Population and biomass dynamics of trees in a northern hardwood forest at Hubbard Brook

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Abstract: We quantified the dynamics of the tree stratum at Hubbard Brook Experimental Forest (HBEF), New Hampshire, to examine why live biomass reached a plateau in about 1980. Total aboveground biomass increased from 209 Mg·ha^{-1} in 1981 to 216 Mg·ha^{-1} in 2001. From 1991 to 2001, in-growth of ≥10 cm diameter at breast height (DBH) trees averaged 4.7 trees·ha^{-1}·year^{-1} with a corresponding in-growth biomass of 0.29 Mg·ha^{-1}·year^{-1}. Mortality of trees ≥10 cm DBH averaged 5.3 trees·ha^{-1}·year^{-1} (1.12% of trees·year^{-1}). Dying trees represented 2.24 Mg·ha^{-1}·year^{-1} of aboveground biomass from 1991 to 2001. The biomass pools of standing dead, snags, and coarse woody debris in this forest currently are near steady state with residence times of 7.5, 15, and 6.2 years, respectively. The plateau in live biomass was mostly associated with lower wood production. Aboveground net primary productivity was estimated at 6.53 Mg·ha^{-1}·year^{-1} (3.28 Mg·ha^{-1}·year^{-1} for aboveground woody tissues and 3.25 Mg·ha^{-1}·year^{-1} for leaf production), considerably lower than published estimates for the 1956–1965 period at the HBEF. Net ecosystem productivity in this young, second-growth forest is near zero, indicating that it may not be a sink for carbon.

Résumé : Nous avons quantifié la dynamique de la strate arborée à la forêt expérimentale de Hubbard Brook, au New Hampshire, pour déterminer pourquoi la biomasse vivante a atteint un plateau vers 1980. La biomasse aérienne totale est passée de 209 à 216 Mg·ha^{-1}·an^{-1} de 1981 à 2001. De 1991 à 2001, le recrutement des arbres de 10 cm et plus (DHP) atteignait en moyenne 4,7 arbres·ha^{-1}·an^{-1} avec une biomasse correspondante de 0,29 Mg·ha^{-1}·an^{-1}. La mortalité des arbres de 10 cm et plus au DHP atteignait en moyenne 5,3 arbres·ha^{-1}·an^{-1} (1,12 % des arbres·an^{-1}). Les arbres morts représentaient 2,24 Mg·ha^{-1}·an^{-1} de biomasse aérienne de 1991 à 2001. Dans cette forêt, les réservoirs de biomasses constitués des arbres morts debout, des chicots et des débris ligneux grossiers sont actuellement presque à l'état stable avec un temps de résidence respectif de 7,5, 15 et 6,2 ans. Le plafonnement de la biomasse vivante était surtout associé à une plus faible production de matière ligneuse. La productivité primaire nette aérienne a été estimée à 6,53 Mg·ha^{-1}·an^{-1} (3,28 Mg·ha^{-1}·an^{-1} pour la production de tissus ligneux aériens et 3,25 Mg·ha^{-1}·an^{-1} pour la production de feuillage), ce qui est beaucoup plus faible que les estimations publiées pour la période de 1956 à 1965 dans cette forêt expérimentale. La productivité nette de l'écosystème dans cette jeune forêt de seconde venue est presque nulle, ce qui indique qu'elle pourrait ne pas être un puits de carbone.

[Traduit par la Rédaction]

Introduction

The complex interactions and feedbacks among forest development, demography and health, energy flow, and changes in environmental resources and conditions present challenges to our general conceptualization of ecosystem ecology and specifically to predictions of ecosystem C balance. An apparently large C sink in the northern hemisphere has been attributed to storage in northern forest ecosystems (Fan et al. 1998); however, the mechanisms controlling this sink are not clear and the future strength of the sink is difficult to predict (Valentini et al. 2000).

Second-growth forests comprise most of the landscape of the northeastern United States and southeastern Canada, having originated following agricultural abandonment or intensive forest harvest in the late 19th and early 20th centuries. At the Hubbard Brook Experimental Forest (HBEF) in the White Mountains of New Hampshire where this research was conducted, there were two distinct phases of forest harvest — early utilization of mature red spruce (*Picea rubens* Sarg.) in the 1870s, followed later (1910–1920) by more intensive harvest of most nondefective overstory stems (Bormann and Likens 1979). These left a mixed-age forest dominated by stems released from competition following

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Fig. 1. Map of the location of the gauged watersheds and four forest plot transects in the Bird Area in the Hubbard Brook Valley.
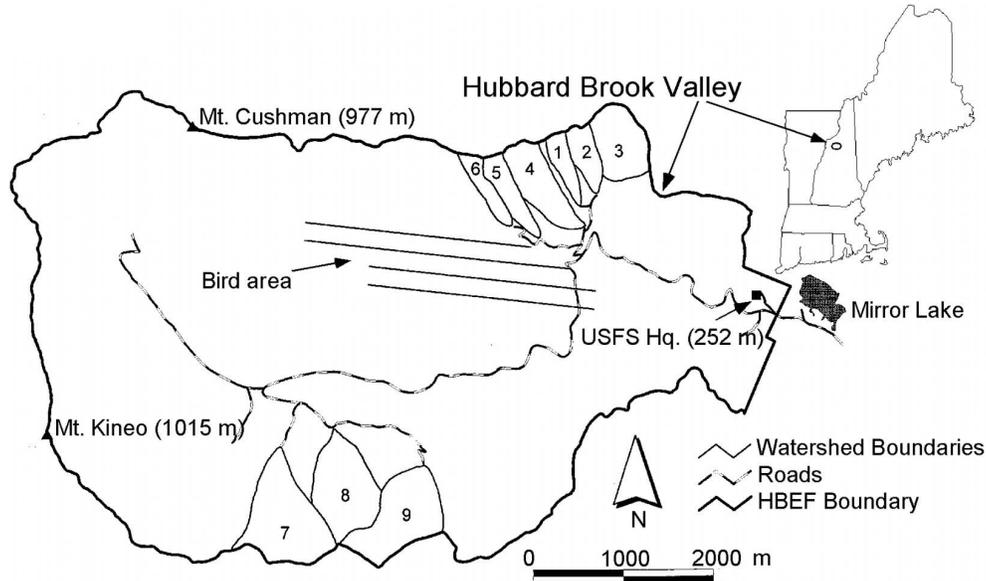
the second harvest, which was further disturbed by a hurricane in 1938 (Merrens and Peart 1992). This sort of complex forest history is typical of upland stands in the Appalachian Highlands and probably representative of most areas that were not suited for agriculture. The dynamics of these forests is now further complicated by widespread occurrence of unusual species-specific mortality owing to introduced insects and pathogens (e.g., beech bark disease; Houston et al. 1979) or complex, pollution-related decline phenomena (e.g., red spruce: Eagar and Adams 1992; sugar maple (*Acer saccharum* Marsh.): Horsley et al. 2000).

At the HBEF, repeated, comprehensive measurements on the biogeochemical reference watershed 6 (W6; Fig. 1) beginning in 1965 (Bormann et al. 1970; Whittaker et al. 1974) have demonstrated that the live biomass of the tree stratum increased rapidly until the early 1980s and has remained essentially constant since that time (Likens et al. 1998; Fig. 2), despite earlier projections of continuing aggradation (Whittaker et al. 1974; Bormann and Likens 1979). Changes in living biomass of the tree stratum reflect the balance between growth of existing stems, recruitment of new individuals (in-growth), and mortality. The contributions of these demographic components in complex, second-growth forests like those at the HBEF have rarely been studied in detail because they require long-term measurement of permanent plots of tagged or mapped trees. In combination with repeated surveys of coarse woody debris (CWD) and other detrital components, such surveys can also provide an alternative means to assess both net primary productivity (NPP; the net carbon gain by vegetation) and net ecosystem exchange (NEE; the net flux of CO_2 between the ecosystem and the atmosphere).

The objectives of this study were to determine the recent patterns of (*i*) tree growth, mortality, and recruitment and (*ii*) detrital C storage in and around the biogeochemical reference watershed (W6) at the HBEF. We used a tagged-tree inventory and other field measurements to identify the contributions of mortality, growth, and recruitment of the dominant tree species to the aforementioned plateau in live tree biomass

observed in W6. We also used these data to test recent modeling work using the forest ecosystem model PnET (Aber et al. 1997), which suggested that NPP of the northern hardwood forest at HBEF currently is considerably lower than was observed in the late 1950s and early 1960s at this site (Whittaker et al. 1974), owing in part to forest maturation (Smith et al. 2002). Finally, we examined the implications of changing demography and forest maturation to NEE at the HBEF.

Site description

The HBEF (3160 ha) occupies most of the drainage area of Hubbard Brook, in the southern portion of the White Mountain National Forest in central New Hampshire (71°45′W, 45°57′N; www.hubbardbrook.org). Most of the published research at the HBEF has been done on six small (12–42 ha) gauged watersheds on the north side of the valley above 500 m elevation (Likens and Bormann 1995). This study was conducted primarily within a 2.5 km² area located immediately to the west of these gauged watersheds, encompassing a forest similar in structure and composition to the lower two-thirds of W6 (Bormann et al. 1970). The forest plots established in this study lie within the portion of the Hubbard Brook Valley used for studies of bird populations during the past 35 years (Holmes et al. 1986). The area is referred to subsequently in this paper as the "Bird Area" (Fig. 1).

Sugar maple, American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt.) compose about 84% of the forest canopy in the Bird Area. There are also patches of red spruce and balsam fir (*Abies balsamea* (L.) Mill.) in the study area. The last broad-scale logging in the area ended in about 1917, although many trees were left uncut owing to poor form, small size, or other reasons. Based on size and age data for the major species (R.H. Whittaker, unpublished data), and the 1965 forest inventory of W6, we estimate that about 58% of the trees with diameter at breast height (DBH, 1.37 m) ≥10 cm present in 1965 pre-dated the time of logging (Bormann et al. 1970). Portions of the Bird Area forest were impacted by a hurricane

Fig. 2. Total live tree biomass (*a*) and dead tree biomass (*b*) (≥10 cm DBH) on the lower two-thirds (hardwoods) of watershed 6 at the HBEF during 1965–2002 and for the Bird Area inventories (1981, 1991, and 2001). Error bars are ±1 SE, based on plot-scale variation.
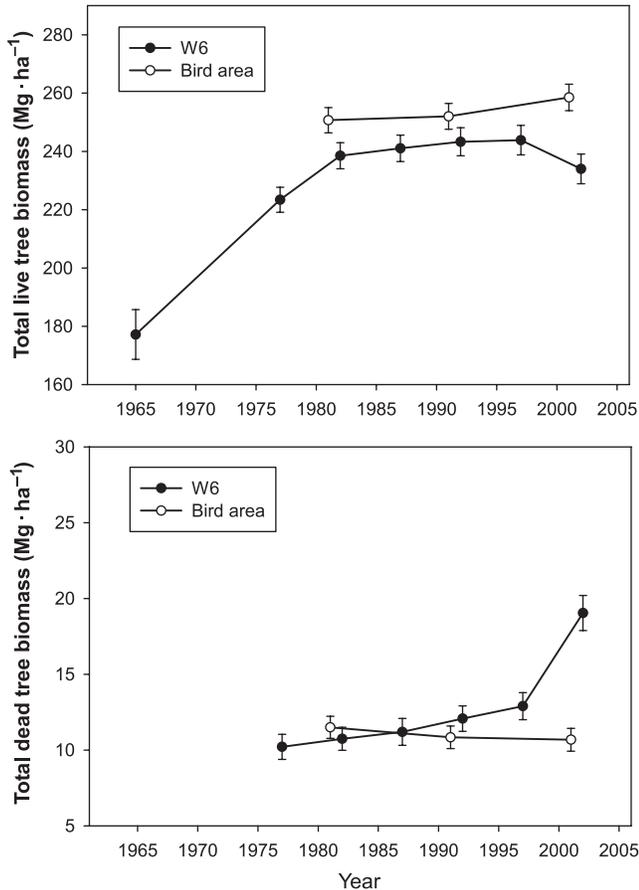
in 1938, which was followed by some salvage logging (Merrens and Peart 1992). There are no large patches of windfall or any historical or physical evidence of fires.

For comparison, we also report on the composition and changes in the forest on W6, a 13.2 ha watershed immediately to the east of the Bird Area (Fig. 1). The forest composition of W6 was measured seven times during 1965–2002 and has been described in detail elsewhere (Whittaker et al. 1974; Bormann and Likens 1979).

Methods

Demographic studies

In 1981, permanent plots were established along four 10 m wide transects, ~2.5 km long and 200 m apart, in the Bird Area (Fig. 1). This set of four transects is considered representative of approximately 2.5 km² of mid-elevation, second-growth northern hardwood forest. Each transect was divided into 25 m segments. Thus the plots are a series of contiguous 10 m × 25 m rectangles, along the four lines, with a total area of 9.96 ha. The diameter and species of all live and dead standing stems ≥10 cm DBH were measured at the establishment of the plots in 1981. In 1991, all live stems ≥10 cm DBH were tagged using numbered aluminum tags and alumi-

num nails and their diameters measured. Diameters of all dead trees with DBH ≥10 cm were also measured and the trees categorized as either standing dead (most branches still present) or snags (dead trees without major branches or broken off above breast height). Dead trees and snags leaning at greater than 45° from the vertical were considered CWD and not included in this inventory. Dead stems were not permanently tagged in 1991; however, there were usually no more than two or three on each plot, so their individual fate was readily determined in subsequent biennial surveys.

The trees on the plots were reassessed at 2 year intervals through 2001. Each tagged tree was categorized as follows: (*i*) live and healthy, (*ii*) unhealthy, (*iii*) standing dead, (*iv*) snag, or (*v*) downed (uprooted or broken off below breast height). Low-vigor trees (unhealthy) had very thin crowns and few or yellowed leaves. These data were used to calculate the transfers of trees among the five categories in each 2 year interval. Diameters were not remeasured at each 2 year survey but were again measured in 2001, the 10th year after tagging. In each 2 year resurvey, in-growth trees, defined as those reaching the 10 cm DBH threshold, were tagged and their species and diameters recorded. In 2001, the 2–9 cm DBH class was sampled in nested 3 m radius subplots centered at the stakes marking the even-numbered plots along the transects (i.e., 171 subplots). Diameter and species of all stems in the 2–9 cm diameter range (DBH) in these plots were recorded and assigned to the same vigor categories used for the larger trees.

Because considerable reference and comparison are made to the forest condition in W6, a brief summary of the methods of monitoring the vegetation on W6 is also presented here. In 1965, W6 was surveyed into two hundred and eight 25 m × 25 m grid cells and the corners were permanently marked. A single 10 m × 10 m sample plot was randomly located in each of the 208 grid cells in 1965. The DBH and species of all live trees ≥2 cm DBH were measured (Bormann et al. 1970). Starting in 1977 and continuing at 5 year intervals through 2002, all live and dead trees ≥10 cm DBH on W6 were measured (i.e., a complete census was employed in place of the 10 m × 10 m sub-plots). Diameter, species, and vigor of 2–9 cm DBH trees were measured beginning in 1982 on subplots within the grid cells. Watershed 6 has been subdivided into three elevation zones for various studies of population structure, biomass, plant nutrient chemistry, and overall biogeochemical cycling (Bormann et al. 1970; Whittaker et al. 1974; Johnson et al. 2000). Effectively, the lower two-thirds of W6 represents typical mid-slope northern hardwood forest and is indistinguishable from the Bird Area forest in species composition. The upper third of W6 is transitional to the boreal spruce – fir – white birch type and is underlain by much shallower soils. Thus, in this study, we compare data from the Bird Area with data from the lower two-thirds of W6.

Biomass estimation

Biomass estimates were made using site-specific allometric equations in which biomass is estimated from parabolic volume of the tree bole (Whittaker et al. 1974). In 1984, a test of the accuracy of these allometric equations against actual measured biomass at the HBEF indicated an

accuracy of ±5% (Siccama et al. 1994). Annual woody aboveground biomass increment (growth) and leaf mass (productivity) estimates were made using two independent methods. First, biomass was estimated for each tree based on its 2001 diameter and its 1991 diameter. The mean annual biomass increment was then estimated by subtracting the 1991 biomass from the 2001 biomass and dividing by 10. Second, rates of diameter growth for the major tree species were obtained from 2008 tree cores taken in the vicinity of the Bird Area in 1992–1996 as part of another project (Schwarz et al. 2003). We fitted functions relating radial increment (Δr, mm) to tree diameter using a three-parameter log-normal model:

$$[1] \qquad \Delta r = a \cdot \exp\left\{ -\frac{1}{2} \cdot \left[\frac{\ln(\text{DBH}/\text{DBH}_0)}{b} \right]^2 \right\}$$

where DBH is the diameter at breast height (1.37 m) and a, b, and DBH_0 are fitted parameters. These functions were then applied to the trees measured in the Bird Area to estimate annual diameter increment in 2001. This value was subtracted from the 2001 diameter and the biomass was estimated as described above. In both biomass estimation techniques, productivity was determined separately for leaves, bole wood, bole bark, live branch wood and bark, dead branches, and twigs (Whittaker et al. 1974). Aboveground woody biomass was computed as the sum of all components except the leaves.

To estimate the biomass of standing dead trees and snags, it was necessary to make some assumptions about tree fragmentation and decay. Standing dead trees and snags differ in the amounts of the tree still standing. We assumed that, on average, standing dead trees retained one-third of their branches (based upon visual estimates), as well as all of their bole bark and wood. We assumed that snags retained no branches, two-thirds of their bole wood, and one-half of their bole bark. In addition, standing dead trees and snags were assumed to decompose while standing; using decay rates for standing dead hardwood trees in Tennessee (Onega and Eickmeier 1991), we estimated a mean 27% mass loss for standing dead and 43% for snag boles over the interval during which they remained standing. This approach may slightly overestimate values for the HBEF, because higher temperatures in the southern hardwood forest probably result in higher decay rates; for example, the exponential decay constant (k) observed by Onega and Eickmeier (1991) for decaying downed boles was slightly higher ($k = 0.110$ year^{-1}) than measurements at the HBEF (0.096 year^{-1}; Arthur et al. 1993). When our demographic data indicated that a living tree had died standing or become a snag, its biomass was reduced accordingly. Although individual trees do not lose their biomass in such an abrupt fashion, the large number of dead and dying trees in our study acts to smooth out this step decrease in biomass.

Finally, the age and radial growth rates of sapling beech (0.3–2.5 cm DBH), by far the most abundant understory species, were measured for 79 stems cut from throughout the Bird Area in 1996. The complete set of tagged tree inventory data used in this study is posted at www.hubbardbrook.org/ under "Datasets."

Results

Comparison of the forest inventories of 1981, 1991, and 2001

A broad overview of the forest dynamics in the 2.5 km^2 study area may be obtained by examining changes in the forest between 1981 and 2001 (Table 1). Over this 2-decade interval, the density of live trees ($\geq$10 cm DBH) declined from 553 to 489 to 486 stems·ha^{-1} in 1981, 1991, and 2001, respectively, mostly accounted for by reduced density of sugar maple and yellow birch. The slowing of the density decline between 1991 and 2001 was explained in part by the in-growth of 28 beech trees·ha^{-1} in this interval. Total live basal area remained essentially constant over the 20 year interval (28.4, 28.3, and 28.8 m^2·ha^{-1} in 1981, 1991, and 2001, respectively). Biomass of live trees (aboveground + belowground) increased slightly over the 2 decades (251, 252, and 259 Mg·ha^{-1} in 1981, 1991, and 2001, respectively), while the biomass of standing dead trees and snags changed negligibly between 1981 and 2001 (11.5, 10.8, and 10.7 Mg·ha^{-1} in 1981, 1991, and 2001, respectively). Biomass change was quite variable spatially within the forest. For example, calculated separately for each of the four transects (~2.5 ha each), two decreased in total biomass by 6–9 Mg·ha^{-1} between 1981 and 2001, whereas the other two increased in total biomass by 20–25 Mg·ha^{-1}. The overall growth pattern, a leveling off in biomass accumulation, is similar to the pattern we have measured on W6 between 1982 and 2002 (Fig. 2). We do not know exactly why the biomass of the Bird Area is about 20% greater than on the lower two-thirds of W6; however, W6 has notably steeper slopes, shallower soils, and a stronger south aspect than the Bird Area, which is on the more or less gently rolling terrain of the mid-valley (Fig. 1).

The tagged-tree inventory

The fates of healthy and unhealthy stems, standing dead trees, snags, and downed trees are presented as the transfers of stems between these categories for each of the five 2 year intervals (Fig. 3). To illustrate the interpretation of this figure, we observed 4608 live trees on the 9.96 ha of Bird Area plots in 1993 . Of these 4608 trees, 4452 remained alive and healthy in the 1995 inventory, 77 were noted as unhealthy in 1995, 39 died and remained standing, 20 died and broke off to become snags, and 20 died and fell to the ground between the two inventories. In addition to the 4452 trees that remained alive and healthy from 1993 to 1995, there were 95 trees that grew into the $\geq$10 cm DBH size-class in the interval, plus 5 trees that had been observed as unhealthy in 1993 that were reclassified as healthy in 1995. Thus, the number of healthy trees in 1995 was 4552 (4452 + 95 + 5).

In-growth

During the 10 year study, a total of 473 trees grew into the permanent plots at the minimum diameter of 10 cm DBH, for a mean in-growth of 4.7 stems·ha^{-1}·year^{-1} (Table 2). In-growth was predominantly beech (58% of stems) and sugar maple (12%). Red spruce and balsam fir contributed about 9%–10% each, while the rest was mostly yellow birch and striped maple (*Acer pensylvanicum* L.). In

Table 1. Phytosociological and biomass summaries for the Bird Area forest in 1981, 1991, and 2001 based on living and dead trees ≥10 cm in diameter at breast height (DBH).
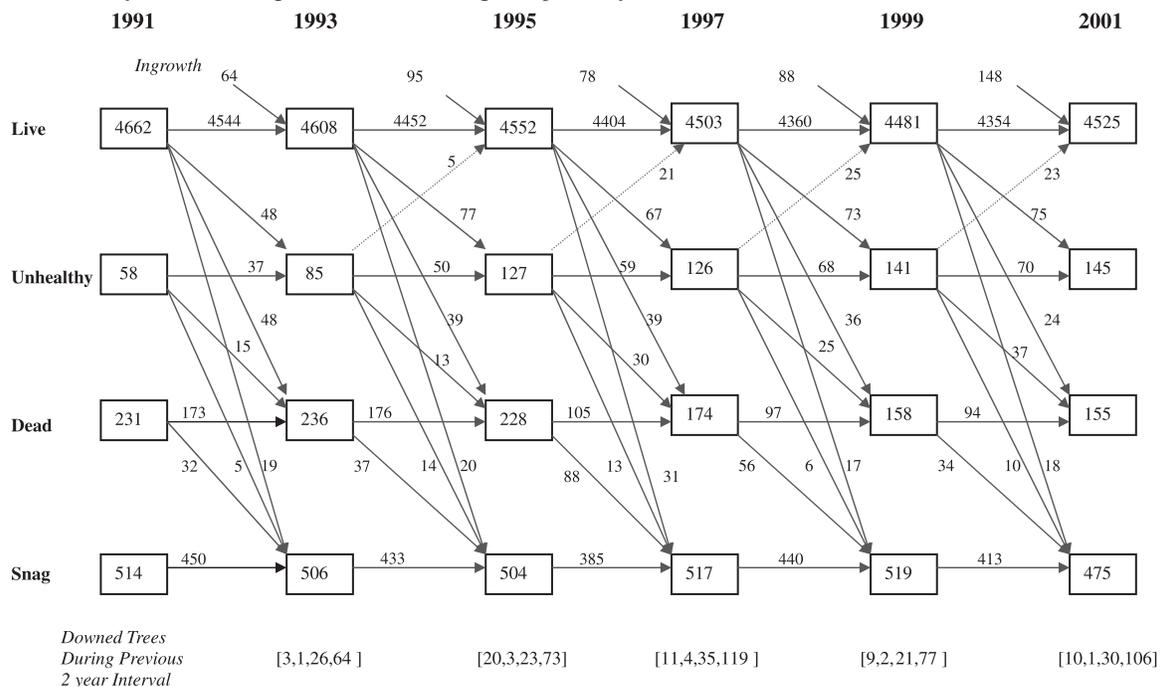
(*a*) Living trees ≥10 cm DBH.

Species	Basal area ($m^2 \cdot ha^{-1}$)	Density (no. of stems·ha^{-1})	Frequency (% of plots)	Biomass (Mg·ha^{-1}) Aboveground	Total
1981					
Sugar maple	8.52	165	83	62.67	74.41
American beech	6.29	153	85	49.14	58.70
Yellow birch	9.60	136	85	69.15	83.76
Balsam fir	0.23	11	14	0.82	1.09
Red spruce	1.10	27	26	4.89	6.53
White birch	0.14	3	5	1.06	1.29
Other*	2.56	58	55	21.11	24.93
Total	28.44	553		208.84	250.71
1991					
Sugar maple	9.13	150	85	68.55	81.17
American beech	6.25	153	89	48.86	58.37
Yellow birch	8.74	109	81	63.44	76.79
Balsam fir	0.28	12	16	1.00	1.32
Red spruce	1.06	22	25	4.69	6.25
White birch	0.15	3	5	1.12	1.37
Other*	2.66	40	43	22.64	26.75
Total	28.27	489		210.30	252.02
2001					
Sugar maple	9.44	142	85	71.62	84.68
American beech	6.49	169	90	50.49	60.35
Yellow birch	8.37	96	78	61.09	73.91
Balsam fir	0.37	15	18	1.36	1.80
Red spruce	1.09	25	27	4.82	6.42
White birch	0.15	3	4	1.13	1.38
Other*	2.93	36	41	25.42	29.99
Total	28.84	486		215.93	258.53

(*b*) Dead trees ≥10 cm DBH.

Species	Basal area ($m^2 \cdot ha^{-1}$)	Density (no. of stems·ha^{-1})	Frequency (% of plots)	Aboveground biomass (Mg·ha^{-1})
1981				
Sugar maple	0.23	6.4	12	0.59
American beech	1.40	16.4	30	3.30
Yellow birch	2.27	37.9	50	4.62
Balsam fir	0.24	6.4	12	0.39
Red spruce	0.29	11.4	19	0.59
White birch	0.01	0.4	1	<0.01
Other*	0.39	19.0	30	0.86
Total	4.83	97.9		10.35
1991				
Sugar maple	0.49	11.8	21	1.62
American beech	0.98	14.6	27	2.46
Yellow birch	2.14	30.1	41	4.45
Balsam fir	0.12	3.0	5	0.21
Red spruce	0.16	5.8	11	0.32
White birch	0.01	0.7	1	<0.01
Other*	0.31	12.1	20	0.75
Total	4.21	78.1		9.81
2001				
Sugar maple	0.77	13.7	22	2.06

Table 1 (*concluded*).

Species	Basal area (m²·ha⁻¹)	Density (no. of stems·ha⁻¹)	Frequency (% of plots)	Aboveground biomass (Mg·ha⁻¹)
(b) Dead trees ≥10 cm DBH.				
American beech	0.95	14.4	26	2.59
Yellow birch	1.97	24.8	39	4.19
Balsam fir	0.07	2.2	5	0.09
Red spruce	0.11	3.0	6	0.21
White birch	0.01	0.3	1	<0.01
Other*	0.21	6.8	12	0.54
Total	4.09	65.2		9.68

*Other includes striped maple (*Acer pensylvanicum* L.), mountain maple (*Acer spicatum* L.), white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), pin cherry (*Prunus pensylvanica* L.), mountain ash (*Sorbus americana* Marsh.), and shadbush (*Amelanchier* sp. Medic.).

Fig. 3. Pools and transfers of trees among various classes in the Bird Area, 9.96 ha of northern hardwood forest at the Hubbard Brook Experimental Forest. Pools are number of trees and transfers are number of stems changing class in the 2 year interval between surveys. The numbers in brackets at the bottom of the figure are the numbers of trees falling to the ground from each of the categories in sequence (healthy trees, unhealthy trees, standing dead trees, and snags, respectively).

Mortality

Of the 4720 live trees tagged in 1991 (4662 healthy, 58 unhealthy), 523 (11.1%) died over the 10 year period (Table 3). Of the 325 in-growth trees that entered the plots from 1993 to 1999 (Table 2), 8 were dead by 2001. Of the 523 dying trees, 306 (59%) died standing, 153 (29%) broke off to become dead snags, and 64 (12%) fell to the ground before the next survey. Few trees fell to the ground by up-rooting; most broke off at or near ground level. The mean annual mortality rate for stems ≥10 cm DBH during the 10 year study was 1.12%·year⁻¹ (Table 3). Of the three major northern hardwood species in the Bird Area, sugar maple

terms of basal area and biomass, in-growth amounted to 0.04 and 0.29 Mg·ha⁻¹·year⁻¹, respectively.

had the lowest mortality rate (0.88% stems·year⁻¹), beech was intermediate (0.93%), and yellow birch was highest (1.35%; Table 3). Intermediate mortality rates were observed for two coniferous species, red spruce (1.04%·year⁻¹) and balsam fir (1.00%·year⁻¹), and highest mortality for "other" species, mostly striped maple (2.19%·year⁻¹).

Biomass and fate of dying trees

The mean aboveground biomass of dying trees ≥10 cm was 2.24 Mg·ha⁻¹·year⁻¹ across the 10 year interval. Based on the assumptions described in the Methods, the transfer of this dead tree biomass to dead wood pools (standing dead, snags, CWD) was calculated (Fig. 4). Only 10.7% of dying tree biomass was transferred directly to the CWD pool by tip-ups. We estimated about 23% respiratory loss

Table 2. Numbers of stems of major species growing into the ≥10 cm diameter class in the Bird Area forest (9.96 ha) at the HBEF, 1991–2001.

Species	In-growth during 2 year interval					Total in-growth	% of total
	1991–1993	1993–1995	1995–1997	1997–1999	1999–2001		
Sugar maple	15	8	8	11	16	58	12
American beech	38	50	42	49	95	274	58
Yellow birch	3	8	3	1	4	19	4
Red spruce	3	9	10	13	12	47	10
Balsam fir	2	10	10	8	11	41	9
Other*	3	10	5	6	10	34	7
Total	64	95	78	88	148	473	100

*Other includes striped maple (*Acer pensylvanicum* L.), mountain maple (*Acer spicatum* L.), white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), pin cherry (*Prunus pensylvanica* L.), mountain ash (*Sorbus americana* Marsh.), and shadbush (*Amelanchier* sp. Medic.).

Table 3. Mortality distribution by tree species in 2 year intervals in the Bird Area forest (9.96 ha).

Species	Alive* in 1991	Number dying during 2 year interval					Total dead	Mean annual mortality[†] (%·year^{-1})
		1991–1993	1993–1995	1995–1997	1997–1999	1999–2001		
Sugar maple	1462	22	25	34	19	26	126	0.88
American beech	1447	23	30	31	30	24	138	0.93
Yellow birch	1067	26	22	38	26	26	138	1.35
Red spruce	214	2	8	4	3	5	22	1.04
Balsam fir	113	0	4	2	3	4	13	1.00
Other[‡]	417	18	20	19	14	15	86	2.19
Total	4720	91	109	128	95	100	523	1.12

*Includes healthy and unhealthy trees.

[†]Mean annual mortality was calculated by first dividing the number of dying trees in each time interval by the number of live trees at the beginning of that interval. After halving this value, to account for the 2 year interval duration, the mortality estimates for the five time intervals were averaged.

[‡]Other includes striped maple (*Acer pensylvanicum* L.), mountain maple (*Acer spicatum* L.), white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), pin cherry (*Prunus pensylvanica* L.), mountain ash (*Sorbus americana* Marsh.), and shadbush (*Amelanchier* sp. Medic.).

of dead tree biomass during detrital processing between the live tree and the CWD pool (i.e., decay of standing dead and snags). Using our visually derived assumptions of fragmentation, roughly equal amounts of organic matter were added to the CWD pool by fragmentation (0.89 Mg·ha^{-1}·year^{-1}) and by fall of trees, standing dead trees, and snags (0.75 Mg·ha^{-1}·year^{-1}). In population terms, we observed a mean of 703 standing dead trees plus snags in the Bird Area over the six inventories (Fig. 3). Of these, 28% were standing dead trees and 72% were snags. The number of stems entering and leaving the standing dead tree category were unequal and, thus, resulted in a decrease in the pool of standing dead trees. A total of 400 trees became snags over the 10 year study, 153 from dying trees and 247 from standing dead trees. Output of trees from snags into the downed tree category was 439 trees, also resulting in a decline in the number of snags. An average stem remained in the standing dead pool for 7.5 years, whereas an average snag remained standing for about 15 years.

Net primary productivity

Annual aboveground woody biomass increment and aboveground NPP (ANPP) were estimated for the Bird Area by two independent approaches. First, the biomass increment calculat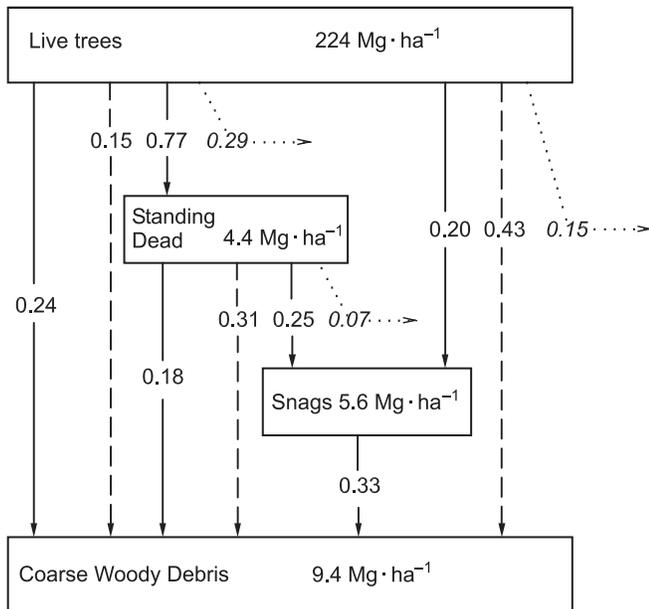ed using the mean annual diameter growth of each tree over the 10 year interval was estimated at 2.81 Mg·ha^{-1}·year^{-1} for trees ≥10 cm DBH. Leaf production estimated from the allometric equations was 3.25 Mg·ha^{-1}·year^{-1}, for a total ANPP of 6.06 Mg·ha^{-1}·year^{-1}. Biomass increment was also estimated on the basis of statistical functions relating diameter growth to tree DBH for each species, based on a total of 2008 tree increment cores obtained in and around the study area (eq. 1; Table 4). The resulting estimate of biomass increment for trees ≥10 cm DBH in the Bird Area for 1991–2001 (2.93 Mg·ha^{-1}·year^{-1}) was within 5% of the value estimated from the mean diameter changes.

Discussion

Tree growth, mortality, and live biomass in the Hubbard Brook forest

Repeated measurements on W6, beginning in 1965, have indicated that live biomass accumulated rapidly until 1982, remained nearly constant for 15 years, and declined over the 1997–2002 interval (Fig. 2). Earlier projections had suggested that biomass aggradation in this second-growth forest would continue much longer (Whittaker et al. 1974; Bormann and Likens 1979). This earlier than expected cessation of live biomass accumulation has important implications for the health and carbon sequestration potential of this and other second-growth northern hardwood forests.

Fig. 4. Fluxes and pools associated with dead wood in the Bird Area forest at Hubbard Brook. All fluxes are Mg·ha^{-1}·year^{-1}. Solid lines indicate direct biomass transfers among pools. Broken lines indicate fluxes to the coarse woody debris (CWD) pool that result from fragmentation of standing dead and snags. Italicized values, associated with dotted lines, are estimated decomposition fluxes associated with standing dead trees and snags. For example, a mean of 0.77 Mg·ha^{-1}·year^{-1} of biomass was transferred annually from the living tree to standing dead pool. This process also delivers 0.15 Mg·ha^{-1}·year^{-1} of biomass to the CWD pool as broken branches and other detritus. An additional 0.29 Mg·ha^{-1}·year^{-1} of biomass was estimated to be lost through decomposition of the standing dead trees (for assumptions underlying these estimates see Methods).

Table 4. Coefficients for functions relating annual radial growth to diameter at breast height (DBH) for the three major hardwood species at the Hubbard Brook Experimental Forest.

Species	a	b	DBH$_0$
Sugar maple	1.186	1.277	63.49
American beech	1.134	1.139	30.71
Yellow birch	0.916	0.848	36.15

Note: The relationships were developed to describe tree growth patterns in the early to mid-1990s (Fig. 3). See eq. 1 for the definitions of a, b, and DBH$_0$.

mortality trends in the HBEF could be influenced by stand age-related factors (Gower et al. 1996) or by diseases or declines affecting particular species (Houston et al. 1979; Horsley et al. 2000).

Woody biomass increment has declined markedly in the HBEF since the original measurements of Whittaker et al. (1974) for 1956–1965. For the Bird Area, we estimated aboveground woody biomass productivity for trees ≥2 cm DBH as 3.28 Mg·ha^{-1}·year^{-1} (2.81 Mg·ha^{-1}·year^{-1} for 10 cm trees + 0.47 Mg·ha^{-1}·year^{-1} for 2–9 cm trees). Applying the recent radial growth data to the stand data for the lower two-thirds of W6 for the mid-1990s yields a similar estimate of aboveground biomass increment for W6 (3.39 Mg·ha^{-1}·year^{-1}). These values are much lower than values reported by Whittaker et al. (1974), who estimated aboveground biomass increment for the lower two-thirds of W6 to be 6.10 Mg·ha^{-1}·year^{-1} in the early 1960s. This 45% decrease in the growth rates of living trees has clearly made a significant contribution to the cessation of live biomass accumulation at the HBEF.

Radial growth measurements for the three dominant tree species provide valuable insights into the factors contributing to the decline in live biomass increment since 1956–1965. We used data from trees cored for the Whittaker et al. (1974) study and cores collected in the vicinity of the Bird Area in 1992–1996 to compare the radial growth rates in 1956–1965 and the early 1990s. Sugar maple and yellow birch both exhibited striking reductions in radial growth between 1956–1965 and the 1990s (Fig. 5); analysis of variance (ANOVA) revealed statistically significant differences in mean radial growth for both species in all size classes (10–20, 21–30, 31–40, and >40 cm). For sugar maple, the mean radial growth declined by more than 50% in all size classes below 40 cm between 1956–1965 and the 1990s. Yellow birch radial growth declined by more than 50% in the 21–30 and 31–40 cm size classes in the same period. Surprisingly, despite widespread infection by beech bark disease beginning in the early 1970s, radial growth rates in American beech have not declined as dramatically (Fig. 5). Declines in mean radial increment for beech between 1956–1965 and the 1990s were only significant in the 21–30 and 31–40 cm DBH classes and were 33% and 29%, respectively, much less than the declines observed for sugar maple and yellow birch. Thus, although declines in tree growth rates are evident in all the principal hardwood species at the HBEF, the changes are not uniform.

Our detailed measurements in the Bird Area forest provide a basis for demonstrating the spatial extent of this pattern and for evaluating the factors contributing to the pattern. The forest of the Bird Area increased only slightly in live biomass over the 20 years between 1981 and 2001 (Fig. 2), suggesting that the observations for W6 apply throughout much of the larger Hubbard Brook Valley.

The dynamics of live biomass in forests depend upon species-specific patterns of tree recruitment, growth, and mortality (Harcombe 1987). Changes in these factors must account for the shift from live biomass aggradation to near steady state that occurred in about 1980 (Fig. 2). A decrease in recruitment rates is unlikely to have accounted for a major portion of the recent reduction in live biomass accumulation. Recruitment into the ≥10 cm DBH class made only a minor contribution to changes in live biomass during 1991–2001 in the Bird Area (0.29 Mg·ha^{-1}·year^{-1}). In 1965–1982, total live biomass of trees ≥10 cm DBH in the lower two-thirds of W6 increased at a mean rate of 3.6 Mg·ha^{-1}·year^{-1}, so the number and biomass of recruited trees would have to have been an order of magnitude larger than at present to explain the observed decrease in biomass accumulation. Hence, either decreased growth rates or increased mortality of pre-existing stems, or both, must account for the sharp slowing of live biomass accumulation. Tree growth and

The contribution of increased mortality to the leveling of live biomass between 1965 and 1982 cannot be quantified

Fig. 5. Mean radial increment in various size classes of sugar maple, American beech, and yellow birch at the Hubbard Brook Experimental Forest in 1956–1965 and the 1990s. Error bars are SEs. All comparisons between 1956–1965 and 1990s values were statistically significant ($P \leq 0.01$), except the two marked not significant (NS).
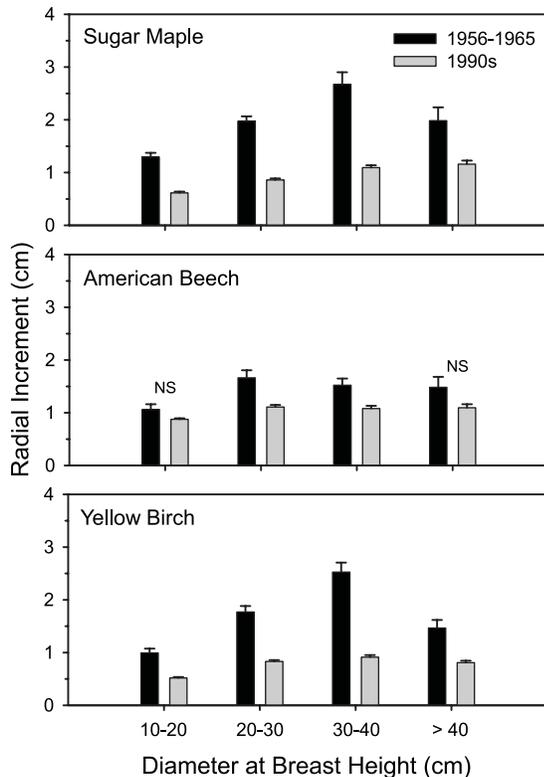
directly, because mortality rates have only been measured since 1991. Nevertheless, the recent mortality observations provide useful insight about its contribution. The present rate of net annual aboveground biomass accumulation in trees ≥ 10 cm on the lower two-thirds of W6 (-0.1 Mg·ha^{-1}·year^{-1}) represents a decrease of 3.7 Mg·ha^{-1}·year^{-1} from 1965–1982 values (3.6 Mg·ha^{-1}·year^{-1}). The mean aboveground biomass of dying trees in the Bird Area was 2.24 Mg·ha^{-1}·year^{-1} during 1991–2001. Therefore, even if mortality was zero in 1965–1982, the present-day mortality could account for only about 60% of the decline in biomass accumulation. Our observations provide no evidence of major changes in mortality. The density of standing dead trees and snags in the Bird Area actually decreased in 1981–2001, and the biomass of those trees remained approximately constant (Table 1*b*). Furthermore, field measurements of CWD on W6 in 1978 (10.9 ±2.2 Mg·ha^{-1}; Tritton 1980) and 1995 (9.4 ± 0.9 Mg·ha^{-1}; Fahey et al. 2005) suggest little or no change in the number or mass of fallen trees.

Interestingly, although we expected relatively high mortality for beech (owing to beech bark disease) and sugar maple (reflecting recent slow growth), these species had much lower mortality rates than yellow birch (Table 3). Furthermore, yellow birch contributed 29% of the aboveground biomass of dying trees; hence, the two species known to be under environmental stress cannot, through their mortality, explain the plateau in live biomass in the Bird Area.

Some additional observations about these three species provide a wider context for interpreting trends in mortality and live biomass accumulation at the HBEF. First, although sugar maple mortality in the Bird Area has been low, this species has exhibited localized high mortality in the experimental watersheds at the HBEF. For example, 40% of the sugar maple stems in the upper elevation zone of W6 died between 1987 and 2002 (~2.7%·year^{-1}; Juice et al. 2006). Although the greatest documented mortality of sugar maple has occurred at elevations above the Bird Area, the reduced growth rates we observed (Fig. 5) suggest more widespread increases in sugar maple mortality at the HBEF in coming years.

Declining growth rates in sugar maple are a regional phenomenon (e.g., Long et al. 1997; Watmough 2002), suggesting that reduced rates of biomass accumulation may be occurring in many forests where sugar maple is a major component. Moreover, it is likely that soil Ca depletion (Likens et al. 1998) is responsible in part for this decline. Calcium treatment on watershed 1 has resulted in amelioration of canopy decline and stimulation of regeneration of sugar maple at the HBEF (Juice et al. 2006). As detailed in recent studies (Juice et al. 2006, Schaberg et al. 2006), low Ca availability appears to limit the distribution, growth, and health of sugar maple through a complex suite of mechanisms.

Second, although changes in growth and mortality of beech have been less dramatic than in sugar maple and yellow birch, infection by beech bark disease is likely to predispose beech to high mortality in the future, as has been commonly observed in other regions (Twery and Patterson 1984). In fact, high beech mortality was observed in parts of the HBEF following a severe ice storm in 1998 (Rhoads et al. 2002). Third, reduced growth and increased mortality of yellow birch reflect trends observed in mature forests of other northern hardwood regions (Manion and Griffin 2001). However, in an old-growth forest at the nearby Bowl Research Natural Area, basal area of yellow birch increased markedly from 1974 to 1994 (Martin and Bailey 1999).

Finally, it is possible that changes in climate may help explain the patterns in live biomass accrual at Hubbard Brook. Modeling results suggest that the northern hardwood forest type is likely to diminish in area under a variety of future climate scenarios (Iverson and Prasad 2001). However, elevation trends in mortality, especially sugar maple, argue against this hypothesis. A warming climate should favor sugar maple at higher elevations, where northern hardwoods currently give way the spruce–fir stands. Yet, we observe the greatest sugar maple mortality in these high-elevation stands.

In sum, the cessation of live biomass accumulation on the south-facing slopes of the Hubbard Brook Valley since 1982 appears to be driven primarily by reduced growth rates, especially of sugar maple and yellow birch. Increased mortality has not been a major factor across the Bird Area, but has had a profound impact in areas affected by the 1998 ice storm and in high-elevation stands with substantial amounts of sugar maple.

Forest demography

In the immediate future, it is likely that the abundance of

American beech in this forest will increase because beech dominates tree recruitment in both the Bird Area and the W6. Moreover, a large cohort of beech currently is moving up through smaller size classes (2–9 cm). This latter cohort is probably related to the impact of beech bark disease. Beech sprouts prolifically from its roots during the decline from beech bark disease (Jones and Raynal 1986), and the mean age of 79 beech saplings (0.3–2.5 cm DBH) in the study area was 26 years in 1996, suggesting an increase in sprouting about the time of the arrival of the beech bark disease (early 1970s). Based on radial growth measurements for these and larger beech saplings, 30–40 years will elapse until this cohort of beech reaches the 10 cm DBH class unless widespread overstory mortality releases these saplings from competition. The dynamics of beech saplings and pole trees is the dominant population process in the forest on the south-facing slope of the HBEF; however, this phenomenon is not as strong in other areas of the Hubbard Brook Valley, where the abundance of beech is lower (Schwarz et al. 2003).

This sort of demographic behavior does not fit simply into the generalized stand development model of Oliver and Larson (1990), both because of the complex history and age structure of this forest and because of the effects of the exotic beech bark disease complex. One would expect the dominant age class that was released from competition by the heavy cutting of 1910–1920 (Likens 1985) to be moving from the stem exclusion to the old-growth stage (Oliver and Larson 1990). However, the recruitment pattern in the HBEF also includes influences from the dynamics of older stems that pre-date the 1910–1920 period, disturbance by the 1938 hurricane and subsequent salvage logging (C. Cogbill, unpublished data), and recent beech sprouting. This complex behavior may be typical of many second-growth northern hardwood forests of the region that were heavily, but selectively, logged at the time of the first cuts of the primary forest (Volk and Fahey 1994; Whitney 1994). In the mid-term future, the overstory composition of this forest is likely to undergo significant changes owing to the rapid shifts in growth, recruitment, and mortality of the dominant species.

Dynamics of woody detritus

The dynamics of the woody detrital pool, as well as its role in both ecosystem organic matter and heterotroph population dynamics (e.g., as animal habitat), depend upon how dying trees move through three broad categories of woody detritus: standing dead trees, snags, and CWD on the ground. In the 10 years of our tagged-tree inventory, most of the dying trees and dead tree biomass entered the standing dead pool (Figs. 3 and 4). Thereafter, a majority of the standing dead trees passed through the snag pool before finally falling to the ground. Because we repeatedly inventoried the populations of standing dead trees and snags between 1991 and 2001, we were able to estimate the residence time of stems in each of these categories. An average standing dead tree remained standing in this forest for ~7.5 years, whereas an average snag remained standing for ~15 years. In terms of animal habitats, the relatively rapid turnover of the standing dead and snag pools in the northern hardwood forest results in a low density of such habitats in a

northern hardwood ecosystem near steady state (65–70 stems·ha^{-1}; Fig. 3). This value is much lower than for subalpine conifer forests in the northeastern United States (Tritton and Siccama 1990).

The aboveground biomass of standing dead wood and snags exhibited negligible changes over 20 years of forest inventory in the Bird Area plots (10.4–9.7 Mg·ha^{-1}; Table 1b). We estimated the input of aboveground biomass to the CWD pool from falling and fragmenting trees to be 1.64 Mg·ha^{-1}·year^{-1} (Fig. 4). Because there has been no significant change in the CWD pool, this large annual addition to the detrital pool on the ground appears to be approximately matched by microbial decomposition. Because both the CWD pool and the mortality rates (Table 3) appear to be at or near steady state, we can estimate the residence time of biomass in the CWD pool using the mean of the two pool estimates (10.2 Mg·ha^{-1}) and the estimated input (1.64 Mg·ha^{-1}·year^{-1}). The resulting value of 6.2 years compares well with the half-life of decomposing bole wood measured on HBEF watershed 2 (7.2 years; Arthur et al. 1993). In the long term, we might anticipate a gradual increase in the CWD pool, because values for old-growth northern hardwood forests in the region are generally higher than for W6 (McGee et al. 1999); presumably the break-up of the largely even-aged overstory canopy in later stages of stand development causes an increase in the CWD pool.

Finally, CWD represents an important source of biomass to the forest floor at Hubbard Brook. Our estimated input to CWD (1.64 Mg·ha^{-1}·year^{-1}) is similar in magnitude to the combined inputs to the forest floor of fine (1.71 Mg·ha^{-1}·year^{-1}) and coarse (0.20 Mg·ha^{-1}·year^{-1}) litterfall reported by Fahey et al. (2005). The pool of CWD on W6 (10.2 Mg·ha^{-1}) is about one-sixth of the organic matter pool in the forest floor in 1997 (65 Mg·ha^{-1}; Fahey et al. 2005). The forest floor measurement technique used at the HBEF excludes CWD, so these values suggest that CWD represents about 15% of the organic matter at the soil surface. Unfortunately, little is known about the rate of incorporation of woody debris into the soil and the rate of decomposition of buried wood.

Primary productivity and ecosystem productivity

The ANPP can be calculated as the sum of woody biomass increment (bole wood and bark, branches, and twigs) and the growth of nonperennial tissues (mostly leaves). The former averaged 3.28 Mg·ha^{-1}·year^{-1} in the Bird Area based on measured diameter changes from 1991 to 2001. The latter is calculated from our site-specific allometric equations, assuming there have been no changes in the relationships between tree volume and leaf biomass since the equations were developed (Whittaker et al. 1974; Siccama et al. 1994). Estimated leaf production under this assumption was similar in 1965 and the mid-1990s at 3.25–3.26 Mg·ha^{-1}·year^{-1}. We can test the assumption by comparing the fine litterfall (leaves, fruits, buds, small twigs, and bark fragments) flux adjacent to W6 in 1969–1970 (3.52 Mg·ha^{-1}·year^{-1}; Gosz et al. 1972) and 1992–1998 (3.42 Mg·ha^{-1}·year^{-1}; Fahey et al. 2005). Hence, ANPP for the northern hardwood forest on the south-facing slope of the HBEF between 500 and 700 m elevation is estimated to be 6.54 Mg·ha^{-1}·year^{-1} (3.28 + 3.26). This level of ANPP is at the lower end of the range for deciduous forests in the north-

ern temperate zone and for *Acer* dominated forests worldwide (Fahey et al. 2005).

The measured ANPP in the northern hardwood forest at the HBEF in the 1990s was 31% lower than estimates for the lower two-thirds of W6 for the 1956–1965 period (9.4 Mg·ha^{-1}·year^{-1}; Whittaker et al. 1974). This 10 year value itself represents the mean of two quite contrasting 5 year estimates (1956–1960: 10.44 Mg·ha^{-1}·year^{-1}; 1961–1965: 8.39 Mg·ha^{-1}·year^{-1}). Whittaker et al. (1974) attributed the decrease in the second pentad to the effects of a severe drought during that interval. Alternatively, the decline observed by Whittaker et al. (1974) may have resulted from forest development patterns following disturbance. Significant overstory damage occurred in W6 as a result of the 1938 hurricane (C. Cogbill, unpublished data). Release from competition may have stimulated tree growth thereafter, with a gradual decline in ANPP accompanying canopy closure.

The more recent decline in ANPP in this forest (between 1965 and 1990s) has not been accompanied by changes in leaf production but, rather, is associated entirely with reduced woody biomass growth. Smith et al. (2002) estimated woody biomass increment on W6 for the late 1990s using a simple model parameterized with hyperspectral measurements of canopy nitrogen concentration. Their estimate (3.71 Mg·ha^{-1}·year^{-1} for stems ≥5 cm DBH) was also much lower than the Whittaker et al. (1974) measurements, a difference that they tentatively attributed to age-related decline in forest NPP (Gower et al. 1996). Our measurements of tree growth rates suggest more complex causes: the magnitude of the recent growth decline is particularly great for sugar maple (Fig. 5), a species that has also exhibited high mortality in parts of W6 and reduced recruitment in the 2–10 cm DBH classes on W6 (Juice et al. 2006). The forest production efficiency of the W6 forest, expressed either on a leaf area basis (ANPP/LAI = 1.12; ANPP in Mg·ha^{-1}·year^{-1}) or on a leaf mass basis (1.76) was lower than for other *Acer* dominated forests around the world (ANPP/LAI = 1.33–1.93; ANPP/mass = 1.80–2.19; Fahey et al. 2005). These observations support the suggestion that unusual stresses may be reducing NPP at the HBEF (Likens et al. 1998).

Net ecosystem productivity (NEP) at the HBEF was near zero in the 1990s, based on minimal changes in live biomass, CWD, and forest floor and mineral soil organic matter (Fahey et al. 2005). Trends in live biomass in the study area are small in magnitude, but not uniform; among four sample transects of 2.5 ha each in the Bird Area, two exhibited decreasing biomass from 1981 to 2001 at the rate of about 0.38 Mg·ha^{-1}·year^{-1}, whereas the other two increased at about 1.13 Mg·ha^{-1}·year^{-1}. Live biomass in the lower two-thirds of W6 decreased slightly from 1982 to 2002 (Fig. 2). Similarly, trends in the biomass of standing dead trees and snags differed slightly among sample areas, decreasing at about 0.04 Mg·ha^{-1}·year^{-1} in the Bird Area forest (Table 1*b*) and increasing at 0.46 Mg·ha^{-1}·year^{-1} in W6. Finally, CWD in W6 showed an insignificant decreasing trend of 0.09 Mg·ha^{-1}·year^{-1}. Although precise bounds cannot be placed on our estimates because of the varied data sources and sampling units (Fahey et al. 2005), these values suggest that NEP in the HBEF is probably slightly positive but departs from zero by less than 0.5 Mg·ha^{-1}·year^{-1}.

By comparison, NEP (measured aerodynamically as NEE) for several European forests in the late 1990s ranged from −1.8 to 13.2 Mg·ha^{-1}·year^{-1} (Valentini et al. 2000). A young beech forest in France exhibited NEP of 4.4–5.1 Mg·ha^{-1}·year^{-1} in 1996–1997, and NEP of a postagricultural mixed-deciduous forest in Massachusetts was estimated at 2.8–5.6 Mg·ha^{-1}·year^{-1} (Goulden et al. 1996). Two sub-boreal broadleaf forests in Canada exhibited a 3 year (1996–1998) mean NEP of 3.0 Mg·ha^{-1}·year^{-1} (Barr et al. 2002). Hence, the current NEP of the HBEF clearly is much lower than for most northern temperate zone broadleaf forests that have been measured aerodynamically. Prior to 1982, however, NEP in the Hubbard Brook forest averaged 3.5–4.0 Mg·ha^{-1}·year^{-1}, which is in line with other deciduous forests cited above.

Northern forests are presently thought to be a large sink for atmospheric carbon (Fan et al. 1998). Aerodynamic measurements have proven valuable for documenting and quantifying that flux (Valentini et al. 2000) and its apparent dependence on annual climatic variations (Goulden et al. 1996; Barr et al. 2002). However, the requirement of unbroken topography for siting such studies (Lee et al. 1999) limits the range of landscapes that can be measured. Our measurements of pool size changes for the HBEF indicate that current NEP is not much different than zero at the age of about 80 years from the last heavy cutting. The HBEF apparently reached that state in the early 1980s, ~60 years after large-scale harvesting. The driving factor for the abrupt decrease in NEP at the HBEF in 1980 was diminished wood growth in two of the dominant species: sugar maple and yellow birch. Interestingly, at Harvard Forest, where positive NEP has been observed (Goulden et al. 1996), the forest is dominated by oak and pine, which appear to be more tolerant of low base cation levels than sugar maple. The growth decline in sugar maple is not a local phenomenon, having been observed in sites as distant as Pennsylvania (Long et al. 1997) and Ontario (Watmough 2002). Taken as a whole, our results may be typical for many forests in the complex landscapes of the Appalachian highlands, and suggest that second-growth forests in the northern temperate zone may not be the substantial carbon sink that some have proposed.

Conclusions

The biomass of the tree stratum on the south-facing experimental areas of the HBEF was essentially constant from the early 1980s to the early 2000s. Our results can be used to draw the following conclusions regarding the causes of this plateau and its implications for ecosystem productivity and carbon cycling:

1. Decreases in the growth rates of living trees were primarily responsible for the cessation of biomass accumulation in living trees. Changes in recruitment and mortality rates can account for only a minor fraction of the change in biomass accumulation rates.

2. Changes in growth rates were not consistent across the major canopy tree species. Sugar maple exhibited the most striking reduction in radial growth, followed by yellow birch. Despite extensive infection with the beech bark disease complex, radial growth in American beech

decreased less dramatically than sugar maple and yellow birch.

3. The current ANPP in this forest is low in relation to other temperate-zone deciduous forests and is 31% lower than in 1956–1965. The decrease in ANPP is entirely due to decreased growth of woody tissues.

4. With pools of live biomass, detrital wood, nonwoody litterfall, and soil organic matter at or near steady-state, it appears that the NEP of this forest is near zero. Like ANPP, this NEP value is low compared to published values for similar forests.

The complex disturbance history at sites like Hubbard Brook makes it difficult to conclusively assign causes to the reduced growth rates that we have observed in this second-growth forest. The hypothesis that reduced growth is due to age-related declines in NPP (Smith et al. 2002) is not fully supported. In particular, growth rate reductions were strongly species dependent, which one would not expect if the forest were reaching steady-state NPP. The causes of growth decline at Hubbard Brook appear to be complex and vary among species. Interestingly, despite widespread evidence of beech bark disease, there is no evidence of increases in mortality, and beech growth rates have declined less than sugar maple and yellow birch. Nevertheless, the high mortality of beech in areas affected by the 1998 ice storm and observations of beech bark disease-related mortality in similar forests (Twery and Patterson 1984; Forrester et al. 2003) suggest that it may be only a matter of time before widespread effects are seen at the HBEF. In the case of sugar maple, we observed decreases in radial growth in mid-elevation forests such as the Bird Area and unusually high mortality (2.7%·year^{-1}) at higher elevations in W6. These observations fit into a regional pattern of declining health of this economically important tree, possibly owing to stresses related to Ca availability (Horsley et al. 2000; Juice et al. 2006). Recent research at the HBEF indicates that decades of acid precipitation have resulted in substantial declines in the pool of available Ca in the soil, perhaps as much as 50% (Likens et al. 1998; Johnson et al. 2000). Therefore, the cessation of biomass accumulation at the HBEF may be at least partly due to anthropogenic causes.

Acknowledgements

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