting flat on the ground, we recorded a height (z-coordinate)

82 as well. All CWD segments were, where possible, identified to species and assigned to an

83 identified stem. We measured heights of stumps and diameter at top of stump (approximating top

84 diameter where it was too high to measure directly) and at ground surface (approximating an

85 average diameter where ground surface was irregular). If there was significant basal flare, the

86  stump was divided into segments to reduce non-linearity of taper.   For snags (standing dead trees

87  with bole intact to diameter > 10 cm), we recorded height and diameter at breast height as well as

88  basal diameter.

89  All CWD segments were scored according to a five-point decay classification similar to that used

90  by other researchers (Angers et al., 2005): Class 1, bark intact and tight; Class 2, significant loss

91  of bark, but wood intact or only slightly decayed; Class 3, outer layers of wood clearly soft and

92  decaying, but log structurally intact, rigid; Class 4, decayed and soft throughout, losing structural

93  integrity ('slumping') but still mostly round in cross-section; Class 5, very soft, disintegrating,

94  often moss-covered, no longer round in cross-section  (Fig. 2).  For the last category, diameters

95  were estimated by averaging approximate vertical and horizontal diameters.

96  *Analyses:*

97  *Estimating living biomass and CWD inputs*:  I used published dbh-based allometric equations to

98  estimate above-ground living biomass for all trees > 12.5 cm dbh (to conform with the 5 inch

99  minimum dbh recorded in 1962 and 1967).  Equations were selected from (Jenkins et al., 2004)

100  on criteria including: location of development, favoring equations developed for the upper Great

101  Lakes region; size range, favoring relationships based on samples including large trees; and size

102  of sample used to develop relationships (see Supplemental Table 1 for equations used and

103  original sources).

104  It is not possible to assess either precision or accuracy of resulting estimates, but significant error

105  and bias are probably inescapable.  For some species, equations were not available for the upper

106  Great Lakes region.  No available allometric equations were fitted using trees larger than about

107  70 cm dbh.  For all major canopy species in the current data-set, individuals of >70 cm dbh are

108  relatively common, with maximum sizes around 100 cm dbh, and large trees account for

109  substantial fractions of total biomass.  Where multiple appropriate equations were available, I

110  compared resulting estimates; estimates for trees up to 50-60 cm dbh were generally similar

111  among equations but, for larger stems, they diverged substantially – by as much as 30% for a 90

112  cm stem.

113  Inputs to the CWD pool were estimated using equations for bole biomass only, applied to trees

114    that died during the interval between two measurements.  In most cases, I used dbh from the last

115    measurement before the tree's death, so any growth after that measurement and before death

116    would be small (annual diameter increments for canopy trees in this study average around 1.0-1.5

117    mm/yr depending on species and interval, and growth rates are typically reduced in the years

118    immediately preceding death (Woods 2000)).  However, for the 22-year interval between 1967

119    and 1989, I used diameter measurements of standing dead trees taken in 1989 where loss of bark

120    and decay were not significant.  As much as 30% of above-ground living biomass, in large trees,

121    can be in branches, twigs, and foliage.  However, only the very largest branches would contribute

122    significantly to CWD as measured here, and allometric equations typically do not allow

123    differentiation of branches by size.  The effects of using dbh for up to several years prior to death

124    and of using bole biomass only will result in some systematic underestimation of CWD input

125    rates. CWD inputs are presented as annualized rates, evenly distributed within each interval

126    between measurements.

127    *Estimating CWD volume and mass*:  I estimated volume of individual CWD segments by treating

128    them as regular conic frusta; the height (length) of the frustum was derived from the mapped

129    polar coordinates of the end-points (using three-dimensional coordinates where appropriate).  For

130    CWD segments lying only partially within the plot, I calculated the length within the plot

131    perimeter and estimated diameter at that point assuming linear taper between measured ends;

132    volume was calculated for the portion within the plot only.  Stumps were also treated as frusta (or

133    multiple frusta where flare led to sectioned measurements).  Snag volume was estimated using

134    similar approaches unless appropriate dbh-based allometric equations for bole volume were

135    available (Supplemental Table 1).  CWD volume was converted to dry biomass using taxon-

136    specific relationships between density and decay class from Liu et al. (2006), which uses decay

137    classes nearly identical to those used here.  For unidentifiable CWD fragments (all in decay class

138    3 to 5), I used density values for 'all species'.

139    *Plot groupings:* For comparisons, I used plog groupings based on location, habitat, and canopy

140    composition dominance (see Woods 2000).  The *Acer* group includes plots in two localities with

141    fine-textured, high-cation soils and near-complete hardwood dominance and with maximum ages

142    > 300 years.  The *Tsuga* group includes two plots in a single stand with high hemlock dominance

143    and apparent maximum age of about 300 years (unpublished increment core data).  Six plots on

144    level, coarse, deep sandy soils, with upper canopy dominated by hardwoods but significant

145     subcanopy and codominant *Tsuga* component were initially assigned to a 'mixed flat' group and

146     three plots in areas of shallower soils on moderate slopes and with mixed hardwood-*Tsuga*

147     canopy were treated as a 'mixed slope'. However, all results and trends were very similar for

148     these two groups, and they are pooled here as a single 'mixed' plot group. Finally, three plots in

149     the 1830 burn area (slight to moderate slopes, and strong *Tsuga* dominance) were assigned to the

150     'burn' group.

151     ***Results:***

152     *Aboveground living biomass:* Aboveground living biomass densities at the most recent

153     measurement date ranged from about 360 to 450 Mg/ha within plot groups (Supplemental Table 2

154     for values by species and plot). Trends over 47 years were not consistent over time or among

155     groups (Table 1, Fig. 3). In the *Acer* and mixed groups total change was less than 10% of initial

156     vales, although the mixed group reached a peak biomass density in 1994 nearly 20% greater than

157     the initial value. Both *Tsuga*-dominated groups ('*Tsuga'* and 'burn'), however, showed more

158     consistent and substantial overall increases in biomass, although biomass density in the 'burn'

159     group decreased by about 10% (after a ca. 25% increase) in the last decade of the study.

160     Averaged over all plots, biomass density increased from 358 Mg/ha in 1962 to 378 Mg/ha in

161     2009, but this change is not statistsically significant (paired t-test, $p > 0.05$).

162     The proportion of total biomass in stems > 70 cm dbh, over all plots, increased from 6% in 1962

163     to 14% in 2009 (paired t-test with arcsin conversion, $p<0.01$) (Fig. 4a). *Acer* plots were most

164     strongly dominated by very large trees over the entire study period (Fig. 5), but proportional

165     representation peaked in 1989. *Tsuga* and mixed plots saw more continuous increases in big-tree

166     fractions, while large stems never exceeded 5% of biomass in the 'burn' plots (all individuals > 70

167     cm dbh were *Populus grandidentata* Michx., and all died by 2004).

168     In all plot groups where *Tsuga* had significant presence, it increased as a proportion of total

169     biomass (Fig. 6, Supplemental Table 2). *Acer* biomass changes varied in absolute values, but its

170     proportional importance decreased except in the *'Acer'* plot group. *Betula alleghaniensis* Britton

171     and *Tilia americana* biomass showed varying trends, but increases were generally modest while

172     declines were substantial in some plot groups. Eleven other species (Woods 2000, Supplemental

173     Table 2) reached diameters of 12.5 cm, but, in total, represented no more than 8% of total

174     biomass except in the 'burn' group, where they were 17% of total biomass in 1962 (*Populus*

175     *grandidentata* constituted more than half of this portion).  In all plot groups, representation of

176     minor species decreased consistently and substantially over the course of the study as large stems

177     died without replacement.

178     *Coarse Woody Debris:* Coarse woody debris pools in 2007, including snags, averaged 151 $m^3$/ha

179     (range among plot groups, 119-178 $m^3$/ha) and 46.0 Mg/ha (38-52 Mg/ha) (Table 2, Fig. 7,

180     Supplemental Table 3).  CWD densities were significantly higher in *Acer*-dominated stands, but

181     were not otherwise different among plot groups (p>0.05, Kruskal-Wallis test, *post hoc* Mann-

182     Whitney pair-wise tests with Bonferroni correction). The proportion of CWD in the first two

183     decay classes was substantially lower in the *Acer* group (31% by mass) compared to other groups

184     (47-61%), and highest for the 'burn' group.  Snag densities ranged from 9.9/ha (*'Acer'* group) to

185     98.8/ha ('burn') with an overall average of 27.3/ha.  Snags constituted 10-20% of total CWD

186     biomass for mixed and hardwood dominated plot groups, but 49% for the *'Tsuga'* group and 99%

187     for the burn group (Supplemental Table 3).

188     Annualized inputs to the CWD pool (total stem mass of dying trees divided by length of

189     measurement interval) averaged 1.9-3.2 Mg/ha/yr, depending on plot group, for the entire 47 year

190     period (Fig. 8).  Fluctuations among measurement intervals can be attributed to the effects of

191     occasional large-tree mortality in relatively small sample areas. However, both mixed and*Tsuga*-

192     dominated fire group showed large increases in CWD input in the second half of the study period,

193     from 1989-2009, compared to 1962-1989 (Figure 7, Table 3).  Rates of CWD input nearly

194     quadrupled over the last two decades, compared to earlier decades, for the 'burn' plot group.

195     Overall, annual input estimates averaged 13% of combined mass of CWD in decay classes 1 and

196     2 in 2007.  By plot group this value ranged from 6% ('burn') to 20% ('*Acer*'); these proportions

197     are likely somewhat underestimated because they do not incorporate large branches that included

198     in the CWD pool as measured.

199     ***Discussion***:

200     *Aboveground biomass*: Total aboveground woody biomass estimates for the Huron Mt. stands are

201     among the highest obtained for eastern North American forests.  Other estimates for old-growth

202  hemlock-northern hardwood forests in the upper Great Lakes range from 200 to 325 Mg/ha

203  (Mroz et al., 1985; Morrison, 1990; Rutkowski & Stottlemyer, 1993); all plot groups in this study

204  exceed this range, with maximum values, in the *Acer* and *Tsuga* groups, at 430 Mg/ha, exceeding

205  the highest previous estimates by a third.  These values are comparable to estimates for southern

206  Appalachian cover forests (Busing, 1993) although temperate coniferous forests in the Pacific

207  northwest attain significantly higher biomass densities (e.g., up to 500 Mg/ha in Janisch 2001).

208  These high values could be, in part, an artifact of original plot selection in 1962, which might

209  have favored stands with more undisturbed appearance, while cited studies might be based on

210  less biased site selection or on larger areas of stands encompassing a range of disturbance.

211  However, Lake Superior coastal climates are distinctive, and mesic forests near the lakeshore

212  appear to experience unusually low frequencies of severe disturbance  (Frelich & Lorimer, 1991),

213  permitting high living biomass accumulation.

214  There were no clear, overall trends in biomass density over the full 47 years of the record; rather,

215  biomass dynamics were dominated by shorter-term fluctuations (Fig. 3).  For example, *Acer* and,

216  to a lesser extent, *Tsuga* groups showed sharp decreases in biomass between 1962 and 1967,

217  while all groups increased in biomass density during the long measurement interval from 1967

218  and 1989.  Biomass increases in the first half of the study were proportionally greatest in the

219  'burn' group, and there was virtually no mortality in this group (Woods 2000), suggesting that,

220  150 years after stand initiation, the stand remained in an aggrading phase.  All groups show both

221  increases and decreases in the four 5-year intervals since 1989, and trends are not synchronous

222  among groups or stands.  This pattern suggests biomass dynamics dominated by generally modest

223  but irregular mortality of large trees superimposed on biomass gains through growth of surviving

224  individuals.  After 1990 (about 160 years after stand initiation), the 'burn' stand no longer shows

225  an aggrading trend.

226  However, even though strong trends were not evident in total living biomass,  directional changes

227  are evident in forest structure, with an approximate doubling of proportions of biomass in trees >

228  70 cm dbh (Figs. 4a, 5).  Higher proportions (ca. 30%) of biomass in stems > 70% were

229  observed by Brown et al. (1997) in old forests of the lower midwest, but the largest stems in

230  many of these stands were *Quercus* spp, while intermediate size-classes were dominated by *Acer*

231  *saccharum* and *Fagus grandifolia*, suggesting that large *Quercus* stems were remnants of forest

232  structures established under past, fire-dominated disturbance regimes.  Tyrrell and Crow (1994)

233    suggest that, in *Tsuga*-dominated forests of the upper Great Lakes, significant representation of

234    stems > 70cm dbh indicates stand ages > 275-300 yr.  Here, biomass proportions in this size

235    category approached or exceeded 20% by 2009 for *Acer* and *Tsuga* stands.   The initial presence

236    (and subsequent mortality without replacement -- unpublished results, K. Woods) of large

237    individual trees of shade-intolerant species (*Quercus rubra, Pinus strobus, Populus*

238    *grandidentata*) in the 'mixed slope' group may be the signature of significant disturbance, but

239    cores of late-successional canopy trees > 250 years old suggest that such disturbances were either

240    partial or ca. 300 years ago.

241    Earlier analysis of compositional trends in non-burned plots over the first 32 years of the study

242    suggested gradual competitive displacement of mid-tolerant species (*Betula alleghaniensis, Tilia*

243    *americana*) with increasing dominance of *Acer saccharum* or *Tsuga canadensis*, depending on

244    soil properties (Woods, 2000). Biomass trends described here are consistent with this picture for

245    the full 47 years of the data-set.  In all plot groups, proportional representation of *Acer* and *Tsuga*

246    has increased at the expense of all other species (Fig. 6). This is particularly evident in the 'burn'

247    group, where  proportional representation of *Tsuga* in the living biomass pool has increased

248    continuously, particularly in the last two decades when total biomass has not been increasing

249    consistently.

250    Taken together, these trends are consistent with the interpretation that old-growth hemlock-

251    northern hardwood stands are typically in varying stages of long-term response to intermediate

252    (or, in the case of the 'burn' plot-group and some individual plots, severe) disturbance (Abrams &

253    Orwig, 1996; Woods, 2004, 2007; Bouchard, Kneeshaw & Bergeron, 2006; Stueve et al., 2011).

254    Most notably, in terms of biomass dynamics, an approximate equilibrium in total biomass density

255    is maintained while both size distributions and species representation show directional shifts.

256    *Coarse woody debris:*  Overall, 2007 CWD volume (averaging 151 m$^3$/ha for all plots) and

257    biomass (46 Mg/ha), with about 25% of these values in standing snags, are within the range of

258    earlier findings for old-growth forests of the upper Great Lakes and northeastern forest regions

259    (Hura & Crow; Tyrrell & Crow, 1994; Goodburn & Lorimer, 1998; McGee, Leopold & Nyland,

260    1999; Angers et al., 2005; D'Amato, Orwig & Foster, 2008).  Conifer CWD generally shows

261    lower decay rates than hardwood CWD of comparable size (Harmon et al., 1986).  However,

262    studies comparing total CWD pools between hardwood and conifer-dominated forests have

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263  shown inconsistent results. Most of these, hoever, have focused on  successional or boreal forests

264  (Lee et al., 1997; Pedlar et al., 2002).  Here, the *'Tsuga'* plot group had relatively low CWD

265  densities compared to other groups in this study, while the strongly hardwood-dominated *'Acer'*

266  group had very high values, suggesting substantially higher recent input rates for hardwood

267  stands.  Tyrrell and Crow (1994) show CWD increasing with age in *Tsuga* stands; values here are

268  in the highest range for their study (suggesting stand ages > 300 yr).  CWD densities for the *Acer*

269  group are among the highest published for cool-temperate deciduous forests. These pools are

270  dominated by wood in the most decayed classes, possibly suggesting results of  a significant,

271  landscape-scale disturbance several decades ago; this may be consistent with the sharp decrease

272  in biomass observed for these plots between 1962 and 1967.

273  Inputs of CWD from 1962-2009 averaged 2.5 Mg/ha/yr over all plots -- equivalent to 5.5% of the

274  2007 total CWD pool and 11.7% of the pool of decay classes 1 and 2.  If CWD pools are

275  relatively stable or equilibrial, this implies an average residence time of around two decades

276  overall and one decade in the relatively intact classes 1 and 2.  Few studies have attempted to

277  estimate residence time for CWD in hemlock-northern hardwood forests, and none have used

278  long-term monitoring of mortality to assess input rates, so it is difficult to draw comparisons.

279  However, existing estimates of residence time vary substantially.  Zielonka (2006) estimates

280  residence times of 13 and 24 yrs in classes 1 and 2 in conifer-dominated forests in Poland --

281  substantially longer than turnover times suggested here under steady-state assumptions.

282  However,  estimates from old-growth hardwood forest in Ontario suggest a half-life for 'down

283  woody debris' (exclusive of snags) of ca. 20 yr, with mean age of wood in classes 1 and 2 of three

284  and five years (Vanderwel et al., 2008), and CWD in a logged, successional forest in New

285  Hampshire decreased in mass by 90% in 20 years (Arthur, Tritton & Fahey, 1993).  Given

286  variations in approach (inclusion of snag mass or not, differences in decay class definitions) and

287  coarseness of estimates, these decay rates could be compatible with current CWD pools being in

288  approximately steady-state.

289  Nearly all previous studies of CWD dynamics are based on one-time measurements and space-

290  for-time substitutions; consequently conclusions about trends over time are strongly assumption-

291  laden.  Direct measurement of trends in CWD input, based on long-term permanent-plots with

292  multiple remeasurements, permits an unusual direct assessment of trends.  Most strikingly,

293  overall per-year CWD input increased by nearly half between the first 27 years of the study and

294    the last 20 years (from 2.1 to 3.1 Mg/ha/yr), suggesting non-equilibrial status of biomass and

295    carbon dynamics at decadal scales.  Such trends might be anticipated in cohort-structured stands

296    where one or more cohorts are reaching senescence; consistent with this interpretation, overall

297    canopy-tree mortality rate increased from 0.6%/yr for 1962-1989 to 0.9%/yr from 1989-2009.

298    These increases were most evident  in the youngest stands -- the  'burn' group -- with an increase

299    in CWD input from 0.8 to 3.0 Mg/ha/yr for these two periods, and in the mixed plots (increase

300    2.1 to 3.9 Mg/ha/yr).

301    Over all plots, size distribution of stems contributing to total mortality and CWD input did not

302    show the increasing dominance of large stems seen in the living biomass pool (Fig. 4b), but size

303    distributions of CWD input do suggest an increased importance of smaller to mid-size canopy

304    trees (ca. 25-50 cm dbh) in the last two decades.  This may be due to enhanced mortality of

305    suppressed sub-canopy trees and sub-dominant canopy trees.

306    The '*Acer*' group, with the highest CWD inputs in 1962-1989, and the *'Tsuga'* group showed less

307    change; if these two groups are in approximate steady-state, implied residence time of CWD is

308    about 16 years overall and 5 years in decay classes 1 and 2 for the hardwood-dominated '*Acer*'

309    plots, and about 22 years and 10 years for the *'Tsuga'* group.  This is in keeping with general

310    expectations of more rapid decay of hardwood CWD.  However, calculations based on steady-

311    state assumptions should be approached cautiously; 47 years is much less than half of canopy

312    turnover time estimates for similar forests (Frelich & Graumlich, 1994; Dahir & Lorimer, 1996).

313    However, several factors make these interpretations very tentative.  First,  input estimates here

314    may be low because of exclusion of branch biomass for dying trees.  Second,  changes in size

315    distribution towards increasing dominance of very large stems suggest that CWD inputs will tend

316    to shift to larger-diameter materials, with correspondingly longer residence-times.  Finally, over

317    longer periods, canopy-tree mortality may be dominated by pulses associated with more severe

318    disturbance (Woods 2004, 2007, Frelich & Lorimer 1991).  No such events have occurred during

319    the study period or, as suggested by size and age structures (Woods 2000), in several decades

320    prior to its initiation.  Thus long-term average inputs are likely to be greater than those observed

321    here.  All of these factors suggest that estimates of recent CWD input for the study plots may be

322    an

323    underestimate of longer-term, future inputs.  If so, CWD pools may be expected to increase.

324 *Sources of error and uncertainty:* While the long-term data-set suppporting these analyses

325 supports unusually detailed insight into carbon/biomass dynamics and relationships between tree

326 growth and mortality and CWD pools in old-growth forests, some important uncertainties and

327 potential errors remain.  Two of these are likely most important.

328 First there are large uncertainties connected with biomass estimation for very large trees (>70 cm

329 dbh) that constitute an increasing proportion (up to 30%) of total above-ground living biomass.

330 Until allometric relationships for large stems become available, it will be difficult to reduce this

331 uncertainty.  All estimates of biomass in late-successional forests are subject to the same potential

332 errors.

333 Second, even though the study period of 47 years is unusually long, canopy-tree mortality rates of

334 < 1%/yr indicate that it remains brief in the innate time-scale for dynamics in these forests.

335 Observed dynamics represent less than half of a single generation of canopy trees.  Further,

336 multiple studies have suggested that dynamics in similar forests are strongly influenced by major

337 disturbance episodes with return times measured in centuries (Woods 2004, 2007, Frelich 1991).

338 Such events would have major consequences for CWD dynamics, but none have occurred at this

339 site during the study period.

340 ***Conclusions***

341 These results provide at least partial answers to my four initial questions; all can be more

342 confidently addressed only with longer-term observation:

343 *Do living biomass pools show consistent trends at decadal time scales* in these old-growth, late-

344 successional forests?  Overall, biomass densities observed here are exceptionally high in the

345 context of published estimates for northeastern North America.  However biomass estimates from

346 seven measurements over nearly five decades indicate no consistent long-term trend.  Live

347 biomass pools are neither aggrading or declining overall, but most stands show significant

348 fluctuations at a decadal scale.  Three plots in an even-aged, post-fire stand appeared to be

349 aggrading for the first 25 years of the study, but this trend ended about 1990 (stand age ca. 160

350 yr). These results do not suggest that above-ground living biomass pools are significant carbon

351 sinks, but longer-term studies will be required to make this conclusion with high confidence.

352 Consistent long-term increases in the contribution of very large trees to living biomass indicate

353 non-equilibrial demography and the potential for sharp biomass fluctuations in future decades

354 with mortality of these trees.

355 *What are patterns of CWD input through tree mortality at decadal scales?* Fluctuation in CWD

356 input rates are large, and individual plots are strongly influenced by occasional mortality of large

357 canopy trees. However, in nearly all plot groups, input rates increased significantly from the first

358 27 years of the study to the last 20 years. This pattern is consistent with the suggestion from

359 previous analyses (Woods 2000) that stand dynamics are influenced by episodic events translated

360 through tree demography; in terms of size-structure and species composition these stands may be

361 cohort-structured and non-equilibrial.

362 *Are historical CWD input rates and current CWD pools consistent with a steady-state*

363 *assumption regarding CWD reserves?* Estimates of CWD input and standing volume here do not

364 allow confident projections regarding wheter CWD pools are stable, increasing, or decreasing.

365 However, increasing dominance of large canopy trees (with the longer residence time of larger

366 tree boles in the CWD pool) and the absence of major disturances during the study period to date

367 may be consistent with an expectation of long-term increases in carbon pools in dead biomass

368 may be increasing even if living biomass is not increasing.

369 *How are forest composition and history related to biomass and carbon dynamics?* While total

370 CWD density did not show marked variation among stand types, *Tsuga*-dominated stands

371 exhibited consistently lower input rates. High fluctuation in CWD input rates may be consistent

372 with cohort-structured mortality related to effects of rare disturbances on tree establishment rates

373 (Woods 2000, 2004, 2007), particularly in hardwood-dominated stands.

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376 Technological University; information about plot location and data from 1962 and 1967

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378 Approximately 25 Bennington College undergraduate students have participated in field

379    measurements since 1989.  The Huron Mt. Wildlife Foundation has provided logistical support

380    through the facilities of the Ives Lake Research Station.

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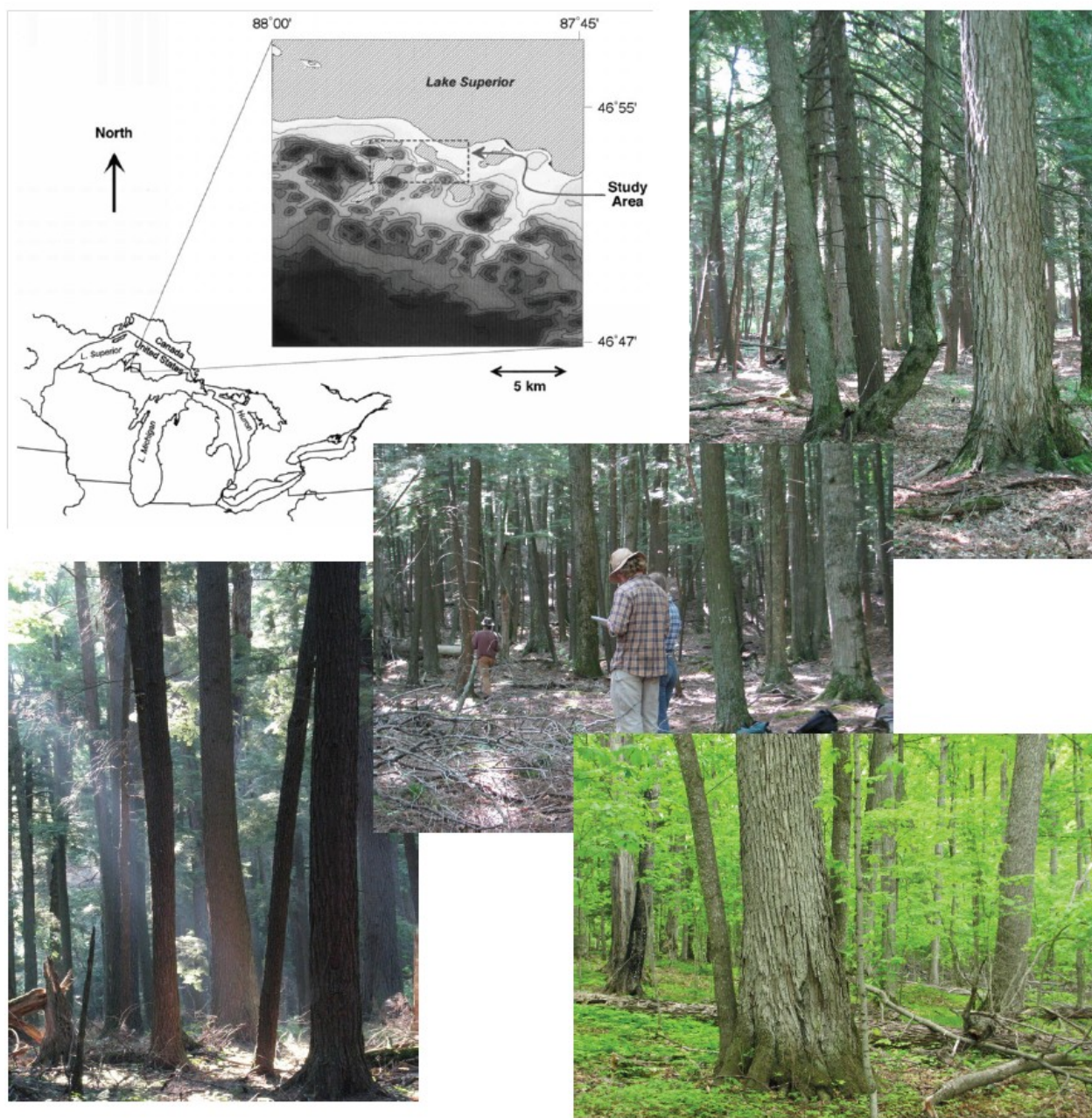


Fig. 1: Examples of community composition represented by plot groupings for analyses: mixed conifer-hardwood stands (upper right), *Acer*-dominated hardwoods (bottom right), *Tsuga*-dominated (bottom left), and plots burned in 1830 with *Tsuga* dominance (center). Inset shows Huron Mts. study area with local topography (Lake Superior surface elevation is 180 m asl; the highest areas in the study area inset are about 550 m asl). (all photos by Kerry Woods)

Fig. 2: Examples of decay classes used in classifying CWD. Clockwise from upper left: recently fallen *Acer saccharum*, class 1; *Acer saccharum* log in class 2; *Tilia americana* log in class 5, *Acer saccharum* log in class 3 or 4. (all photos by Kerry Woods)

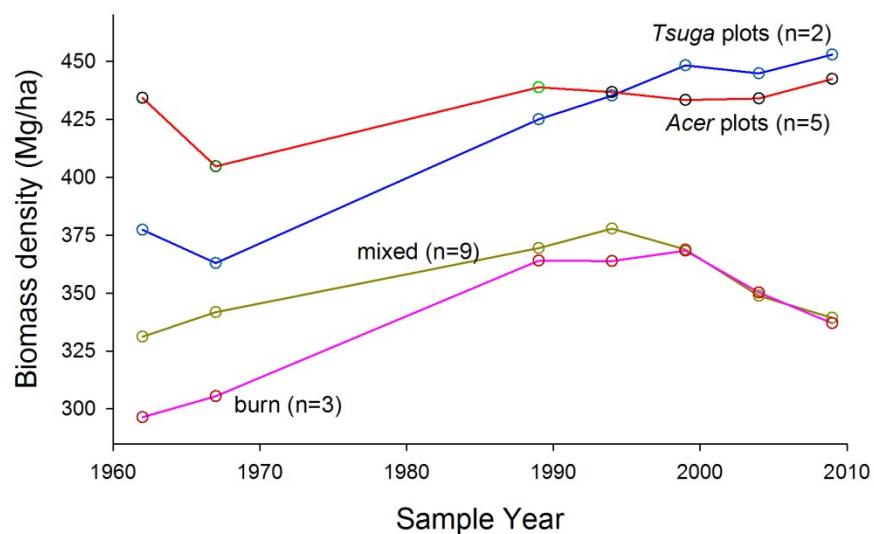
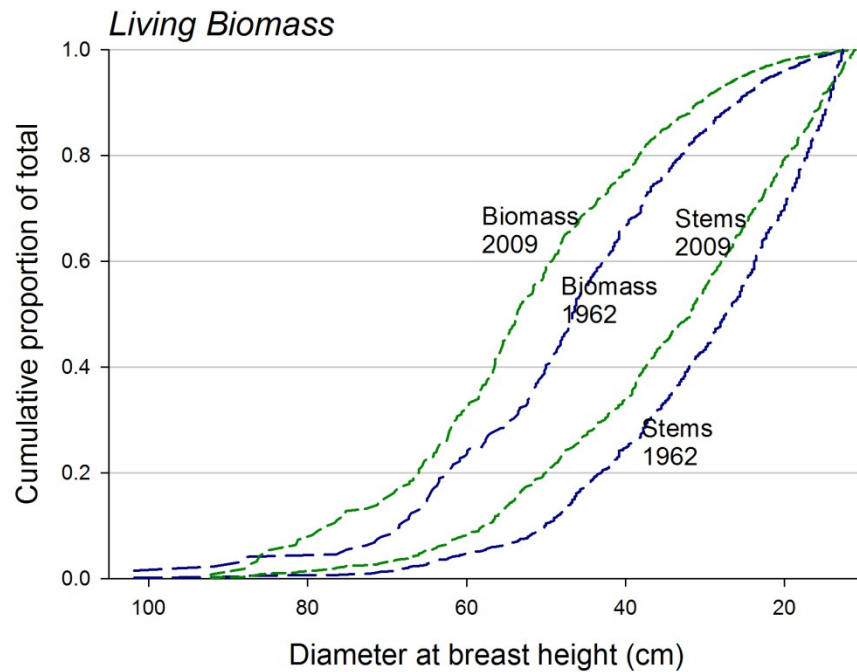



Fig. 3: Trends in above-ground living biomass over time and among composition-based plot groups.  Overall average biomass density increased slightly, from 358 Mg/ha to 378 Mg/ha from 1962 to 2009.  All plot groups show changes in direction of change over time.  Highest values, for strongly *Acer* and *Tsuga*-dominated stands, are among the highest reported for eastern North America.

382  A.

B.

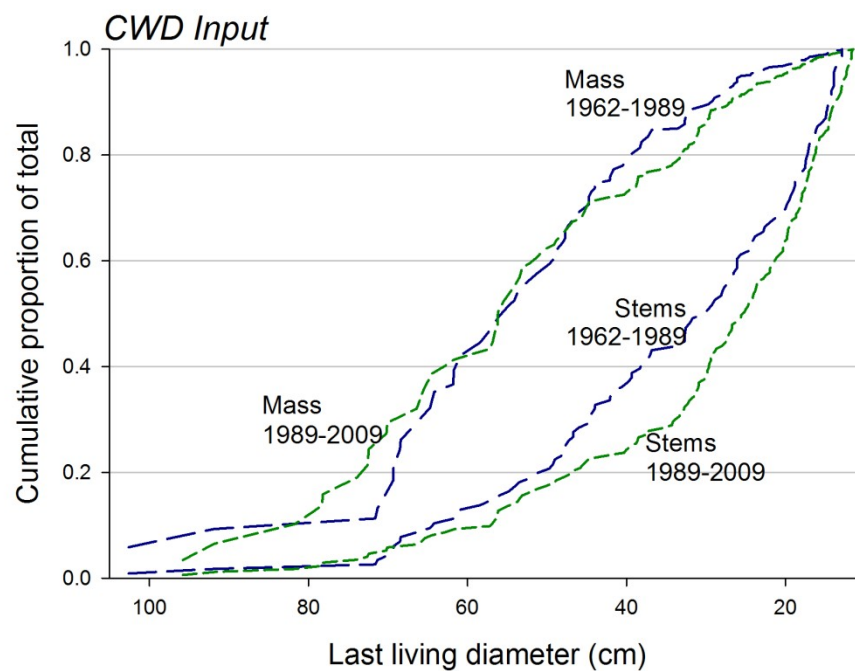



Fig. 4: Cumulative distribution of BM and CWD input with respect to tree size. Large
trees increasingly dominate both living biomass and stem density over the study period
(A), but CWD inputs through mortality do not show similar trends (B). Cumulative
curves (from largest to smallest stems) for total biomass and stem density are higher for
2009 over nearly the full span of stem diameters (A). CWD input curve for the first 27

years of the study does not differ from curve for the last twenty years; numerically, mid-size canopy trees dominate inputs in the earlier period, but smaller stems dominate in the later period (B).

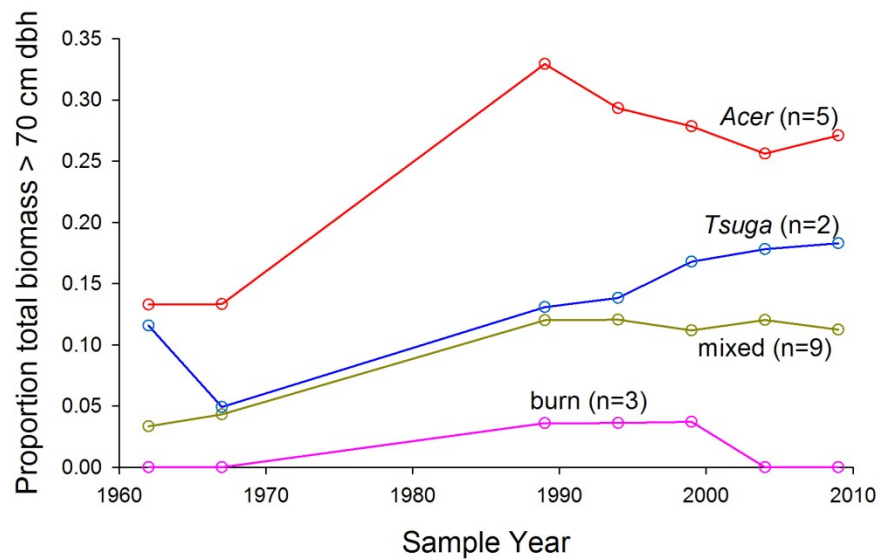



Fig. 5: Proportion of living biomass in large trees (>70 cm dbh) increases over time for all plot groups except the 'burn' group.  Mortality of early-successional species accounts for the loss of large trees in the burn group after 1999.

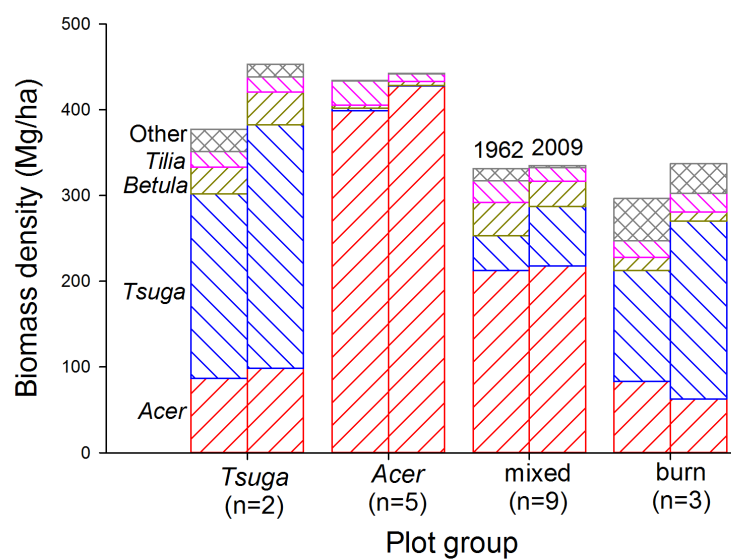



Fig. 6: In all plot groups, the most shade-tolerant canopy species (*Tsuga canddensis* and *Acer saccharum*) increasingly dominate biomass pools over the course of the study. *Tsuga*, where present, shows the largest proportional increase, while other species show generally decreasing biomass contributions.

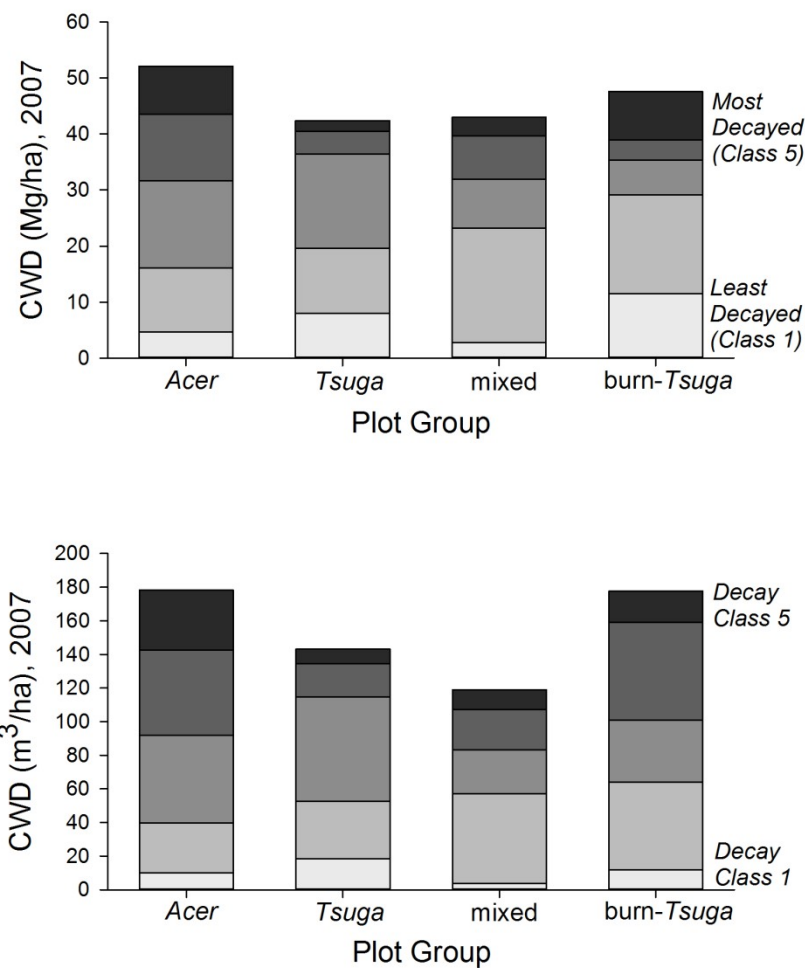



Fig. 7: Coarse woody debris (CWD) pools in 2007 were highest in *Acer*-dominated plots in both total mass and voume. *Acer* plot group CWD pools -- composed entirely of hardwood species -- are proportionally more dominated by more fully decayed material.

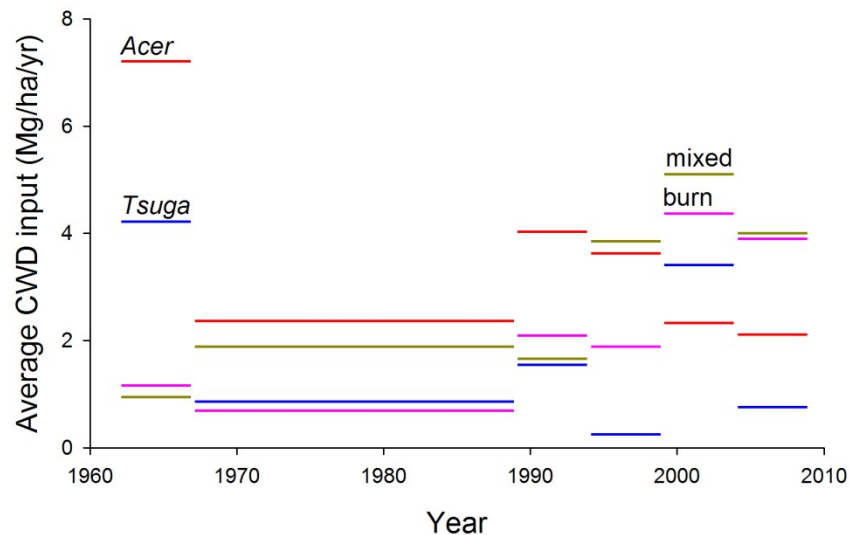



Fig. 8: Annualized coarse woody debris (CWD) inputs, estimated as bole mass of trees dying during each measurement period, are generally higher during the last two decades than for the first 27 years of the study. No systematic differences in trend are evident among plot groups. Mass of trees dying during each measurement period is allocated uniformly across years within the measurement period.

Table 1: living biomass by plot group, yr

## Table 1: Total aboveground biomass, stems > 12.5 cm dbh (Mg/ha)

| | Year | | | | | | |
|---|---|---|---|---|---|---|---|
| **Plot Group** | 1962 | 1967 | 1989 | 1994 | 1999 | 2004 | 2009 |
| *Acer* (n=5) | 434.2 | 404.7 | 438.8 | 436.7 | 433.3 | 434.0 | 442.4 |
| *Tsuga* (n=2) | 377.3 | 363.0 | 425.0 | 435.2 | 448.2 | 444.8 | 452.9 |
| Mixed (n=9) | 331.2 | 341.8 | 369.5 | 377.9 | 368.9 | 348.9 | 339.4 |
| burn (n=3) | 296.5 | 305.5 | 364.0 | 363.9 | 368.3 | 350.3 | 337.0 |

Table 2: Coarse woody debris, average values by plot group, 2007

| | Decay Class | | | | | |
| Plot Group | I | II | III | IV | V | Total |
|---|---|---|---|---|---|---|
| **I. CWD volume (m³/ha)** | | | | | | |
| *Acer* (n=5) | 10.0 | 29.8 | 52.2 | 50.7 | 35.6 | 178.3 |
| *Tsuga* (n=2) | 18.5 | 34.0 | 62.3 | 19.8 | 8.6 | 143.2 |
| Mixed (n=9) | 6.4 | 53.0 | 29.6 | 35.5 | 14.1 | 138.6 |
| burn (n=3) | 26.5 | 45.9 | 22.8 | 17.1 | 37.8 | 150.1 |
| **II. CWD dry biomass (Mg/ha)** | | | | | | |
| *Acer* (n=5) | 4.7 | 11.4 | 15.5 | 11.9 | 8.5 | 52.1 |
| *Tsuga* (n=2) | 8.0 | 11.7 | 16.8 | 4.0 | 1.9 | 42.4 |
| Mixed (n=9) | 2.8 | 20.5 | 8.7 | 7.8 | 3.3 | 43.0 |
| burn (n=3) | 11.5 | 17.6 | 6.2 | 3.6 | 8.6 | 47.6 |

Table 3: CWD inputs by plot group and period

*CWD input (Mg/ha/yr)*

| Year | 1962-67 | 1967-89 | 1989-94 | 1994-99 | 1999-2004 | 2004-2009 | Overall | 1962-1989 | 1989-2009 |
|---|---|---|---|---|---|---|---|---|---|
| *Acer* (n=5) | 7.21 | 2.44 | 4.03 | 3.60 | 2.33 | 2.33 | 3.21 | 3.32 | 3.10 |
| *Tsuga* (n=2) | 5.78 | 0.92 | 1.82 | 0.31 | 3.77 | 2.03 | 1.89 | 1.82 | 1.96 |
| Mixed (n=9) | 0.95 | 2.04 | 1.73 | 3.87 | 5.11 | 3.68 | 2.59 | 1.84 | 3.40 |
| burn (n=3) | 1.18 | 0.72 | 2.68 | 2.05 | 4.30 | 4.09 | 1.86 | 0.81 | 3.00 |