Late-Successional Biomass Development in Northern Hardwood-Conifer Forests of the Northeastern United States

William S. Keeton, Andrew A. Whitman, Gregory C. McGee, and Christine L. Goodale

Abstract: Managing the contribution of forest ecosystems to global carbon cycles requires accurate predictions of biomass dynamics in relation to stand development. Our study evaluated competing hypotheses regarding late-successional biomass dynamics in northern hardwood-conifer forests using a data set spanning the northeastern United States, including 48 mature and 46 old-growth stands. Continuous data on dominant tree ages were available for 29 of these and were used as an indicator of stand development. Aboveground live biomass was significantly ($P < 0.001$) different between mature (195 Mg/ha) and old-growth (266 Mg/ha) sites. Aboveground biomass was positively ($P < 0.001$) and logarithmically correlated with dominant tree age; this held for live trees ($r^2 = 0.52$), standing dead trees ($r^2 = 0.36$), total trees ($r^2 = 0.63$), and downed woody debris ($r^2 = 0.24$). In a Classification and Regression Tree analysis, stand age class was the strongest predictor of biomass, but ecoregion and percent conifer accounted for ~25–33% of intraregional variability. Biomass approached maximum values in stands with dominant tree ages of ~350–400 years. Our results support the hypothesis that aboveground biomass can accumulate very late into succession in northern hardwood-conifer forests, recognizing that early declines are also possible in secondary forests as reported previously. Empirical studies suggest a high degree of variability in biomass development pathways and these may differ from theoretical predictions. Primary forest systems, especially those prone to partial disturbances, may have different biomass dynamics compared with those of secondary forests. These differences have important implications for both the quantity and temporal dynamics of carbon storage in old-growth and recovering secondary forests. FOR. SCI. 57(6):489–505.

Keywords: aboveground biomass, northern hardwoods, stand development, carbon cycles, old-growth

MANAGING THE CONTRIBUTION OF FOREST ECO-SYSTEMS to global carbon budgets requires accurate predictions of biomass dynamics in relation to stand development and management. Accurate predictions have become particularly pertinent with the development of domestic and international carbon markets and proposals for forest sector participation in both voluntary and compliance systems (Ruddell et al. 2007, Ray et al. 2009b). There remain critical issues regarding the long-term net effects of different forest management approaches, such as intensive versus less intensive management, on carbon sequestration and storage (Harmon et al. 1990, Thornley and Cannell 2000, Harmon and Marks 2002). Consideration of alternate management systems often entails a projection of long-term in situ forest biomass accumulation under a "no management" scenario, and comparison of this trajectory with carbon storage in multiple sinks (e.g., forest, wood products, or landfills) under active harvest scenarios (Harmon et al. 2009, Nunery and Keeton 2010). Estimating the carbon storage capacity of recovering secondary forests, such as those now dominant in the northeastern United States, similarly necessitates estimation of biomass dynamics in relation to forest stand development processes (Brown et al. 1999). Consequently, improving our understanding of carbon storage dynamics in primary (i.e., never cleared), old-growth, and unmanaged forests has become increasingly important for characterizing these baseline, reference, and future potential conditions (Hudiburg et al. 2009, Keith et al. 2009, Rhemtulla et al. 2009).

Forest Biomass and Stand Development

For decades, models relating biomass development to forest age for northern hardwoods have been based on ground-breaking research performed in the 1970s at the Hubbard Brook Experimental Forest in New Hampshire, USA. This widely cited model, developed by Bormann and Likens (1979), predicts peaks in biomass after less than two centuries (approximately 170 years) of stand development, followed by declining biomass in stands 200–350 years of age, and "steady-state" biomass dynamics in stands >350 years of age. Bormann and Likens broke this timeline into four phases of development, which they called "reorganization," "aggregation," "transition," and "steady state." Net ecosystem productivity (NEP) was predicted to decline to zero "at full maturity" (Odum 1969, Whittaker et al. 1974). Biomass accumulation curves for the first two development stages were based on empirical data collected in secondary

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stands located at Hubbard Brook and elsewhere. Biomass dynamics projected for the latter stages of development were largely theoretical, although grounded in observational studies and derived from predictions made by the JABOWA model (Botkin et al. 1972), one of the early gap-based forest succession simulators.

Bormann and Likens (1979) cited a lack of old-growth forests in the northeastern United States as the reason for relying on theoretical projections for late-successional biomass development models. But since the 1970s researchers have discovered and mapped more old-growth in the Northeast than was previously known to exist (McMartin 1994, Davis 1996, D'Amato et al. 2006). For instance, by some estimates there are more than 80,000 ha of old-growth forest in the Adirondack region of New York alone, one of the largest concentrations east of the Mississippi River (Dunwiddie et al. 1996). These forests span a wide range of sites and biophysical diversity and thus are not anomalous (e.g., restricted to inaccessible or low-productivity sites) but are in fact representative of landscape-scale ecological variability (McMartin 1994). More than 30 years of research has described the structural characteristics (e.g., Tyrrell et al. 1998, Hale et al. 1999, McGee et al. 1999, Ziegler 2000, Keeton et al. 2007, Whitman and Hagan 2007), successional dynamics (e.g., Foster 1988, Abrams and Orwig 1996, Goodburn and Lorimer 1999, McLachlan et al. 2000), and disturbance regimes (e.g., Runkle 1982, Ziegler 2002, Lorimer and White 2003, D'Amato and Orwig 2008) of late-successional/old-growth northern hardwood-conifer forests. These studies allow us to revise our understanding of late-successional forest dynamics using real-world reference stands and empirical rather than theoretical data.

Competing Hypotheses Describing Biomass Dynamics in Relation to Forest Age

Studies conducted in primary (never cleared, but containing a mix of successional stages) and old-growth (a stand development condition) forests have provided different and sometimes conflicting perspectives on late-successional biomass dynamics. For example, research in the US Upper Midwest (Tyrrell and Crow 1994) showed basal area peaks somewhat later than predicted by Bormann and Likens (1979), achieving maximum values in 230- to 260-year-old forests, but with subsequent declines in older forests. In contrast with Tyrrell and Crow (1994), Ziegler (2000) showed continued basal area increases in a chronosequence spanning forest ages in excess of 400 years, with little evidence of asymptotic relationships or declines as age increased. There is also growing recognition of the potential for continued net positive carbon uptake (NEP) very late into stand development in temperate forests globally (Pregitzer and Euskirchen 2004, Luyssaert et al. 2008, Keith et al. 2009), although this has been poorly explored in northern hardwoods specifically. Taken together, this body of literature supports a hypothesis that there may be potential for biomass accumulation in northern hardwoods of both greater magnitude and duration than previously recognized.

A competing hypothesis is offered by recent work at Hubbard Brook, based on long-term plot remeasurements in the unmanipulated (or control) watershed (W6). These have shown biomass accumulations slowing much earlier than expected, leveling off after only 80 years of stand development (Fahey et al. 2005, Siccama et al. 2007). Live tree biomass actually decreased over the most recent remeasurement period (1997–2002); total biomass (including standing dead trees) continued to increase. Fahey et al. (2005) suggested a number of possible explanations for the trends they detected, including growth reductions due to acid deposition, declines caused by beech bark disease (*Nectria* spp.), altered stand development processes related to land use history, and the possibility of climate change effects. However, they could not reject the possibility that biomass accumulation potential in secondary forests may be lower than previously predicted. Remaining unexplored is whether the biomass dynamics observed in primary forests reflect fundamentally different stand development processes than those in secondary forests.

Biomass curves based on the Bormann and Likens (1979) model continue in use as the basis for regional carbon budget assessments and methodologies for estimating future forest carbon storage potential (e.g., Turner et al. 1995, Smith et al. 2006). The curves also underpin algorithms used in individual tree-based forest growth and development models (Dixon 2002, Ray et al. 2009a), which are increasingly relied on to predict carbon storage under alternate forest management strategies (Nunery and Keeton 2010). Because of their wide use and importance to carbon budget estimation, ensuring their accuracy has taken on new significance. In this study, we examine whether generalized biomass curves are sufficiently representative or predictive of biomass dynamics playing out across the northern hardwood region. We evaluate the competing hypotheses described above and include our own empirical evidence, exploring biomass relationships in a data set spanning most of northern New York and New England.

Determination of Tree and Stand Ages

In this study we examine stand age-related trends for a subset of our data points. However, assigning an "age" to primary northern hardwood forests can be problematic. Unlike western temperate coniferous forests, in which stand origin often can be traced to a single high severity or "stand-replacing" fire event (Keeton and Franklin 2004, 2005), return intervals for stand-replacing disturbances, such as hurricanes, in northern hardwoods often exceed 1,000 years (Seymour et al. 2002, Lorimer and White 2003). These are more than double the maximum lifespans of the constituent late-successional tree species. Structure and age distributions in primary temperate hardwoods are shaped, rather, over centuries by high- to moderate-frequency partial disturbances, such as gap-forming events, that result in fine- to intermediate-scaled regeneration and release effects (Hanson and Lorimer 2007, D'Amato and Orwig 2008).

Methods for assigning "stand age" in primary northern hardwood systems typically require an estimation of the age of canopy trees, either as an average for all codominant and dominant trees over a given minimum diameter (e.g., Woods and Cogbill 1994) or as an average of the largest,

dominant trees (e.g., Keeton et al. 2007, Stovall et al. 2009). For all of these methods, the result is an estimate of canopy tree age, rather than time since high-intensity disturbance. Determination of tree ages in old-growth stands is challenging because of the prevalence of rotten heartwood. Repeated coring is usually required to obtain a single intact core. However, coring the largest trees increases the precision of stand age estimates from relatively small samples because of the close correspondence between age and diameter for the larger trees in uneven-aged stands (Leak 1985). In this study we determined the average ages of the largest trees, and thus our ages are weighted toward the maximums encountered in the sample trees. We use the term "dominant tree age," recognizing that our values are not true estimates of stand age but rather more probably are an indicator of variation in disturbance history, large tree survivorship, and related degree of stand structural development. We propose that this is as a useful analytical approach for comparing old forest sites and assessing development potential and related ecological processes (see, e.g., Stovall et al. 2009, Warren et al. 2009).

Because of the difficulties associated with age determination, many forest inventory data sets have assigned sites or plots to age classes (e.g., mature versus old-growth). Previous studies (e.g., McGee et al. 1999, Goodale and Aber 2001), consequently, often have used categorical comparisons, rather than modeling age relationships using continuous variables. In this study, we use a combination of both methods depending on the available age data. Using mature stands as a benchmark for comparison against old-growth helps contrast the conditions encountered in different age classes. These contrasts probably would be even more distinct if old-growth structure were compared with young and partially harvested forest stands (McGee et al. 1999, Crow et al. 2002, Angers et al. 2005).

Methods
Overview of Data Sets and Study Region

Our study combined data from four existing data sets, hereafter referred to as the "Goodale," "Keeton," "McGee," and "Whitman" data sets. The data set includes 94 independent data points, 46 old-growth and 48 mature sites (Table 1). It thus provides a robust sampling of the remaining old-growth forests in the Northeast. For the purposes of our study, we defined "old-growth" as primary (never cleared) forest with dominant canopy trees >150 years of age and uneven-aged (more than three age classes) structure. Our "mature" forest designation refers to stands that are approximately 80–150 years of age, exhibiting even to multiaged (two or three age classes) structure. The mature stands originated after logging and human-caused wildfires in the late 19th and early 20th centuries and have had little or no logging since establishment, which minimizes variability associated with management history. Our sites included both northern hardwood-dominated as well as mixed-wood stands (see Table 1 for data on conifer percentages by site), with varying components of *Betula alleghaniensis* (yellow birch), *Fagus grandifolia* (American beech), *Acer saccharum* (sugar maple), *Acer rubrum* (red maple), *Picea rubens*

(red spruce), *Tsuga canadensis* (eastern hemlock), and *Abies balsamea* (balsam fir). There were scattered *Pinus strobus* (eastern white pine), including remnant old-growth trees, at some sites.

Collectively our data set provides a well-distributed, representative sample of the northern hardwood region of the northeastern United States. The data focus on three subregions within this area, the Adirondack Mountain region of upstate New York, the White Mountains of New Hampshire, and the west-central highlands to northern hills of Maine. For clarity throughout the article we refer to these respectively as "New York" (Keeton and McGee data sets), "New Hampshire" (Goodale and Whitman data sets), and "Maine" (Whitman data set). These subregions share a moist temperate climate characterized by cold winters and warm summers, with even distribution of precipitation throughout the year. Surficial geology within our study areas is dominated by postglacial plateaus, hills, and montane landforms with relatively fertile soils derived primarily from glacial and alluvial tills and deposits.

Data Collection

Site selection and sampling methods differed for each of the four data sets, and thus are described separately. Sample sizes by state and biomass variable are provided in Table 2.

Keeton Data Set

The Keeton data set includes data from 29 sites, 19 of which were described in Keeton et al. (2007); 10 sites were sampled subsequently. These sites were selected from the available known occurrences of old-growth and comparable secondary forests within the Adirondack region based on site-matching criteria described in Keeton et al. (2007). The sites, sampled in 2002–2006, are located along 200- to 300-m-long, first- and second-order stream reaches. Elevations ranged from 450 to 600 m. At each site forest structure and composition (live and standing dead trees >5 cm dbh) were sampled within 6–10 (proportionate to reach length) variable radius (2.3 metric basal area factor) prism plots randomly placed within 30 m of the stream bank (well distributed, even ratio per side). Tree heights were measured in alternating plots with an Impulse 200 Laser Rangefinder; snags were assigned to decay stages (1–9). Downed coarse woody debris (DCWD) (downed logs ≥10 cm diameter at intercept, ≥1 m length) volume by decay class (1–5) was measured along multiple, systematically placed transects using the line-intercept method and layout scheme described in Keeton et al. (2007). Transects were 200- to 300-m-long, depending on reach length. Age at breast height was determined from increment cores for four to six randomly selected, large dominant *B. alleghaniensis*, *P. rubens*, or *T. canadensis* at each site. Cored trees were randomly selected from among the larger canopy dominants. Ages were estimated in the field following McGee et al. (1999), with one core per site randomly selected and returned to the laboratory for examination, after sanding and mounting, under a dissecting microscope to assess field error (mean = ±9 years; SD = ±5).

Table 1. Site information, including data on stand structure and composition.

Site	Data set	State	Ecoregion[1]	Age class	Percent conifer	Aboveground live tree biomass (Mg/ha)	Basal area (live) (m²/ha)	Stem density (live) (trees/ha)
Mountain Pond	Whitman	ME	M212A	Old-growth	0.00	305.09	35.10	467
Deadriver4	Whitman	ME	M212A	Mature	29.20	390.58	51.70	683
Deadriver5	Whitman	ME	M212A	Mature	41.75	209.67	32.00	600
Little Bigelow	Whitman	ME	M212A	Old-growth	5.92	225.19	31.83	600
Borestone Mtn. 1	Whitman	ME	M212A	Old-growth	23.45	224.15	29.98	517
Borestone Mtn. 2	Whitman	ME	M212A	Old-growth	0.00	226.26	26.99	417
Greatpond9	Whitman	ME	M212A	Mature	0.00	205.32	29.74	583
Kibby1244	Whitman	ME	212B	Mature	3.51	191.44	24.86	333
Kibby1508	Whitman	ME	212B	Mature	11.90	202.27	26.42	333
Merrill1	Whitman	ME	212B	Mature	0.00	121.30	15.77	267
PiercePond1	Whitman	ME	M212A	Mature	0.00	284.32	36.84	717
Skinner153	Whitman	ME	M212A	Mature	0.00	189.19	25.90	550
Skinner267	Whitman	ME	212A	Mature	17.10	175.43	26.17	633
T11R15 WELS0	Whitman	ME	M212A	Mature	12.38	339.51	44.85	933
T11R15 WELS1	Whitman	ME	M212A	Old-growth	8.18	333.28	37.65	383
T11R15 WELS4	Whitman	ME	M212A	Old-growth	52.35	245.97	37.70	633
Yankeetuladi	Whitman	ME	M212A	Old-growth	2.53	266.05	32.33	617
Yankeetuladi	Whitman	ME	M212A	Old-growth	0.00	163.69	22.34	433
T28MD27	Whitman	ME	M212A	Mature	0.00	121.08	15.57	300
T29MD30	Whitman	ME	M212A	Mature	12.97	224.59	33.26	917
T2R4BKPWKR	Whitman	ME	M212A	Mature	9.52	224.83	29.84	500
T3R8 WELS	Whitman	ME	212C	Old-growth	3.06	232.90	31.20	617
Boody Brook	Whitman	ME	212C	Old-growth	8.09	568.85	64.17	733
Big Reed 1	Whitman	ME	M212A	Old-growth	2.10	370.67	43.48	583
Big Reed 2	Whitman	ME	M212A	Old-growth	15.74	318.03	41.20	667
Big Reed 3	Whitman	ME	M212A	Old-growth	35.12	410.30	54.57	717
Big Reed 4	Whitman	ME	M212A	Old-growth	50.63	104.21	16.45	367
Big Reed 5	Whitman	ME	M212A	Old-growth	64.17	158.81	27.26	533
Big Reed 6	Whitman	ME	M212A	Old-growth	0.00	348.49	38.93	383
T8R16 WELS9	Whitman	ME	M212A	Mature	0.00	317.33	39.30	583
T9R10 WELS13	Whitman	ME	M212A	Old-growth	7.48	314.68	40.30	633
T9R8 WELS10	Whitman	ME	M212A	Mature	56.18	215.04	34.11	700
T9R8 WELS14	Whitman	ME	M212A	Mature	21.56	145.78	20.08	400
WELD5	Whitman	ME	M212A	Mature	0.00	169.46	22.90	383
WYMAN130	Whitman	ME	M212A	Mature	23.56	343.11	39.58	500
Bartlett26	Whitman	NH	M212A	Old-growth	20.77	361.67	48.25	717
Bartlett40	Whitman	NH	M212A	Old-growth	5.06	297.50	35.92	417
Carrabasset11	Whitman	NH	M212A	Mature	13.70	221.55	63.60	1,350
The Bowl 1	Whitman	NH	M212A	Old-growth	10.77	256.34	34.15	550
Lafayette Brook	Goodale	NH	M212D	Old-growth	7.46	287.57	33.85	363
Gibbs Brook	Goodale	NH	M212D	Old-growth	10.21	200.58	24.76	375
Glen Boulder	Goodale	NH	M212D	Old-growth	15.43	251.14	29.61	600
Spruce Brook	Goodale	NH	M212D	Old-growth	0.00	316.92	35.10	775
The Bowl 2	Goodale	NH	M212D	Old-growth	0.00	250.25	30.46	588
Mt. Bickford	Goodale	NH	M212D	Mature	1.77	170.45	31.58	313
Zealand Valley	Goodale	NH	M212D	Mature	0.00	186.70	28.74	550
George's Gorge	Goodale	NH	M212D	Mature	0.00	233.05	32.25	663
Wild River	Goodale	NH	M212D	Mature	0.00	204.51	29.37	1,213

(*Continued*)

McGee Data Set

McGee collected data from seven old-growth and four mature study sites in upland Adirondack northern hardwood old-growth forests, sampled in 1995–1997. Sites were located on mid to upper slope positions at elevations ranging from 470 to 770 m. Stand structural and compositional data for live and standing dead trees >10 cm dbh were collected on two 0.1-ha (20 × 50 m) randomly established sample plots at each site. Length and end diameters were measured for downed log sections and stumps >10-cm diameter within nested subplots or across the whole 0.1-ha area

depending on log diameter (see McGee et al. 1999). Structural and compositional data for six of the seven old-growth stands and the four maturing (postfire, 90- to 100-year-old) stands are reported by McGee et al. (1999). Insufficient data are available to estimate dominant tree age for the McGee sites.

Whitman Data Set

Whitman collected data from 20 old-growth and 20 mature study sites in upland northern hardwood forests in

Table 1. Site information, including data on stand structure and composition (*cont*).

Site	Data set	State	Ecoregion[1]	Age class	Percent conifer	Aboveground live tree biomass (Mg/ha)	Basal area (live) (m²/ha)	Stem density (live) (trees/ha)
Mt. Chocorua	Goodale	NH	M212D	Mature	0.00	124.93	23.48	613
Cascade Brook	Goodale	NH	M212D	Mature	4.82	227.80	29.77	400
Mt. Tom	Goodale	NH	M212D	Mature	2.18	139.67	21.20	425
Lost Pond	Goodale	NH	M212D	Mature	0.00	188.96	29.12	613
Carter Dome Tr.	Goodale	NH	M212D	Mature	13.10	265.25	35.07	488
Mt. Paugus	Goodale	NH	M212D	Mature	10.30	180.38	32.59	875
Ampersand Mt.	McGee	NY	M212D	Old-growth	12.99	357.57	39.55	380
Gill Brook	McGee	NY	M212D	Old-growth	15.33	258.01	31.20	405
Whalestail Mt.	McGee	NY	M212D	Old-growth	3.24	356.50	38.25	345
Huntington 1	McGee	NY	M212D	Old-growth	4.85	234.93	28.30	405
Sucker Brook	McGee	NY	M212D	Old-growth	3.26	267.56	31.90	470
Mason Lake	McGee	NY	M212D	Old-growth	4.88	328.56	36.70	370
Moose Mountain	McGee	NY	M212D	Old-growth	2.57	358.70	38.95	405
Bigsby Pond	McGee	NY	M212D	Mature	7.80	220.21	29.90	500
Van Hoevenberg	McGee	NY	M212D	Mature	0.00	198.00	24.55	390
Hennessy Mt.	McGee	NY	M212D	Mature	0.00	240.84	34.10	650
Gooseberry Mt.	McGee	NY	M212D	Mature	0.00	207.25	27.85	490
Constable Inlet	Keeton	NY	M212D	Mature	61.00	130.17	23.30	714
Darby Brook	Keeton	NY	M212D	Mature	19.00	145.62	22.60	555
Pigeon Lake	Keeton	NY	M212D	Mature	84.00	135.26	26.40	1,380
Witchopple 1	Keeton	NY	M212D	Old-growth	34.00	165.99	26.80	827
Witchopple 2	Keeton	NY	M212D	Mature	45.00	160.08	27.20	1041
Combs Brook	Keeton	NY	M212D	Mature	13.00	150.15	21.90	563
Clearlake Outlet	Keeton	NY	M212D	Old-growth	36.00	188.26	29.30	1,398
Clearlake 2	Keeton	NY	M212D	Old-growth	29.00	201.04	31.80	1,627
Panther	Keeton	NY	M212D	Mature	29.00	178.27	27.30	848
Oxbow	Keeton	NY	M212D	Mature	34.00	126.62	21.60	951
Limekiln	Keeton	NY	M212D	Old-growth	33.00	241.52	37.50	1,348
Limekiln Trail	Keeton	NY	M212D	Old-growth	14.00	176.86	27.10	1,062
Little Moose Trib 1	Keeton	NY	M212D	Old-growth	44.00	195.66	29.30	609
Otter Brook	Keeton	NY	M212D	Mature	32.00	190.52	31.40	733
Little Moose Outlet	Keeton	NY	M212A	Old-growth	43.00	232.17	35.30	710
Little Moose Trib 6	Keeton	NY	M212A	Old-growth	70.00	341.76	51.40	705
Little Moose Trib 5	Keeton	NY	M212A	Mature	68.00	191.19	32.50	748
Upper Sylvan	Keeton	NY	M212A	Old-growth	59.00	214.97	33.30	1,010
Little Moose Trib 3	Keeton	NY	M212A	Mature	88.00	89.81	19.10	820
Dutton Brook	Keeton	NY	M212A	Old-growth	69.00	262.03	37.90	602
Beth's Brook	Keeton	NY	M212A	Mature	18.00	138.60	21.40	497
Camp Nine	Keeton	NY	M212A	Mature	57.00	127.63	24.10	661
Arbutus Outlet	Keeton	NY	M212A	Mature	3.00	195.54	29.50	731
Wolf Lake Outlet	Keeton	NY	M212A	Mature	45.00	171.06	32.10	2,572
Huntington 2	Keeton	NY	M212A	Old-growth	27.00	193.66	26.30	472
Huntington 3	Keeton	NY	M212A	Old-growth	68.00	206.81	32.10	406
Pico	Keeton	NY	M212A	Mature	7.00	147.46	23.00	1,222
McKenna	Keeton	NY	M212A	Old-growth	50.00	212.70	31.10	843
MellonBerry	Keeton	NY	M212A	Old-growth	75.00	217.35	33.50	792

[1] M212 = New England-Adirondack Province: M212A, White Mountains section; M212D, Adirondack Highlands section; 212 = Laurentian Mixed Forest Province: 212A, Aroostook Hills and Lowlands section; 212B, Maine-New Brunswick Foothills and Lowlands section; 212C, Fundy Coastal and Interior Section

Maine (Whitman and Hagan 2007). Sampling was conducted in 2003 and 2004. Sites occurred on elevations ranging from 150 to 700 m and on mesic slopes and hilltops. Previous researchers had visited the old-growth sites and established the lack of human and catastrophic disturbance and the fact that tree ages exceeded 150 years (Maine Critical Areas Program 1985). Whitman sampled all old-growth northern hardwood stands in the study area that could be relocated using existing reports. Mature stands were randomly selected from stand maps for selected large (>100,000 ha) landowners dispersed across central and northern Maine. Live and standing dead trees (≥10 cm dbh,

at a height of 1.37 m) were measured in a randomly established 0.06 ha (3 × 200 m) plot at each site. DCWD (≥10 cm intercept diameter, ≥1 m in length) was sampled using the line intercept method (Van Wagner 1968) on a 200-m transect. Tree age data were not collected at the Whitman sites.

Goodale Data Set

Study site selection, location, and sampling design for the Goodale data set are described in detail in Goodale and Aber (2001). Five study areas in the White Mountains of

Table 2. Results of Tukey tests comparing biomass characteristics in mature (80- to 150-year-old, even to multiaged) versus old-growth (>150 years old, uneven-aged) northern hardwood-conifer forests.

	Aboveground biomass								
	Means		95% Confidence Intervals (±)		Sample size (*n*)		Statistical results		
	Mature	Old-growth	Mature	Old-growth	Mature	Old-growth	*T* critical	*T* statistic	*P*
	. . . .(Mg/ha)								
Live Trees									
Region	194.95	266.33	17.56	23.65	48	46	1.663	−4.749	<0.001
ME	226.13	283.33	36.05	51.93	18	17	1.699	−1.774	0.043
NH	194.84	277.75	24.47	34.09	11	8	1.761	−3.872	<0.001
NY	165.49	248.22	17.22	27.17	19	21	1.692	−5.041	<0.001
Standing dead									
Region[1]	21.49	41.44	4.07	7.89	37	38	1.673	−4.407	<0.001
ME	20.82	36.78	7.06	12.81	18	17	1.708	−2.139	0.021
NY	22.12	45.21	4.43	9.79	19	21	1.701	−4.212	<0.001
Total									
Region[1]	216.48	305.37	22.43	29.93	37	38	1.668	−4.659	<0.001
ME	246.95	320.11	37.45	54.62	18	17	1.699	−2.165	0.019
NY	187.61	293.43	18.38	31.70	19	21	1.694	−5.660	<0.001
Downed coarse woody debris									
Region[1]	27.10	35.94	5.07	4.79	37	38	1.666	−2.569	0.006
ME	24.16	28.15	6.00	6.12	18	17	1.692	−0.985	0.166
NY	29.88	42.25	8.47	6.21	19	21	1.691	−2.467	0.009

Sample sizes varied because of differences among the four subregional data sets. Comparisons were significant at $\alpha = 0.05$.

[1] Includes Maine and New York only; sufficient sample sizes were not available for New Hampshire for these variables.

New Hampshire were identified from historical maps, each containing sites originating from fires or logging (the mature sites) or in old-growth. There was one location at each study area for each of the three site histories, for a total of 15 sites (10 mature and 5 old-growth). Elevations ranged from 600 to 700 m; the sites were sampled in 1996. At each site, two randomly placed, 20 × 20-m (0.04-ha) plots were established on drained, midslope topographic positions. dbh and species were recorded for all live trees >9.5 cm dbh and 1.37 m in height. The data set does not include data for standing dead trees, DCWD, or tree ages, and thus sample sizes in the regional data set are lower for those variables.

Data Analysis

Our analysis consisted of four elements designed to evaluate the competing hypotheses regarding late-successional biomass development in northern hardwoods. These were 1) processing and standardization of field data to generate a regional-scale set of biomass estimates and stand structure metrics, 2) comparisons of age classes to provide a regional perspective based on the available categorical data (see Table 2 for sample sizes), 3) regression modeling of biomass in relation to dominant tree age for the subset of sites ($n = 29$) from which continuous age data were available, and 4) a multivariate analysis to test the sensitivity of biomass estimates to multiple sources of variability ($n = 94$). These elements are described sequentially below. All statistical analyses were run in TIBCO Spotfire S+ 8.1. Tests were significant at $\alpha = 0.05$.

Field data from the four data sets were processed in either Microsoft Excel (Goodale, McGee, and Whitman data sets) or the Northeast Ecosystem Management Deci-

sion Model (Keeton data set) (Twery et al. 2005) to generate a suite of stand structure biometrics. All tree-related metrics were standardized to a >10-cm dbh minimum size threshold. Aboveground tree biomass estimates were calculated from dbh measurements using species-specific allometric equations. For the Keeton, McGee, and Whitman data sets, the equations followed Jenkins et al. (2003). The Goodale data were processed using equations from Whittaker et al. (1974) with modifications by Siccama et al. (1994) for yellow birch, sugar maple, American beech, and red spruce; equations from Hocker and Early (1983) were used for paper birch (*Betula papyrifera*), red maple, aspen (*Populus tremuloides*), and eastern hemlock.

DCWD volume estimates were calculated differently for line-intercept versus fixed-area plot surveys. The former relied on equations from Warren and Olsen (1964) as modified by Shivers and Borders (1996), whereas the latter used geometric equations described in McGee et al. (1999). Our procedure for converting DCWD volumes to biomass involved two steps. First, we conducted an analysis using the subset of sites (New York) for which decay class data were available. Decay class-specific conversion factors (i.e., specific gravity values) from Harmon et al. (2008) were applied to the volume data sorted by age class. Then we calculated an average conversion factor that accurately estimated biomass for each age class, given the differences in decay class distributions (see Results below). These values were 0.325 and 0.285 g/cm³ for mature and old-growth, respectively, and were consistent with conversion factors generated from bulk density measurements of DCWD in the Adirondacks (McGee et al. 1999). In the second step, volume data for all the sites were converted to biomass using these age class-specific values.

We used linear regression modeling to analyze relationships between dominant tree age and biomass/stand structure variables. Alternate curve-fitting techniques were used to assess the relative fit of linear, logarithmic, polynomial (second to fourth order), and negative exponential curves, applied as transformations of the dependent variable. Residuals were plotted and examined for evidence of heteroscedasticity. Where nonlinear curves explained equal or greater variance compared with a linear trend and where asymptotic relationships were the most mechanistically plausible, we selected the nonlinear (in all cases logarithmic) curve as the final model.

We used Tukey honestly significant difference tests, assuming unequal variance for all categorical comparisons of biomass and stand structure variables by age class (mature versus old-growth) and state. We also used Tukey tests and one-way analysis of variance to examine differences in basal area estimates between data sets as a function of sampling intensity and subregion. Basal area was selected as the indicator metric for these analyses because of its sensitivity to sampling intensity in spatially heterogeneous systems (Shivers and Borders 1996).

For the final step in our analytical procedure we conducted a classification and regression tree (CART) analysis. This allowed us to examine the relative influence of forest age class versus ecoregion and the proportion of conifers (by basal area) at each site (independent variables) on aboveground biomass (dependent variable). Sites were assigned to ecological units (sections) according to the National Hierarchy of Ecological Units (Table 1) following Smith and Carpenter (1996). Our rationale was that subregional ecological variability (e.g., climate, soils, productivity, and disturbance regime) might account for variability in biomass levels independent of forest age class (McNab et al. 2007). Likewise, the shade-tolerant conifer component in mixed stands or increasing late in succession has the potential to influence biomass development (Stoy et al. 2008). Because our sites encompass a range of percent conifer values, it was important to distinguish this source of variability from the effects of forest age. CART is robust, a nonparametric, binary procedure, accommodating both categorical and continuous variables (De'ath and Fabricius 2000). The procedure hierarchically partitions values of the independent variables through successive splits based on the amount of variance explained in values of the dependent variable. We used cost-complexity pruning to eliminate nonsignificant nodes. CART was not used in our study to establish definitive threshold values for the predictor variables. Rather, CART provided a way to rank the relative predictive strength of the independent variables of interest.

Results

Categorical Comparisons between Mature and Old-Growth Forests

Old-growth sites in our data set had significantly higher mean levels of aboveground tree biomass in comparison with mature stands. This held true for live, standing dead, and total (live + standing dead) tree biomass as well as for DCWD. We found old-growth biomass to be significantly greater at both subregional and regional scales (Table 2). As an average for the region, old-growth forests contained 266 and 41 Mg/ha of live and standing dead aboveground tree biomass, respectively. These values were compared with regional means of 195 (live) and 25 Mg/ha (standing dead) for mature stands. Thus, the mature (80- to 150-year-old) stands contained 73% of the live biomass and 61% of the standing dead tree biomass found on average in old-growth forests. The biomass contrasts were consistent with other measures of structural complexity. For instance, basal areas (live and standing dead), large tree densities (live and standing dead), and quadratic means diameters were all significantly greater in old-growth compared with mature forest sites. Stem densities were not significantly different between age classes.

Although the biomass means were statistically different, there was considerable variation across the region. For example, mature live tree biomass ranged from 90 Mg/ha at a site in New York to as high as 391 Mg/ha in a productive, well-developed stand approaching 150 years of age in Maine. Old-growth live tree biomass, in comparison, ranged from 104 Mg/ha at a recently disturbed site to 569 Mg/ha, a value almost twice the regional average for old-growth; both sites were in Maine. The highest average live tree aboveground biomass levels for old-growth were reached in Maine (283 Mg/ha), with New Hampshire (278 Mg/ha) intermediate and New York (248 Mg/ha) the lowest, although these subregional means were not statistically different. Live biomass in mature forests was proportionately lowest, relative to that in old-growth, in New York (67%) compared with New Hampshire (70%) and Maine (80%); again these contrasts between subregions were not statistically significant.

Both DCWD volume and biomass were significantly greater in old-growth relative to that in mature forests for New York and the region; DCWD biomass was not significantly different between age classes for Maine although volumes were (Table 3). Regional mean volumes were 83 m³/ha in mature stands (or 32% lower) compared with 122 m³/ha in old-growth stands. The mature sites in New York had a larger percentage (55%) of DCWD volume in less-decayed classes (1–2), whereas old-growth sites had a larger proportion (61%) in well-decayed classes (3–5). Biomass contained in the downed log pool represented 11.1 and 10.5% of the total aboveground biomass (DCWD + live and standing dead trees), not including understory vegetation and fine litter, for mature and old-growth stands, respectively. Thus, we did not find a significant difference between age classes in DCWD biomass as a proportion of total aboveground biomass. Old-growth stands had significantly higher mean DCWD biomass values (36 Mg/ha) in relation to mature stands (27 Mg/ha). Like the other structural variables, DCWD biomass varied widely throughout the region and within age classes (Table 2). Levels ranged from 6 to 71 Mg/ha for mature stands and from 11 to 65 Mg/ha for old-growth, similar ranges although the means differed. At the subregional scale, New York had higher DCWD biomass levels than Maine for both mature and old-growth sites; these differences were statistically significant.

Biomass Development in Relation to Dominant Tree Age

Aboveground tree biomass showed positive relationships with dominant tree age for our sites in the Adirondack region of New York (Figure 1). There were significant relationships for live ($r^2 = 0.52$, $P < 0.001$), standing dead ($r^2 = 0.36$, $P < 0.001$), and total ($r^2 = 0.63$, $P < 0.001$) aboveground tree biomass. In each case we fitted logarithmic curves to the data because these explained the greatest amount of variation, although linear trends exhibited similar correlation coefficients. The logarithmic curves exhibited moderately strong asymptotic relationships, showing evidence of leveling off at values close to 280, 230, and 50 Mg/ha for total, live, and standing dead aboveground tree biomass, respectively, in stands with dominant tree age >400 years. However, the trend lines did not reach clear asymptotes over the range of dominant tree ages evaluated, suggesting the potential for continued net positive biomass accumulations into greater ages. There was no evidence of peaks or declines in biomass before the maximum dominant tree age achieved in the data set. This conclusion was based on fitting polynomial curves capable of detecting such relationships. The regression results were limited by the relative lack of data points for age values between 150 and 250, although the 205-year-old site had aboveground live biomass very close to the trend line (Figure 1). Although the predicted biomass trends for this gap in the age range are similar to basal area trends previously reported for the Adirondacks (Ziegler 2000), we cannot rule out the possibility that the asymptote is reached earlier than predicted by our regression equations.

The strong positive relationship between biomass and dominant tree age reflects, in part, the increasing density of large trees (>50 cm dbh) as stands develop (Figure 2). Large tree densities were strongly related to dominant tree ages based on regression results. A logarithmic curve explained the greatest variation for live large trees ($r^2 = 0.64$, $P < 0.001$), whereas a linear relationship had the best fit for large standing dead trees ($r^2 = 0.41$, $P < 0.001$). Large tree density is, in turn, strongly correlated ($r^2 = 0.48$, $P < 0.001$) with aboveground biomass, as demonstrated by a regression of live large density against live tree biomass across all 94 sites in our data set (Figure 2, bottom panel). Neither total (all sizes) live tree nor total standing dead densities were significantly correlated with age across the age range examined, with linear regressions exhibiting slopes near zero.

That total aboveground biomass is increasing across the range of dominant tree ages in our data set is demonstrated also by the positive relationship between age and DCWD biomass (Figure 3). Although DCWD biomass was highly variable among sites, a logarithmic curve explained 24% of the variation in the relationship with dominant tree age. DCWD biomass approached an asymptote of approximately 55 Mg/ha in stands 400 years of age or older, but like standing tree biomass, did not level off over the range of ages assessed. Thus, continued DCWD biomass accumulations are possible into older dominant tree ages.
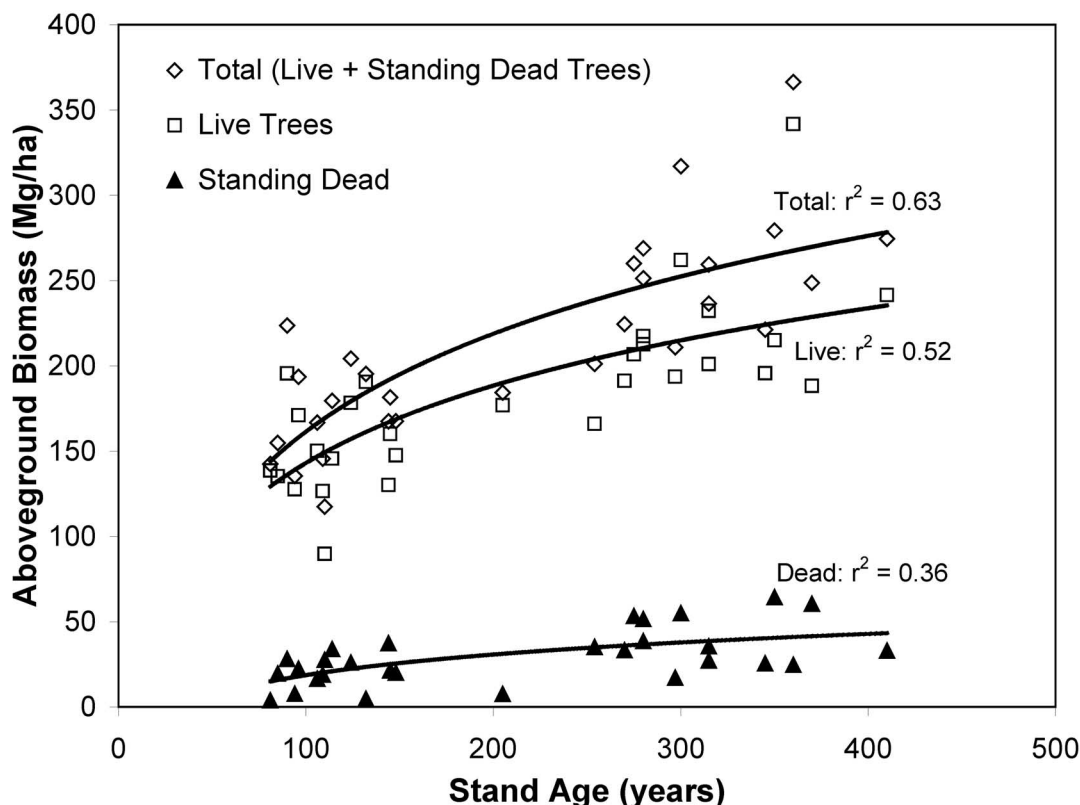

Figure 1. Aboveground biomass in relation to dominant canopy tree age in the Adirondacks, New York ($n = 29$). Shown are logarithmic models for live [$y = 65.39\ln(x) - 158.19$], standing dead [$y = 17.389\ln(x) - 61.633$], and total [live + standing dead, $y = 82.779\ln(x) - 219.83$] trees.
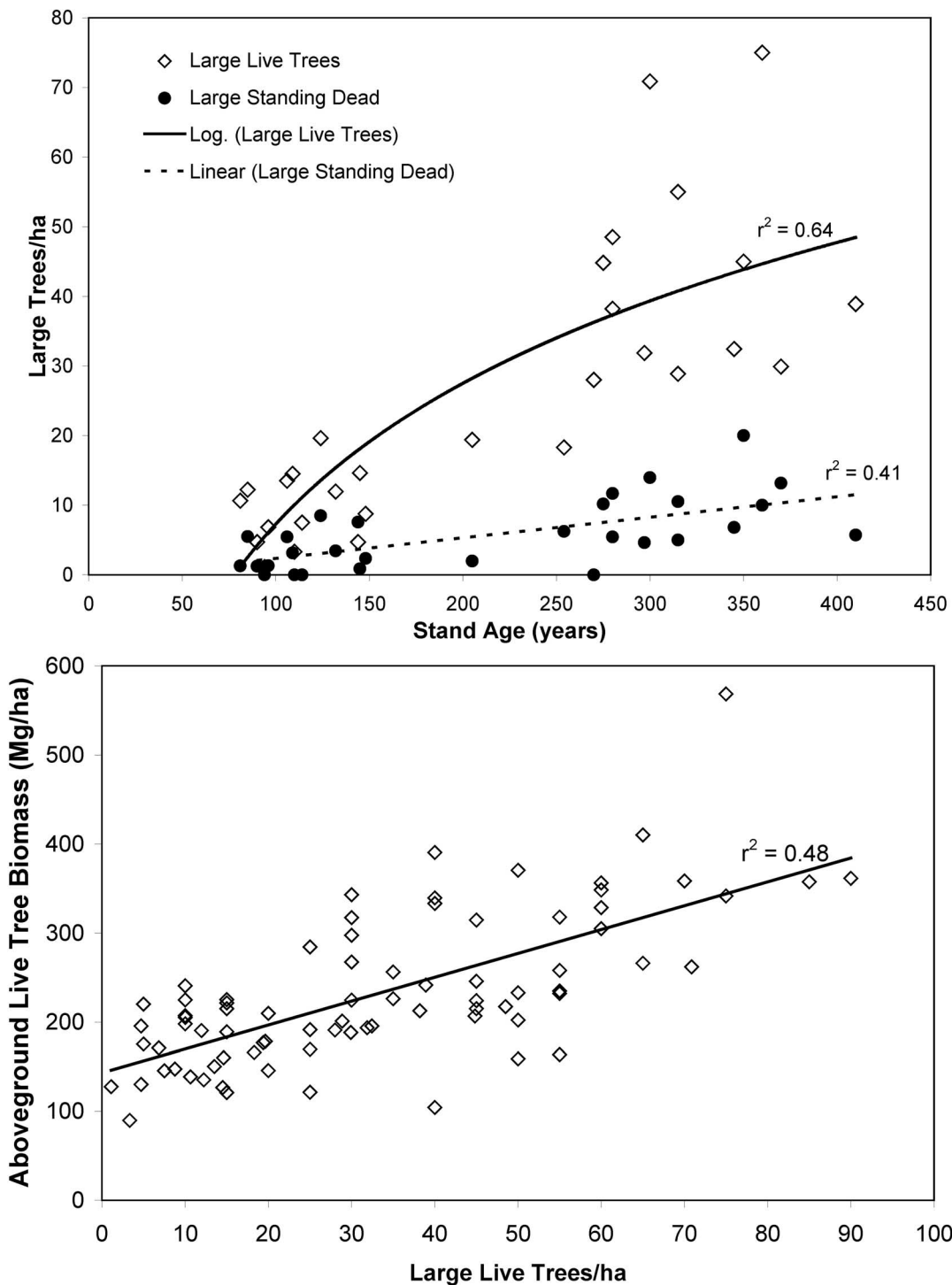
Figure 2. Top panel: Density of large trees (>50 cm dbh) in relation to stand age ($n = 29$). A logarithmic model [$y = 29.166\ln(x) - 127.03$] explained the most variation for live trees, whereas standing dead trees exhibited a linear relationship ($y = 0.0295x - 0.584$). Bottom panel: Relationship between live large tree density and aboveground live tree biomass ($n = 79$), exhibiting a linear model fit ($y = 2.6814x + 143.09$).

Relative Influence of Age Class, Ecoregion, and Species Composition

Forest age has a controlling and dominant effect on biomass development relative to ecoregional variability and the conifer component in mixed hardwood-conifer stands. This conclusion was clearly supported by CART results, in which age class emerged as the primary (top tier) predictor of aboveground live tree biomass (Figure 4). However, both

ecoregion and percent conifer were included in the CART (and thus were statistically significant) as secondary (lower tiered) predictors. For old-growth sites, percent conifer explained variation in aboveground biomass, with sites comprising between 5 and 22% conifer basal area having the greatest aboveground biomass (mean = 301 Mg/ha). Sites falling to less than 5% were intermediate (mean = 288 Mg/ha) and sites greater than 22% were lowest (mean =
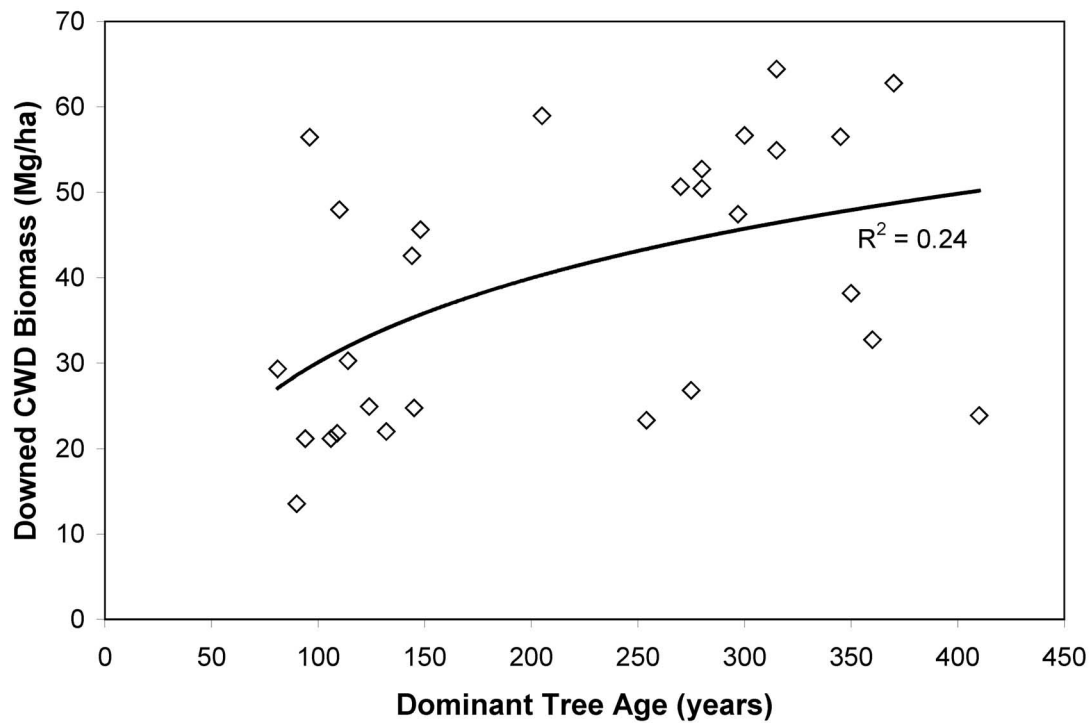
Figure 3. Relationship between DCWD biomass and stand age ($n = 29$). A logarithmic curve explained the greatest variation in this relationship [$y = 18.463\ln(x) - 57.495$].
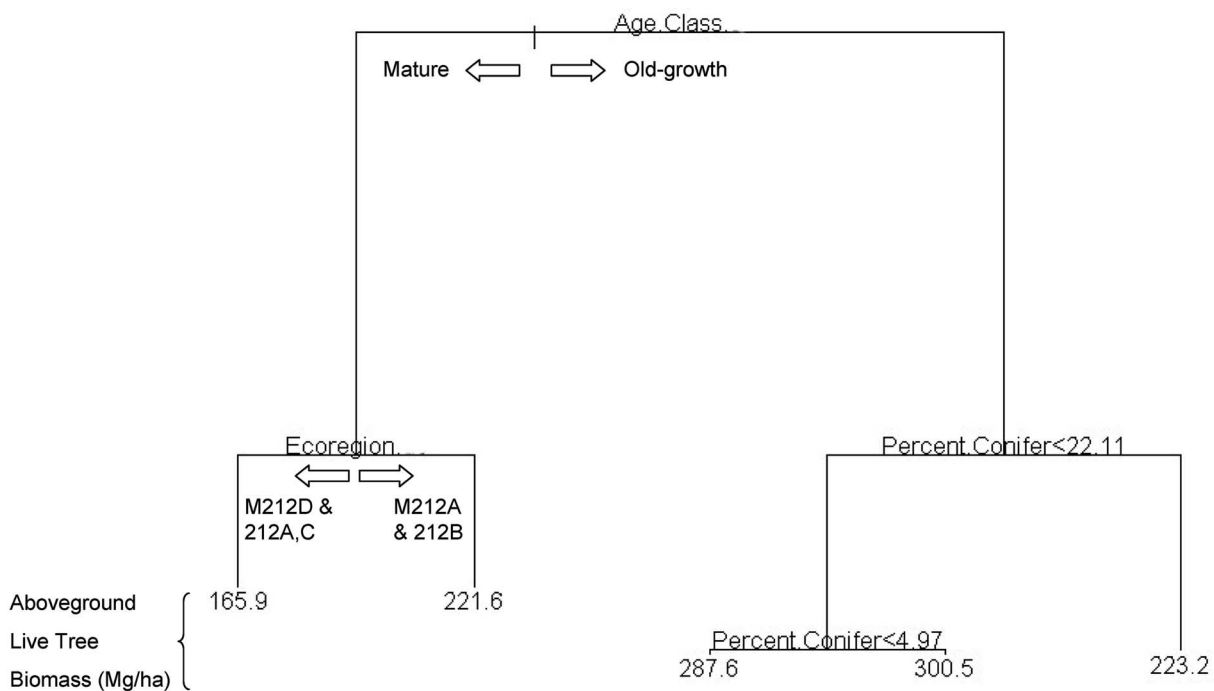

Figure 4. CART model, showing statistically significant ($\alpha = 0.05$) independent variables selected, split values, and partitioned mean values (bottom) of the dependent variable (aboveground live tree biomass, $n = 94$). The figure ranks variables by predictive strength (top to bottom). Length of each vertical line is proportional to the amount of deviance explained. Minimum observations required for each split = 15; minimum deviance = 0.01.

223 Mg/ha) in biomass within the old-growth age class. Together these results signaled a range in which a minor conifer component is sometimes associated with elevated biomass in old mixed stands, provided this does not exceed approximately one-quarter of total live tree basal area. Variance (or deviance) in our data set explained by percent

conifer was approximately one-third of that explained by age class alone on the basis of the CART output.

Biomass development was also associated with ecological variability attributable to differences among ecoregions (or sections). Ecoregion was selected in the CART as a secondary explanatory variable for mature sites. Within the

mature age class, aboveground biomass was lowest (mean = 166 Mg/ha) at sites in the Adirondack Highlands section (M212D) of New York, and two sections (212A and 212C) in the Laurentian Hills and Lowlands Province of southeastern to northeastern Maine. Mature forest biomass was higher (mean = 222 Mg/ha) in the White Mountains section (M212A) of New Hampshire and western Maine, and one section (212B) of the Laurentian Province in Maine. Ecoregion explained approximately one-fourth of the variation explained by age class alone.

Error Related to Subsampling Intensity

An important difference among the data sets was the intensity of subsampling (i.e., use of multiple plots) within sites. In one data set, subsampling consisted of 6–10 plots per site, whereas for the other data sets there were only 1 or 2 plots. Because total gap area in late-successional/old-growth northern hardwood forests can range from 5 to 10% (Runkle 1982, Ziegler 2002), sampling methods that fail to capture fine-scaled spatial variability (Curzon and Keeton 2010) are prone to error in terms of estimating forest structure attributes. For instance, excluding gaps from the sample may cause an overestimation of basal area and aboveground biomass in both mature and old-growth stands, although the error will be greater for the latter because of their higher gap fractions (Dahir and Lorimer 1996).

Despite these limitations, single plot per site data from old forests are commonly used for regional and even global estimates of biomass dynamics and carbon stocks (see, for example, sources reviewed in Luyssaert et al. 2008 and Keith et al. 2009). Nevertheless, it is important to recognize that the data derived from sites sampled more intensively are probably more robust. However, we found no statistically significant difference in basal area estimations for the Adirondacks in a comparison of the sites sampled intensively versus those sampled with only two plots. This comparison held for both old-growth ($P = 0.35$) and mature ($P = 0.27$) forest sites. Likewise, there were no statistical differences when we compared mature ($P = 0.16$) and old-growth ($P = 0.47$) basal areas among all four data sets based on analysis of variance results. These results suggest that the random plot placement used in all four data sets may have minimized this source of error.

Discussion
Evaluation of Competing Hypotheses

Our results support the hypothesis that biomass has the potential to increase very late into stand development, showing only slight declines as dominant trees pass 300 years of age, and continued additions to 400 years and beyond. Our data showed no evidence of peaks in early old-growth (e.g., approximately 200 years of age), declines subsequently (i.e., a "transition" phase), or steady-state dynamics as predicted by Bormann and Likens (1979). Correlations between total aboveground biomass and dominant tree age were related not just to increases in the standing dead tree component but also to substantial biomass accrual in live trees. Large tree densities (live and standing dead)

were strongly correlated with both age and aboveground biomass, whereas total live and standing dead stem densities showed no relationship with age across the range represented in our data set, a phenomena observed previously (Keeton et al. 2007). These results suggest that large trees make a proportionately greater contribution to total biomass as stands undergo late-successional development (Brown et al. 1997) and where disturbance dynamics allow persistence of some canopy dominants to very old ages.

Continued biomass development leads to substantially greater carbon storage levels in both live and standing dead tree pools (standing and downed), in comparison to levels achieved during maturation stages of development (Franklin et al. 2002). This inference was strongly supported by the categorical comparisons of age classes, which resulted in consistent findings for all of the subregions examined. Collectively the results suggest the potential for biomass additions (positive NEP) and related high-magnitude carbon storage over longer time frames than predicted previously for the northern hardwood region (Figure 5, top panel). Maximum attainable biomass levels and accrual rates are likely to vary by site, species composition, and ecoregion, as suggested by the CART results. For instance, total aboveground biomasses reached at our oldest sites (approximately 250–350 Mg/ha in stands >350 years old) are still only equal to or slightly below peak levels initially predicted for Hubbard Brook by the JABOWA model (350 Mg/ha, reached at approximately 200 years, declining to a long-term average of 300 Mg/ha after 400 years) (Whittaker et al. 1974).

Our findings did not directly support the alternate hypothesis offered by Fahey et al. (2005) regarding biomass stabilization or decline earlier than predicted by Bormann and Likens (1979). Likewise, they were not consistent with Martin and Bailey (1999) who, working at the Bowl Research Natural Area in New Hampshire, found that a logged stand recovered biomass comparable to average levels (208 Mg/Ha) after 100 years in a mosaic of (variable structure) old-growth areas. However, there are several possible explanations for these discrepancies. We propose three, each of which warrants further investigation and none of which is mutually exclusive.

Intraregional Variability

The first is that discrepancies among empirical studies may reflect regional- and site-level variability in late-successional biomass development processes. By this explanation, the Hubbard Brook findings may represent a lower point within this spectrum, whereas the highest values reported in this and other articles (e.g., Woods and Cogbill 1994, Ziegler 2000) may define the upper limits. Evidence supporting this line of thinking include the documented effects of anthropogenic stressors on forest productivity, expressed heterogeneously throughout the northern hardwood region (e.g., Aber et al. 2001, Schaberg et al. 2001), the region's pronounced site-specific edaphic variability (Seymour 1995), and variable stand dynamics attributable to different natural disturbance histories (Seymour et al.
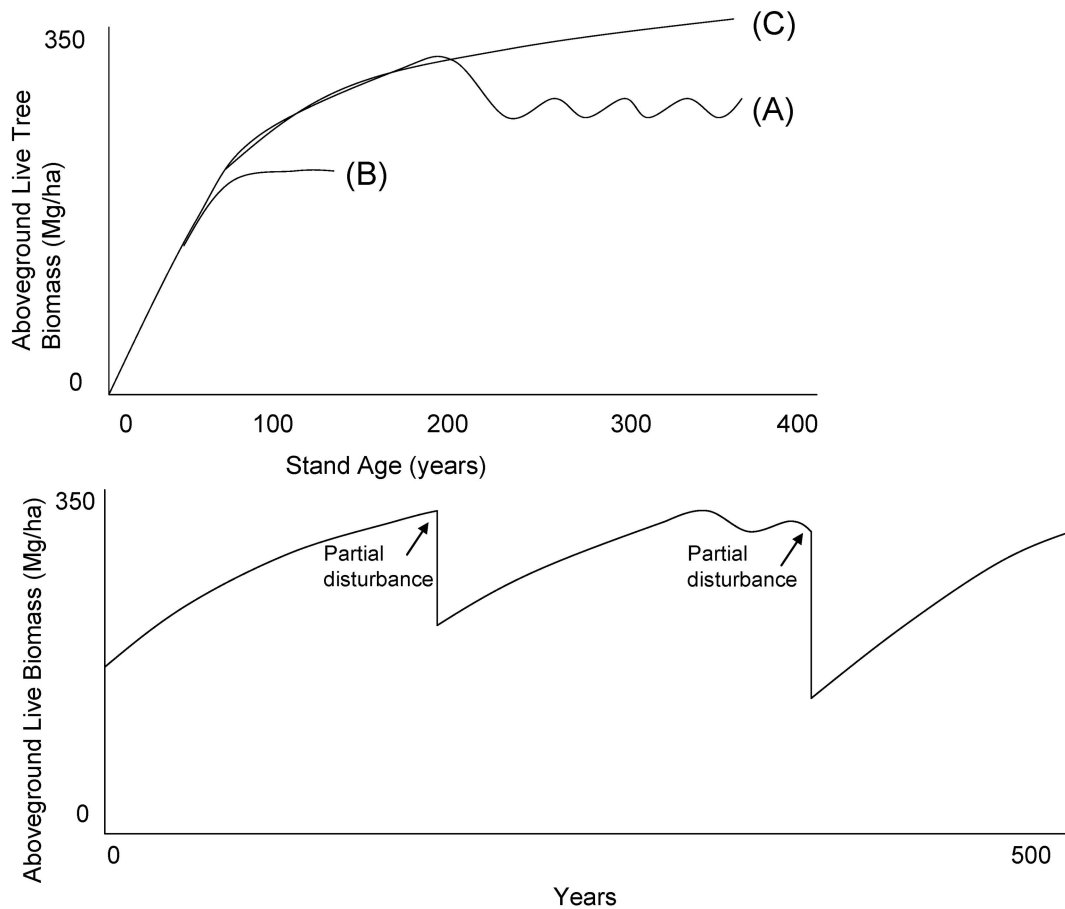
Figure 5. Conceptual models of stand-scale aboveground biomass development pathways for northern hardwood-conifer forests. Top panel: Pathway A depicts the widely referenced Bormann and Likens (1979) model, based on empirical data for young stands and theoretical projections for late-successional stands. Pathway B shows observed live tree biomass trends in a secondary stand at Hubbard Brook Experimental Forest, with earlier than predicted stabilization and possible decline (Fahey et al. 2005). Pathway C is based on empirical data presented in this and other studies (e.g., Ziegler 2000), suggesting continued long-term biomass accumulation potential in late-successional forests. Collectively these pathways may represent a range of variability for the northern hardwood region. Bottom panel: Hypothetical aboveground biomass dynamics in response to partial disturbances, such as microbursts, moderate-severity hurricanes, tornadoes, and ice storms. Note that live tree biomass declines following each disturbance, but it is hypothesized to recover asymptotically due to maintenance of multiaged to uneven-aged structures. If the time between partial disturbances is long enough, steady-state dynamics driven by gap dynamics (indicated in the panel by the dip before the second disturbance) are theoretically possible, although these were not evident in our data set.

2002). Land-use history is another major source of variability affecting stand development rates and trajectories in secondary forests (Foster et al. 1998, McLachlan et al. 2000).

The CART results showed that although forest age was the dominant factor, other sources of variability are important determinants of biomass development potential. Likewise, our data set contained a wide range of aboveground biomass values, with substantial overlap between the lower values obtained in the old-growth age class and the higher values presented in the mature age class. This variability clearly reflected the range of conditions encountered in all stands, including extent of recent wind throw and ice damage (Manion and Griffin 2001, Curzon and Keeton 2010), site quality (Keeton et al. 2007), and mortality related to beech bark disease (Gavin and Peart 1993, McGee et al. 1999). It also may reflect varying degrees of historical

harvesting effects in mature stands. For instance, some of our unmanaged mature stands fell within the range of highly disturbed old-growth stands.

Past versus Present

A second explanation is that biomass development may have occurred differently in the past than it does in the present. It is important to recognize that our study is a space-for-time substitution, and there are limitations to the inferences that can be drawn from chronosequence research. Our data do not track the individual pathways along which each stand has developed over past centuries or recent decades, and, therefore, they do not provide a basis for evaluating current biomass dynamics. It is thus possible that sustained positive biomass development may have been more likely in the past, whereas anthropogenic stressors

may have reduced this potential in the present as proposed by Fahey et al. (2005).

Primary versus Secondary Forest Dynamics

A third possibility is that biomass dynamics may be fundamentally different in primary forests compared with that in the secondary forests now recovering across the northeastern United States and observed at Hubbard Brook. This difference, in turn, may relate to the natural disturbances affecting primary forest landscapes over past centuries. The literature for the northeastern United States has emphasized either high-frequency, low-intensity disturbances, such as fine-scaled gap-forming events or very low-frequency (e.g., return intervals exceeding 1,000 years), high-intensity disturbances, such as high-severity hurricanes, and may have underreported intermediate intensity disturbances (Seymour et al. 2002). However, there is a growing recognition of intermediate-intensity events operating across centennial-scale frequencies, such as microbursts, tornadoes, insect outbreaks, and ice storms (North and Keeton 2008). They are also caused by low- to moderate-severity hurricanes in interior and northwestern portions of the region (Boose et al. 2001). Intermediate-intensity disturbances cause partial mortality with high, although spatially variable, densities of residual live trees (Millward and Kraft 2004, Woods 2004, Hanson and Lorimer 2007). They have been shown to produce nonequilibrium dynamics in Adirondack old-growth forests (Ziegler 2002, Curzon and Keeton 2010).

Nonequilibrium dynamics attributable to partial disturbances would produce biomass responses very different from those for the Bormann and Likens (1979) model for secondary forests. The latter predicted an early peak in biomass primarily due to an initial period of even-aged development. The predicted point of maximal biomass development was a function of efficient growing space allocation. Canopy disturbances, mortality in the dominant cohort, and changing species composition were predicted to result in subsequent declines and steady-state dynamics in stands composed of a "shifting mosaic of patches" (Whittaker et al. 1974). However, in a forest landscape subject to spatially heterogeneous, variable frequency but periodic partial disturbances, complete reinitiation of stand development would seldom occur (Schulte and Mladenoff 2005, D'Amato and Orwig 2008), and thus there would rarely, if ever, be an early stage of true even-aged structural development at the stand scale. Instead, stand-scale biomass would drop after each disturbance, only to recover subsequently while maintaining multiaged structure (Woods 2004, Hanson and Lorimer 2007) (Figure 5, bottom panel). This type of dynamic would produce the same logarithmic relationships with dominant tree age we found across our chronosequence. Bormann and Likens (1979) actually suggested that such a dynamic might be possible in uneven-aged systems characterized by partial disturbances. Thirty years later there is emerging empirical evidence that may support this prediction. We propose this as a hypothesis worthy of further investigation.

Error in Biomass Estimation

A potential source of error in our study was the use of diameter-based allometric equations to estimate large trees biomass. The equations of Jenkins et al. (2003) incorporate a correction factor for large trees based on Freedman (1984) but do not account for rotten wood specifically. Lacking an estimate of heartrot frequency, we may have overpredicted biomass for large trees in some cases. Error also may have been introduced by the assumed relationship between tree diameter and height as predicted by the equations of Jenkins et al. (2003). However, the assumption of a positive relationship for dominant and codominant trees was supported by the significantly greater canopy heights at the old-growth compared with those at mature sites in New York as reported by Keeton et al. (2007). Having higher mean stand diameters, large tree densities, and canopy heights, the predicted biomass differences are probably robust.

Standing dead tree biomass estimates were not corrected for height or fragmentation because of incomplete data across the full regional data set. This is an important limitation given that snapped stems can be common in late-successional northern hardwood-conifer forests (Curzon and Keeton 2010). However, an analysis of tree height data in the Keeton data set showed significantly higher mean snag heights at the old-growth sites, consistent with the inferred biomass trends. In addition, there were no differences in snag density or basal area distributions by decay stage (which incorporate evidence of stem breakage and deterioration) in relation to age class or dominant tree age. Thus, these sources of error are not likely to have altered the fundamental age-related contrasts reported in this article, although we are likely to have overestimated standing dead tree biomass, possibly by as much as 22%.

Implications for Carbon Dynamics and Storage in Northeastern Temperate Forests

Our results add to a growing body of literature showing that old-growth temperate forests have greater carbon sequestration and storage potential than previously realized (Keeton et al. 2010). A key finding of recent research, including gas exchange studies, has been that equilibrium NEP conditions, as previously predicted and modeled in regional and global carbon budgets (Houghton 2005), are seldom reached at stand scales in temperate and boreal forests (Pregitzer and Euskirchen 2004, Luyssaert et al. 2008). Instead, net positive carbon uptake frequently continues very late into stand development (Carey et al. 2001, Keith et al. 2009). For example, high levels of net annual carbon storage (3.0 Mg/ha) have been measured by the eddy covariance method in a ~200-year-old old-growth eastern hemlock stand in New England (Hadley and Schedlbauer 2002). Hadley and Schedlbauer accounted for known sources of error in the eddy covariance method (see Field and Kaduk 2004), such as incorrect instrument response and footprint size of the flux system but could not rule out error due to advective CO_2 flux. There are conflicting findings, such as the observed declines at Hubbard Brook, attributed to reduced growth in live trees, leading Siccama et al.

(2007) to conclude that W6 is no longer a carbon sink. Long-term, net positive NEP has been attributed both to increases in the dead wood and soil carbon pools (Harmon and Marks 2002) as well as to efficient three-dimensional allocation of growing space in uneven-aged, old-growth forests (Luyssaert et al. 2008). The latter is a recognition that tree mortality in the upper canopy of uneven-aged stands is compensated for by fast colonization of available growing space by co- and subdominant trees, a function of the vertically complex canopies and wide range of tree sizes/ages characteristic of old-growth forests (Franklin and Van Pelt 2004). However, research has also shown subordinate trees to have lower light use efficiencies, which may contribute to lower NPP in some forests with heterogeneous canopies (Binkley et al. 2010).

In this context our results suggest that there is a significant potential to increase total carbon storage in the Northeast's northern hardwood-conifer forests. Young to mature secondary forests in the northeastern United States today have aboveground biomass (live and dead) levels of ~107 Mg/ha on average (Turner et al. 1995, Birdsey and Lewis 2003). Thus, assuming a maximum potential aboveground biomass range for old-growth of approximately 250–450 Mg/ha, a range consistent with upper thresholds in our data set and the lower threshold observed at Hubbard Brook, our results suggest a potential to increase in situ forest carbon storage by a factor of 2.3–4.2, depending on site-specific variability. This would sequester an additional 72–172 Mg/ha of carbon. A reconstruction of pre-European settlement forest carbon storage in Wisconsin produced estimates within similar ranges for both old-growth carbon storage and current recovery potentials (Rhemtulla et al. 2009).

Although secondary forests may have the potential to more than double their aboveground carbon storage in some cases, there are many factors that will influence future trajectories of biomass development. Type and intensity of forest management approach will play a major role (Keeton 2006; Harmon et al. 2009). With development of carbon markets, this may include both reserve-based approaches, leading to development of late-successional/old-growth conditions, as well as those designed to optimize net carbon storage in actively managed forests (Harmon and Marks 2002, Seidl et al. 2007, Nunery and Keeton 2010). Carbon management probably will entail a combination of more intensive approaches intended to achieve net emissions reductions though product and energy substitution (Eriksson et al. 2007) and less intensive approaches, such as extended rotations and structural retention, favoring maintenance of high levels of in situ forest carbon storage (Ray et al. 2009b). Thus, carbon storage recovery is likely to be heterogeneous at landscape scales as a function of management alone.

However, there other important sources of uncertainty that must be considered. Global change, including climate system disruption and spread of exotic organisms, ranks foremost among these. Climate change may influence both rates and pathways (e.g., successional dynamics) of future biomass development (Aber et al. 2001, Iverson et al. 2008). Whether these result in negative or positive effects on late-successional forest carbon storage potential will depend on many factors, including atmospheric CO_2 fertilization effects, intensity of warming and precipitation changes, extent of species range shifts, and interactions with other stressors, such as disturbances, disease, airborne pollutants, and land use (Ollinger et al. 2002, Beckage et al. 2008). Thus, although old-growth reference stands suggest an inherent capacity within the system, future carbon storage dynamics are likely to differ from historic benchmarks as environmental boundary conditions change (Seidl et al. 2008, Ollinger et al. 2008).

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