

OLD-GROWTH FORESTS: AN ECOSYSTEM APPROACH

Structural characteristics and aboveground biomass of old-growth spruce–fir stands in the eastern Carpathian mountains, Ukraine

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Abstract

Temperate old-growth forests are known to have ecological characteristics distinct from younger forests, but these have been poorly described for the remaining old-growth *Picea abies*–*Abies alba* forests in the eastern Carpathian mountains. In addition, recent studies suggest that old-growth forests may be more significant carbon sinks than previously recognized. This has stimulated interest in quantifying aboveground carbon stocks in primary forest systems. We investigated the structural attributes and aboveground biomass in two remnant old-growth spruce–fir stands and compared these against a primary (never logged) mature reference stand. Our sites were located in the Gorgany Nature Reserve in western Ukraine. Overstory data were collected using variable radius plots; coarse woody debris was sampled along line intercept transects. Differences among sites were assessed using non-parametric statistical analyses. Goodness-of-fit tests were used to evaluate the form of diameter distributions. The results strongly supported the hypothesis that old-growth temperate spruce–fir forests have greater structural complexity compared to mature forests, including higher densities of large trees, more complex horizontal structure, and elevated aboveground biomass. The late-successional sites we sampled exhibited rotated sigmoid diameter distributions; these may reflect natural disturbance dynamics. Old-growth Carpathian spruce–fir forests store on average approximately 155–165 Mg ha⁻¹ of carbon in aboveground tree parts alone. This is approximately 50% higher than mature stands. Given the scarcity of primary spruce–fir forests in the Carpathian region, remaining stands have high conservation value, both as habitat for late-successional species and as carbon storage reservoirs.

Keywords: *Old-growth, temperate spruce–fir, forest carbon, stand structure, forest development, ecosystem services*

Introduction

Temperate old-growth forests are recognized as having ecological characteristics distinct from younger forests, including high levels of carbon storage (Luyssaert et al. 2008; Keith et al. 2009), structurally complex habitats for late-successional species (Stoyko 1998; Lindenmayer & Franklin 2002), and effects on habitat structure in forested streams (Keeton et al. 2007). There is growing understanding of the processes associated with development of these characteristics over time, such as interactions between successional dynamics and natural disturbances (Franklin et al. 2002). As our knowledge of these dynamics has advanced,

scientists have experimented with new silvicultural systems designed to reproduce or restore a degree of old-growth character in actively managed forests (Keeton 2006; Bauhus et al. 2009; Chernyavskyy 2009). The objective is to increase ecological connectivity, for instance, linking and buffering reserves, by providing late-successional habitat characteristics where these are currently under-represented on the landscape (Keeton 2007). The development of restorative silvicultural systems is guided by improved understanding of the structural characteristics associated with old-growth forests. Similarly, efforts to protect high conservation value forests require information on the ecosystem services provided by different forest types and

developmental conditions. Yet these remain poorly described in some temperate forest systems, particularly where old-growth examples are rare.

In this paper we describe the structural characteristics of old-growth *Picea abies* (Norway spruce)–*Abies alba* (European silver fir) stands in the Carpathian mountains of western Ukraine and compare these against a younger reference stand. Our objective is to identify key structural attributes associated with late stand development in Carpathian temperate spruce–fir ecosystems, by contrasting the conditions encountered in different late-successional age classes (i.e., mature vs. old-growth). The hypothesis tested is that old-growth temperate spruce–fir forests exhibit a higher degree of structural complexity compared to mature stands, based on an evaluation using selected indicator metrics (see Keeton 2006; McElhinny et al. 2006).

We also explore the question of whether temperate spruce–fir forests exhibit similar structural characteristics associated with old-growth systems in other regions of the world. In this respect a particular focus is aboveground biomass, due to the importance of understanding forest carbon storage dynamics in relation to global climate change. A critical source of uncertainty pertains to the dynamics of carbon accumulation and net ecosystem productivity (NEP) in late-successional systems. Whereas long-standing theoretical models predicted attainment of equilibrium (or stable) NEP in mature to early old-growth developmental stages (Odum 1969; Bormann & Likens 1979), the recent empirical evidence suggests the potential for continued net positive biomass accumulations very late into stand development (Luyssaert et al. 2008). Sustained biomass accumulations over long time periods result in high levels of carbon storage, signaling an important role for old-growth forests in global carbon cycling and climate change mitigation (Pregitzer & Euskirchen 2004; Rhemtulla et al. 2009). By contrasting biomass in mature and old-growth stands, our objective is to evaluate whether there is evidence of similar trends in Carpathian spruce–fir forests.

While there is a rich literature on stand dynamics in old-growth boreal spruce ecosystems (e.g., Hofgaard 1993; Hornberg et al. 1995; Holeksa et al. 2008), and managed spruce plantations (e.g., Fries et al. 1997; Seidl et al. 2008), such as those that now dominate much of the Alps and Carpathian region of central and eastern Europe, considerably less is known about the old-growth developmental stage in primary (never cleared or logged) spruce–fir forests. Previous research has identified the potential for very high levels of biomass development in remnant stands of primary spruce–fir in the eastern Carpathians of Czech Republic, Poland, and Slova-

kia (Szwagrzyk & Gazda 2007; Holeksa et al. 2009). However, it remains uncertain whether these are representative of the broader region. Moreover, the previous work has often relied on single-plot inventories, which do not capture horizontal structural complexity, such as canopy gaps and associated variations in stand density and disturbance histories. Patch heterogeneity is considered as a distinguishing characteristic of temperate old-growth ecosystems with fine-scaled disturbance regimes (Leemans 1991; Runkle 2000; Franklin & Van Pelt 2004). Inadequate sampling of horizontal variability can lead to over-estimates of aboveground biomass and other structural characteristics linked to gap or patch dynamics. Our intent was to address this limitation in some previous research through intensive subsampling of multiple stands.

Research on Carpathian forests has taken on a new significance with the growing awareness of the region's unique ecological values (Palang et al. 2006; Soloviy & Keeton 2009), cultural traditions tied to forest resources (Sikor 2003; Elbakidze & Angelstam 2007), and increasingly prevalent anthropogenic stress and land cover change (Grodzki et al. 2004; Kuemmerle et al. 2007, 2009; Main-Knorn et al. 2009). The Carpathian mountains harbor the largest stands of old-growth European beech (*Fagus sylvatica*) remaining in Europe, and have both high levels of floristic endemism as well as a full complement of native mammal diversity. Conservation and sustainable forest management in the region are thus of high priority for Carpathian nations and international environmental organizations (Soloviy & Cubbage 2007; Keeton & Crow 2009), as evidenced by the Carpathian Convention of 2003. Old-growth beech and mixed beech–conifer stands have been the focus of much past and on-going research (e.g., Szwagrzyk & Szewczyk 2001; Chernyavskyy 2005; Commarmot et al. 2005; Nagel et al. 2006). However, the available data for primary spruce–fir systems in the eastern Carpathians are more limited, though information is available for several well-studied stands in the western Carpathians and Austrian Alps (e.g., Hasenauer et al. 2005; Splechtna et al. 2005; Szwagrzyk & Gazda 2007). One reason is the extreme rarity of native, old-growth spruce–fir due to landscape scale conversion of primary forests to secondary plantations, which included widespread planting of genetically non-endemic (e.g., central European) varieties of *P. abies* (Irland & Kremenetska 2009). The loss of native spruce–fir has contributed to the spruce dieback and forest health problems now being experienced across the Carpathians (Badea et al. 2004); the dieback has been especially severe in the western portion of the range (Longauer et al. 2004; Main-Knorn 2009). Consequently, data on old-growth characteristics are

needed to guide conservation of remaining primary forests and long-term restoration of endemic late-successional forest composition and structure on the managed landscape.

Methods

Study area and sites

Our study was conducted in the 5344 ha Gorgany Nature Protection/Scientific Reserve (or “zapovidnik”) located in the central portion of the Carpathian mountains in the Ivan Frankivski region of western Ukraine (Figure 1). The Gorgany Reserve was established in 1996 to protect examples of rare primary forest types, including 460 ha of old-growth spruce and fir. The topography is characterized by steep, asymmetric slopes, including sandstone talus, with elevations ranging from 710 to 1755 m above sea level (m a.s.l.). Soils are predominantly brown neopodzols and podzols, while the montane surficial geology is Carpathian flysch with additions of sand, clay, and marl slates of Cretaceous and Quaternary origins. Average temperature of the warmest month (July) is +16°C, and for the coldest month (January) is +1°C (mean annual temperature is +7°C). Mean annual precipitation ranges from 680 to 900 mm. Mean annual relative humidity is approximately 80%.

Our study sites were located in the mixed temperate spruce–fir elevation zone, which extends from approximately 870 to 1200 m a.s.l. The sites are dominated by Norway spruce and silver fir, with only minor (<1%) components of deciduous hardwoods, including European beech, silver birch (*Betula pendula*), and sycamore maple (*Acer pseudo-platanus*). Spruce and fir at our sites achieve maximum ages of approximately 350–400 years, with maximum heights and diameters of 53 and 1.6 m, respectively (Chernyavskyy unpublished data). The natural disturbance regime is characterized by fine-scaled mortality agents, including insects, fungal pathogens, and low to moderate intensity wind events causing damage to single or small groups of trees (Lavnyy & Lassig 2003). Popa (2008), however, reported an increase of high intensity windthrow events for the eastern Carpathians of Romania over the twentieth century. This indicates that larger disturbances do occur in the Carpathian range.

Previous researchers identified two core areas (contiguous stands > 100 ha) of old-growth spruce–fir forest within the preserve, one northwestern facing and the other on a southwestern aspect. These comprised our two “old-growth” sites and had average dominant tree ages of approximately 250 years based on an examination of several



Figure 1. Map showing the location of the research area. The map displays a portion of the Carpathian mountain region in western Ukraine.

(illegally) cut stumps on the periphery of each area. An area of primary forest with dominant canopy tree ages of approximately 100–150 years (based on increment coring) was located adjacent to the south-western-facing old-growth site and at the same elevation. This site was designated as the “mature” site and used as a reference stand (Figure 2). The mature stand was most likely established following a high intensity windthrow event, which is reflected by the presence of a few scattered residual old-growth trees.

Data collection

The field data were collected in October 2008. At each site, we established non-permanent, variable radius prism plots (2.3 metric basal area factor) to inventory forest structure and composition. Species, diameter at breast height (dbh, 1.37 m ht.), and vigor Classes (1–9) were recorded for all live and dead trees. Tree heights were measured using a laser range finder. There were nine plots at one old-growth site, four at the other, and seven at the mature site. Sampling intensity varied due to time limitations, but was generally proportionate to stand area. Plots were distributed throughout each stand and located through a randomized survey method. This involved establishing plot coordinates at vari-

able distances and bearings (generated from a random number table) from a point of origin located in the center of each stand. The inventory plots did not coincide with any visible cut stumps.

Downed coarse woody debris (CWD) was inventoried using a line intercept method following Warren and Olsen (1964) as modified by Shivers and Borders (1996). This was conducted along line transects linking each prism (overstory) plot. Transects thus varied in length from 30 to 70 m and had randomized orientation and location. We surveyed downed logs >10 cm diameter at intercept and >1 m length. Logs were assigned to decay Classes (1–5) following Sollins (1982).

Data analysis

Field data were input into the Northeast Ecosystem Management Decision Model (Twery et al. 2005) or Microsoft Excel spreadsheets to generate an array of stand structure and composition metrics, including key variables, such as large tree density and CWD volume, determined by previous studies to be indicative of stand structural complexity (McElhinny et al. 2006; Whitman & Hagan 2007). We used a threshold of 50 cm dbh for large tree classification, both live and dead. CWD volume was evaluated both as a total for all decay classes and as a sub-total for Classes 3 and



Figure 2. Left: One of the old-growth study sites (Gorgany 2). Note the stand structural complexity as indicated by large snags, downed woody debris, and spatial heterogeneity in tree density. Right: The mature reference site. Note the lesser degree of structural complexity, including the relatively homogeneous spatial distribution of trees.

4, the latter classes being well decayed, though physically intact, and often the most biologically available as habitat (McKenny et al. 2006). The variable set also included estimates of aboveground tree biomass produced by diameter-based allometric equations from Jenkins et al. (2003), which we modified for the central/eastern European region following Zianis et al. (2005).

We used PASW Statistics 17.0 software (SPSS, Inc.) for statistical analyses of the dataset. All variables were checked for normality using the Shapiro–Wilk test, with the data stratified by site. This revealed evidence of significant site-specific departures from normality for 10 of the 16 structural variables we assessed. Consequently, we used non-parametric tests to compare all the biometrics between sites. These analyses employed the Kruskal–Wallis test followed by multiple comparisons using the Mann–Whitney *U*-test. Our statistical population of interest was the diversity of patches within each site. Thus, inventory plots or transects were treated as independent data points, which was appropriate for an analysis at this spatial scale (Peterson 2000; Burrascano et al. 2008).

We analyzed live tree diameter distributions to determine whether their forms were statistically different from a rotated sigmoid distribution, which is frequently associated with old-growth forest structure (O’Hara 1998; Goodburn & Lorimer 1999). A sigmoidal curve was generated by distributing the total live stem density for each stand among 5 cm diameter classes, using a *q* factor (the ratio of tree densities in successively larger diameter classes) of 2.0 in the smallest size classes, 1.1 for medium size trees, and 1.3 in the largest size classes. The application of a non-constant *q* factor has been shown to approximate the form of a rotated sigmoid diameter distribution (Keeton 2006). Both the hypothesized sigmoidal and observed diameter distributions were log transformed to enhance sigmoidal tendencies (Leak 2002). We then examined the statistical congruence between the sigmoid and observed distributions using the Kolmogorov–Smirnov (KS) two-sample goodness-of-fit test. All statistical tests were considered significant at $\alpha = 0.05$.

Results

Aboveground biomass

There were significant differences between the sites in aboveground biomass and stand structural complexity based on the Kruskal–Wallis and multiple comparison results (Table I). Both old-growth sites had significantly greater aboveground total (mean = 309.53 Mg ha⁻¹) and live (mean = 279.14 Mg ha⁻¹) biomass compared to the mature site (202.83 and 181.25 Mg ha⁻¹, respectively). There

were also statistically significant contrasts between the two old-growth sites, with one (northwestern facing) having intermediate biomass levels and the other (southwestern facing) having the highest biomass. These differences signal a range of structural variability within the old-growth age class, attributable to site-specific differences.

While the two old-growth sites had higher mean aboveground dead tree biomass, these were not statistically different from the mature site due to the high degree of spatial variation, as indicated by the wide error range generated from sub-sampling at each old-growth site (see Table I). However, this spatial variation itself was statistically greater for the old-growth sites ($p < 0.001$), based on a Kruskal–Wallis test comparing standard deviations.

Stand structure characteristics

There were other structural characteristics that differed between the sites. In comparison to the mature site (see Table I for values), the two old-growth sites had significantly lower live tree densities (mean = 532 stems ha⁻¹), and significantly greater mean stand diameters (mean = 31.05 cm), quadratic mean diameters (QMDs, mean = 35.12 cm), and large tree densities (mean total = 84 stems ha⁻¹; mean live = 76 stems ha⁻¹). Consistent with its higher aboveground biomass (Brown et al. 1997), the southwest-facing old-growth site also had higher large live tree densities compared to the other old-growth site. This difference between the two old-growth sites held true also for mean stand diameter and QMD (which is the diameter of the tree of average basal area).

Canopy closure did not differ significantly, but the lowest level (80%) was achieved in an old-growth site (Gorgany 2, northwest facing) with a high frequency of canopy gaps. Mean values for live and total basal areas appeared somewhat higher in the old-growth sites, but these differences were not statistically significant, possibly indicating that basal area and aboveground biomass do not consistently co-vary in these systems. We observed that basal area varied widely among sample plots at the old-growth sites, reflecting horizontal structural complexity influenced by gap dynamics, whereas horizontal structure was more homogenous in the mature stand (i.e., lower variance among sample plots). At the old-growth sites, our sample plots encountered recent canopy gaps with very low basal areas, older gaps with high densities of small diameter stems, and closed canopy matrix with widely spaced large trees and little tree regeneration.

Spatial heterogeneity lowered mean basal area values, resulting in the aforementioned lack of statistical significance, and supporting the need for either

Table I. Kruskal–Wallis test ($df = 2$) results and Mann–Whitney U multiple comparisons for structural variables.

Forest structure variable	Mean values (\pm one standard error)			Kruskal–Wallis test Statistic	Significance	Multiple comparisons ($\alpha = 0.05$)
	Gorgany 1 (mature)	Gorgany 2 (old-growth)	Gorgany 3 (old-growth)			
Stocking						
Basal area ($m^2 ha^{-1}$)						
Total	45.26 (2.33)	47.70 (2.59)	53.95 (1.15)	4.034	$p = 0.133$	
Live	40.67 (8.46)	43.62 (2.13)	47.63 (1.44)	2.192	$p = 0.334$	
Dead	4.59 (1.94)	4.08 (1.37)	6.31 (1.96)	1.045	$p = 0.593$	
Aboveground biomass ($Mg ha^{-1}$)						
Total	202.83 (8.44)	280.04 (18.89)	339.02 (9.48)	12.573	$p < 0.002$	Gorgany 2 & 3 > Gorgany 1 Gorgany 3 > Gorgany 2
Live	181.25 (14.99)	255.49 (13.78)	302.98 (8.26)	12.573	$p < 0.002$	Gorgany 2 & 3 > Gorgany 1 Gorgany 3 > Gorgany 2
Dead	21.59 (1.94)	24.55 (9.37)	36.04 (10.29)	2.987	$p = 0.225$	
Stem density (trees ha^{-1})						
Live	1540.60 (260.50)	725.17 (190.45)	339.40 (36.40)	9.562	$p = 0.008$	Gorgany 2 & 3 < Gorgany 1 Gorgany 3 < Gorgany 2
Dead	203.05 (111.19)	62.56 (24.21)	117.96 (135.17)	0.604	$p = 0.739$	
Tree diameters						
Average diameter (cm)	17.16 (1.43)	28.24 (3.38)	33.86 (4.58)	7.658	$p = 0.022$	Gorgany 2 & 3 > Gorgany 1 Gorgany 3 > Gorgany 2
Quadratic mean diameter (cm)	19.23 (1.46)	31.89 (3.12)	38.34 (3.63)	10.172	$p = 0.006$	Gorgany 2 & 3 > Gorgany 1 Gorgany 3 > Gorgany 2
Large tree structure						
Density (no. trees ha^{-1})*						
Total	6.62 (4.41)	64.34 (13.28)	102.93 (9.09)	13.032	$p < 0.001$	Gorgany 2 & 3 > Gorgany 1 Gorgany 3 > Gorgany 2
Live	4.19 (2.87)	59.84 (11.95)	93.07 (6.38)	14.211	$p < 0.001$	Gorgany 2 & 3 > Gorgany 1 Gorgany 3 > Gorgany 2
Dead	2.43 (1.57)	4.51 (3.16)	9.86 (4.61)	2.775	$p = 0.250$	
Canopy closure (%)	91.27 (5.08)	80.73 (5.49)	92.60 (3.05)	1.491	$p = 0.475$	
Coarse woody debris						
Volume ($m^3 ha^{-1}$)						
Total	76.70 (28.78)	176.13 (55.78)	157.26 (42.31)	4.186	$p = 0.123$	
Decay Classes 3 and 4	52.96 (21.46)	139.66 (66.78)	113.55 (34.79)	1.667	$p = 0.434$	

*Trees > 50 cm dbh; statistically significant p values are shown in bold.

Note: The table presents these as a comparison of two old-growth and one mature forest site.

an intensive sample consisting of multiple plots or sub-sampling within very large (e.g., 10–20 ha plots) to capture finely scaled patch structure. Studies relying on a single-plot per site (i.e., of a size that does not exceed the scale of patch representation) and placed deliberately to avoid gaps, will over-estimate basal area, canopy closure, aboveground biomass, and other attributes based on our results.

The Kruskal–Wallis tests also did not result in statistically significant differences for dead tree biometrics, including dead tree densities (all stems or large trees only) and CWD volume, either as a sum of all decay classes or for decay Classes 3 and 4 (well-decayed wood) as a subset. However, on closer examination, several interesting relationships emerged in the CWD decay class distributions

(Figure 3). The old-growth sites had consistently higher mean volumes for all decay stages except Class 5. For total CWD, the old-growth means were more than double that of the mature site; the north-west-facing old-growth site (Gorgany 2) had mean decay Class 4 volumes more than triple the debris loading in the mature stand. But these contrasts were not statistically significant because of the wide variance in the data for all the sites. Again this reflected a high degree of variability between individual survey transects, signaling pronounced spatial heterogeneity in CWD availability in both the mature and old-growth sites. In some cases, comparisons between pairs of sites were statistically significant. For instance, both old-growth sites had significantly higher ($p < 0.001$) volumes of decay Classes 1 and 2 relative to the mature site. The southwest-facing old-growth site (Gorgany 3) had significantly higher volumes of decay Class 3 compared to the mature site.

Diameter distributions

Live tree diameter distributions differed significantly among the sites (Figure 4). The mature site exhibited a larger number of trees in smaller size classes, with exponential decline in stem density across larger

size classes, tapering to 60 cm dbh, with exceedingly low (<1 tree ha^{-1}) densities in size classes above that threshold. The old-growth sites had lower tree densities in small sizes and a more gradual density decline trend across medium and large size classes. Relatively high densities (from 1 to 18 stems ha^{-1} depending on size class) were maintained in size classes extending above 60 cm to 95 cm dbh. Despite these differences, none of the sites were statistically distinguishable from the hypothesized rotated sigmoid distribution (Table II). While the old-growth diameter distributions had closer fit with the rotated sigmoid (i.e., lower D_{max} values, see Table II), the mature distribution was not determined to be statistically different based on the KS goodness-of-fit test.

Discussion

Aboveground biomass and carbon storage

Old-growth temperate spruce–fir forests in the eastern Carpathians have the potential to achieve significantly higher aboveground biomass compared to mature stands. We found aboveground biomass levels more than 50% greater than the mature reference stand, which was itself approaching the upper end of both age and structural complexity achieved over standard timber harvest rotations in Ukraine

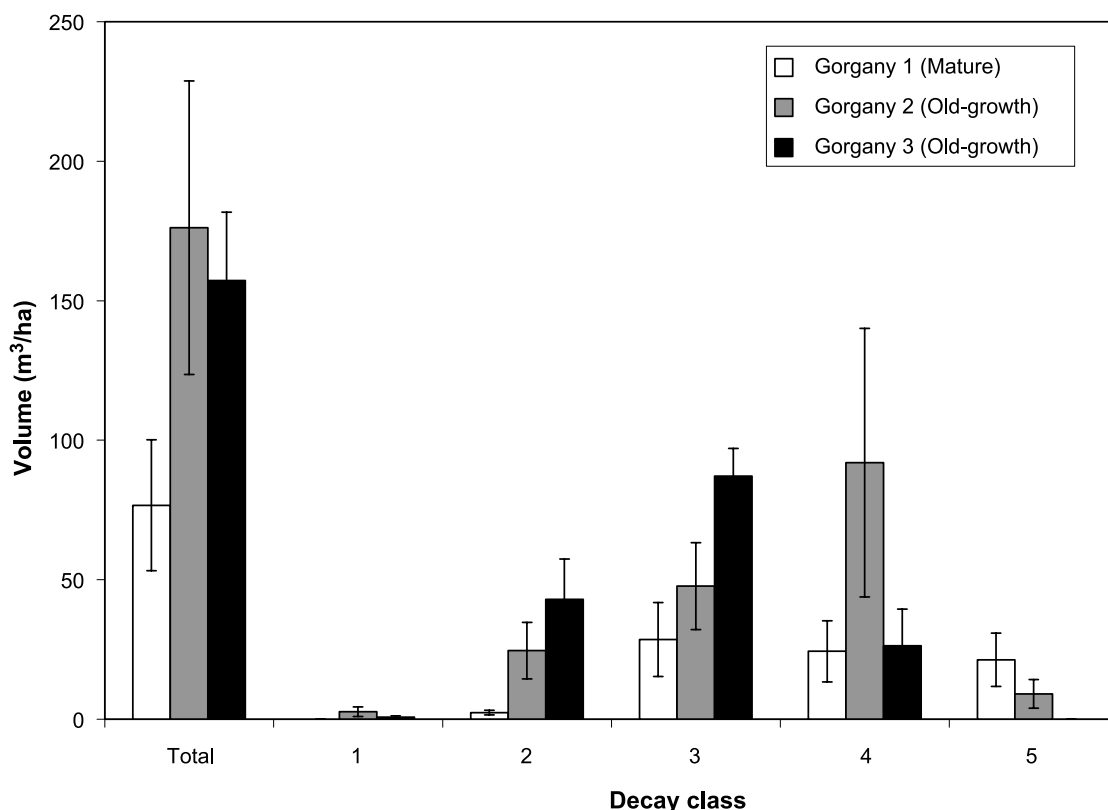


Figure 3. Downed coarse woody debris volume by decay class and site. Total volumes are shown to the left. Error bars are \pm one standard error of the mean. Decay Class 1 is the least decayed, while Class 5 is the most decayed.

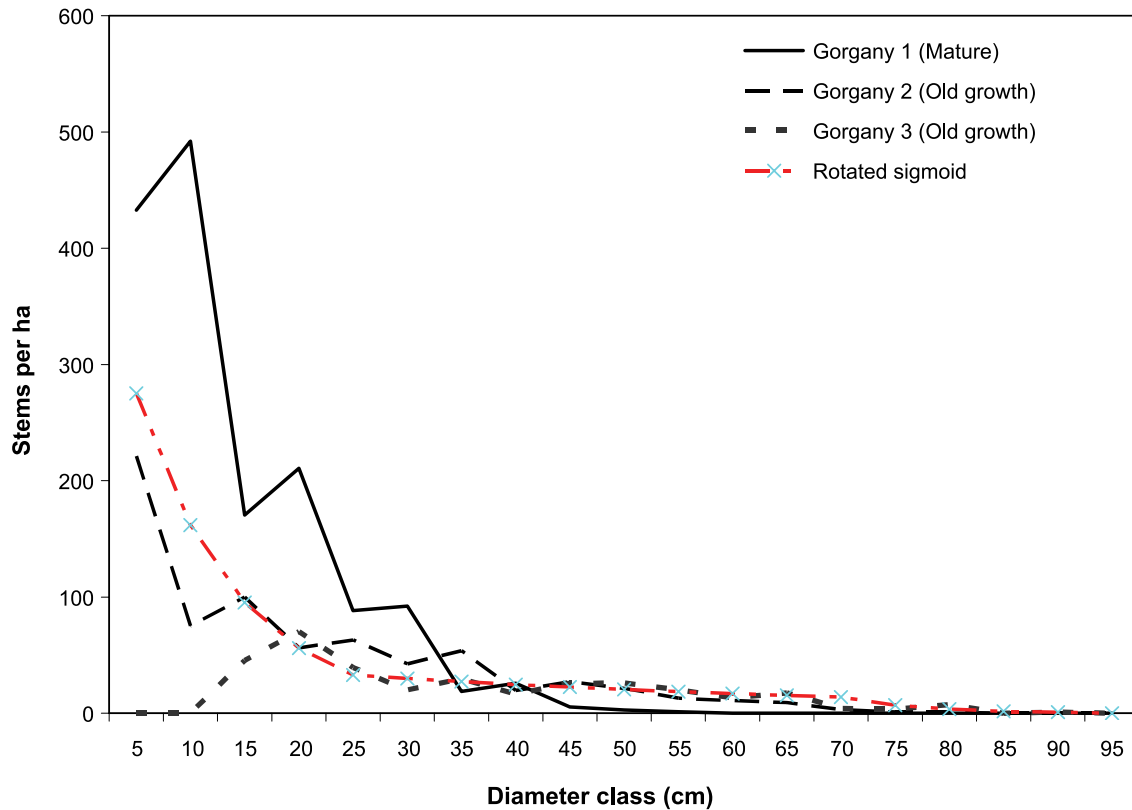


Figure 4. Tree diameter distributions by site and compared to a hypothesized rotated sigmoid form. Note the long, flat tail spanning large size classes for the old-growth sites, matching very closely the rotated sigmoid distribution.

Table II. Parameters and results of the KS two-sample goodness-of-fit tests. These were used to compare live tree diameter distributions against a hypothesized rotated sigmoid distribution.

Site	D_{\max}	D_{crit}	Statistical conclusion
Gorgany 1 (mature)	0.3454	0.4586	$p > 0.05$; not significant
Gorgany 2 (old-growth)	0.1165	0.4328	$p > 0.05$; not significant
Gorgany 3 (old-growth)	0.1216	0.4418	$p > 0.05$; not significant

D_{\max} is the maximum difference (or distance) between distributions detected by the KS test. D_{crit} is the critical value of the test statistic for the given comparison at $\alpha = 0.05$.

(Strochinskii et al. 2001). Rotations are relatively long under Ukrainian forest code for montane spruce forests, ranging from 81 to 140 years depending on regulatory zonation. Our findings, however, suggest that there is continued potential to accumulate aboveground biomass at stand ages above this age range.

It is important to consider, however, that there are fundamental differences between the primary forests investigated in this study and the monocultured spruce plantations now predominant on the landscape (Polyakov & Sydor 2006). These may be increasingly susceptible as they age to decline and mortality caused by acid deposition, disease, and spruce bark beetles (*Ips typographus*) (Badea et al. 2004; Grodzki et al. 2004; Shparyk & Parpan 2004). Thus, the concept of enhancing carbon stor-

age by extending rotations or allowing old-growth structure to develop in unmanaged forests (Keeton & Crow 2009) applies more readily to primary forests and areas restored to endemic species composition and genetic varieties.

The average aboveground biomass we found in old-growth stands (310 Mg ha^{-1}) was very similar to the mean value (331 Mg ha^{-1}) reported for 36 primary spruce stands in the western Carpathians (Szwagrzyk & Gazda 2007), although the latter encompassed a broader range ($169\text{--}536 \text{ Mg ha}^{-1}$). The aboveground biomass in our reference mature site (203 Mg ha^{-1}) was also remarkably similar to the average (207 Mg ha^{-1}) found in 54 mature spruce stands (81–150 years of age) in Poland (Main-Knorn, unpublished data). Our study sites were representative of montane spruce–fir forests in the

Ukrainian Carpathians. However, the collective findings of this and previous research suggest a commonality across the Carpathian mountain range of increasing aboveground biomass and carbon storage late into stand development.

That biomass reaches maximal levels in old-growth Carpathian spruce–fir stands is consistent with an emerging view of temperate old-growth forests as significant carbon sinks in terms of carbon storage capacity (Luyssaert et al. 2008). While young to mature forests have higher rates of carbon uptake, old forests have both higher carbon storage capacity and, in many cases, the ability to maintain net positive NEP for long time periods. Thus, old-growth forests, such as the Carpathian spruce–fir described in this study, play an important role in global carbon cycling.

Stand structural complexity and old-growth forest functions

The results strongly supported the hypothesis that old-growth temperate spruce–fir forests in the East Carpathians of western Ukraine have greater structural complexity compared to mature (and therefore younger) age classes. Key indicators of structural complexity, identified by previous studies as related to late-successional/old-growth development (Whitman & Hagan 1997; Franklin et al. 2002; McElhinny et al. 2006), achieved consistently higher values in our old-growth sites. These indicators included live aboveground biomass, QMD, and large live tree densities. That old-growth Carpathian forests develop very high levels of structural complexity is consistent with similar findings for old-growth beech in the Carpathians (Commarmot et al. 2005) and southern Europe (Merino et al. 2007; Burrasano et al. 2008), as well as spruce and mixed-forests in the western Carpathians (Szwagrzyk & Gazda 2007) and Alps (Splechtna et al. 2005).

Old-growth spruce–fir stands are thus more likely to provide late-successional habitat functions associated with these attributes, such as large tree-related roosting and cavity platforms and canopy openings associated with large tree mortality (Dahir & Lorimer 1996). Gaps created by large tree mortality are, in turn, associated with a range of habitat functions, including vertical structural complexity (i.e., tree regeneration and release), variable below-canopy light regimes (Van Pelt & Franklin 2000), and more diverse understory plant communities compared to closed canopy stands (Burrascano et al. 2008; Smith et al. 2008). Heterogeneous light regimes and large tree availability have been shown to affect forest–stream interactions along low-order streams in other regions, for instance, by creating

“hotspots” of elevated periphyton production (Stovall et al. 2009) and CWD recruitment into stream channels (Keeton et al. 2007).

Mean values for dead tree metrics, including dead aboveground biomass, large dead tree densities, and downed CWD, were two to three times higher at the old-growth sites. However, most dead tree metrics were not statistically different among the age classes we evaluated. There were exceptions as noted above, such as higher volumes of recently recruited CWD at the old-growth sites, and more well-decayed CWD (decay Class 3) at one of the old-growth sites. But the lack of consistency in these results was surprising due to the disparity with previous research contrasting age classes in temperate forest systems (e.g., Spies et al. 1988; McGee et al. 1999), including work in boreal and sub-alpine *P. abies* systems (Fries et al. 1997; Linder & Ostlund 1998; Zielonka 2006). It is unlikely that CWD volumes at our sites were influenced by fuel wood collection due to their remoteness and the prohibition on all timber harvesting within the reserve. However, the high standard deviations in our dataset reflected both the greater spatial variability (i.e., patch heterogeneity) at the old-growth sites and a degree of legacy structure in the mature site. As noted previously, the mature site contained several remnant old-growth logs. These lessened the contrast with the old-growth sites. Spatially aggregated, and therefore patchy, CWD patterns related to gap dynamics have been described previously for boreal old-growth Norway spruce in Sweden (Mattias & Jonsson 2001). Thus, the within-site variation we found in structural characteristics may reflect spatially heterogeneous gap and mortality processes operative to a greater degree in the old-growth stands, though we did not evaluate this directly.

The biological legacies we observed consisted of scattered large remnant trees (live and dead) from which the occasional very large (>80 cm diameter) downed log had recruited. This structural condition is highly consistent with primary mature forests originated following partial disturbances (Keeton & Franklin 2004, 2005) and has been reported in other temperate forest systems (Franklin et al. 2002; Keeton et al. 2007). Intermediate to high intensity windstorms, for instance, can leave relatively high densities of residual live trees, both dispersed and aggregated in small patches (Hanson & Lorimer 2007). Similarly, high intensity storms thinned the stands rather than creating large gaps in a central European old-growth forest (Splechtna et al. 2005). Disturbances can result in two-aged or multi-aged stands and a carryover of CWD, both standing and downed (North & Keeton 2008), similar to the conditions encountered at our mature site. Thus, while old-growth spruce–fir forests have greater

potential to recruit dead tree structure, carryover in natural disturbance originated, unmanaged stands may blur contrasts between age classes.

Diameter distributions and stand dynamics

A long-standing hypothesis is that density-dependent mortality results in constant mortality rates across all size classes in uneven-aged, late-successional forests, in turn producing negative exponential (or “reverse J”) diameter distributions (Meyer 1952). However, support for this hypothesis has been mixed, with studies finding alternate distributions in North America (O’Hara 1998; Goodburn & Lorimer 1999) and Europe (Commarmot et al. 2005; Nagel et al. 2006; Westphal et al. 2006). Diameter distributions can change dynamically over time and space in primary forest landscapes, for instance, as reported for mixed-species old-growth in Bialowieza National Park, Poland (Bernadzki et al. 1998). Dynamics of understory tree species may strongly affect diameter distributions in old-growth forests (Gratzer et al. 1999) and further relax the assumption of negative exponential diameter distributions as a distinguishing characteristic.

The stands we investigated exhibited diameter distributions with rotated sigmoidal form, though the old-growth sites matched this more closely. Rotated sigmoid distributions are produced by non-constant mortality rates, related both to suppression of shade-tolerant species and reduced mortality in rapidly growing mid-sized trees. Partial disturbances and associated episodic regeneration and release can also create discontinuous, unbalanced age class structure. For example, Splechtina et al. (2005) found considerable temporal variation in disturbance frequency and severity during the last 300 years, with resulting peaks in tree establishment after disturbance events. This type of stand dynamics related to variable disturbance intensities contrasts with the conventional view that age structure in old-growth European spruce systems is driven strictly by fine-scaled gap disturbances (e.g., Hornberg et al. 1995). It is consistent with stand dynamics models emphasizing interactions with variable frequency and intensity disturbances.

Conclusions and management implications

Old-growth temperate spruce–fir forests have ecological characteristics distinct from younger forests, including high densities of large trees, complex horizontal structure, and elevated above-ground biomass. They store on average approximately 155–165 Mg ha⁻¹ of carbon in aboveground tree parts alone, based on this and previous studies. This is approximately 50% higher than mature

stands of similar species composition. Given the scarcity of primary spruce–fir forests in the Carpathian region, remaining stands have high conservation value, both as habitat for late-successional species and as carbon storage reservoirs.

In secondary forests, management for old-growth characteristics (see Keeton 2006) might emphasize several ecological objectives. These include restoration of site-endemic species and genetic varieties (Chernyavskyy 2009), redevelopment of under-represented structural characteristics, such as large snags (Linder & Ostlund 1998) and downed woody debris (Fries et al. 1997), and aboveground biomass accumulation (Keeton 2006). Similarly, transition from even to uneven-aged silviculture is likely to enhance landscape carbon storage in European spruce systems (Seidl et al. 2007), even accounting for altered successional dynamics and productivity under climate change scenarios (Seidl et al. 2008). In this context, remaining old-growth spruce–fir forests represent important benchmarks needed to inform ecologically based silviculture.

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