ČESKÁ ZEMĚDĚLSKÁ UNIVERZITA
V PRAZE

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Konštrukcia a vedecká implementácia matematických modelov stromových komponentov listnatých drevín v štádiách nálet, nárast a mladina

Disertační práce

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Podpis autora

ABSTRAKT

Dôležitosť presného určenia zásob biomasy stromov v lesoch stále narastá. Dôvodom je, že v kontexte prebiehajúcej klimatickej zmeny museli vedci začať posudzovať všetky stromové komponenty, jednak z hľadiska ich energetického využitia, tak aj pre odhad uhlíkových zásob. Zároveň v ostatných rokoch narastá záujem o modely biomasy pre malé stromy v súvislosti s významným zväčšením plôch mladých porastov v dôsledku zániku starých porastov pôsobením disturbančných javov (najmä: víchrice, premnoženie podkôrneho hmyzu, suché obdobia a lesné požiare). Modely na určenie zásob biomasy v porastoch mladších ako 10 rokov sú v odbornej literatúre zriedkavé a venujú sa zväčša iba nadzemnej biomase. Táto práca sa preto zameriava na doplnenie chýbajúcich poznatkov v tejto oblasti. Jej hlavné ciele sú:

1) konštrukcia regresných modelov slúžiacich na výpočet hmotnosti sušiny jednotlivých stromových komponentov (tzn. kmeň, konáre, listy, korene) pre mladé porasty vybraných listnatých drevín,
2) aplikácia regresných modelov pri výpočtoch expanzno-konverzných faktorov biomasy (biomass conversion and expansion factors; BCEF), alokačných koeficientov, rastovej účinnosti a indexu listovej plochy (LAI) a ich medzidruhové porovnanie,
3) uplatnenie alometrických vzťahov na odhad potravinového potenciálu pre prežúvavú raticovú, najmä jeleniu zver na lesných drevinách (odhryz konárov, resp. listov, prípadne obhryz kôry).

Pri tvorbe modelov sa využili vzorníky stromov, ktoré boli vykopané na vybraných stanovištiach, rozseparované na jednotlivé komponenty, vysušené na konštantnú hmotnosť a odvážené. Na následnú konštrukciu regresných modelov sa použili logaritmicky transformované alometrické rovnice.

Kľúčové slová: model biomasy, štruktúra biomasy, stromové komponenty, listová plocha, potravinový potenciál

ABSTRACT

Importance of precise estimation for tree biomass in forests has been continuously increasing. Regarding to the climate change, scientists have started to quantify all tree components not only in terms of energetic utilization but also for carbon stock estimation. At the same time, increasing relevance of biomass models for young trees relates to expanding area of young forest stands during the last period due to decay of old forests often caused by disturbances (especially: windstorms, outbreaks of bark beetles, drought episodes, and forest fires). Models for biomass stock estimations constructed for stands with age to 10 years are rare and usually are focused on aboveground tree parts. Thus, this work aims at filling knowledge gaps in this field. Its main objectives are:

1) construction of regression models applicable for estimation of dry mass in the particular tree components (i.e. stem, branches, foliage, roots) for young stands of some broadleaved species,
2) implementation of regression models for calculation of biomass conversion and expansion factors (BCEF), allocation coefficient, growth efficiency and leaf area index (LAI) and their inter-specific comparison,
3) utilisation of allometric relations for estimation on forage potential for ruminating ungulate game, especially red deer (i.e. browsing on branches and foliage, bark stripping).

To make up the models, destructive tree sampling will be implemented. The sample trees will be excavated, separated into tree components, dried for constant weight and weighed. Log-transformed relationships will be used for construction of regression models.

Keywords: biomass model, biomass structure, tree components, leaf area, forage potential

OBSAH

1 ÚVOD

Rámcová dohoda OSN o zmene klímy (UNFCCC – United Nations Framework Convertion on Climatic Change) z roku 1997 stanovila za cieľ dosiahnutie stabilizácie koncentrácie skleníkových plynov v atmosfére a dostatočné zníženie úrovne nebezpečného antropogénneho zasahovania do klimatického systému. V decembri 2015 sa konala Parížska konferencia OSN o ochrane klímy, ktorá po ratifikácii od roku 2020 nahradí Kjótksy protokol. Parížska konferencia zaviazala 196 krajín sveta udržať globálne otepľovanie výrazne pod dvomi stupňami Celzia. Pritom rozvinuté krajiny pomôžu rozvojovým krajinám sumou sto miliárd dolárov ročne pre napĺňanie zámeru redukovať emisiu skleníkových plynov do atmosféry. Zároveň rozvinuté krajiny, vrátane európskych, musia hospodáriť so skleníkovými plynmi tak, aby sa tento zámer naplnil aj na národnej úrovni. Jedným z najefektívnejších spôsobov redukcie koncentrácie skleníkových plynov, najmä CO_2 v atmosfére, by mohlo byť zvyšovanie zásob biomasy lesnej vegetácie.

Klimatická zmena a jej inherentné javy majú rôznorodé negatívne vplyvy na životné prostredie, vrátane deštrukčného pôsobenia na lesné ekosystémy (extrémne prejavy počasia, resp. vznik vhodných existenčných podmienok pre škodcov). Tu treba zdôrazniť, že lesy nie sú iba pasívnym objektom vplyvu klimatickej zmeny, ale vďaka schopnosti absorbovať a akumulovať uhlík môžu tento proces významne ovplyvňovať. Napr. Dixon (1994) už v polovici 90-tych rokov predpovedal, že uhlíková sekvestrácia v lesoch môže hrať dôležitú úlohu ako jeden z komplexu faktorov zmierňujúcich klimatickú zmenu. White et al. (2000) odhadli, že zhruba polovica všetkej uhlíkovej zásoby je umiestnená v terestriálnych ekosystémoch, pritom významná časť z nich sa vyskytuje na severnej hemisfére. Všeobecne sa akceptuje fakt, že európske lesy sú dôležitou zásobárňou uhlíka v celosvetovom meradle (Janssens 2003), a preto treba posilňovať ich funkciu pre uhlíkovú sekvestráciu v blízkej budúcnosti (Karjalainen et al. 2003). Množstvo uhlíka v biomase stromov v stredoeurópskych lesoch v štádiu kmeňovín spravidla presahuje jeho množstvo v lesných pôdach (Brunner a Godbold 2007), pričom v globálnom meradle lesné pôdy viažu približne dvakrát toľko uhlíka ako stromová biomasa (Dixon et al. 1994).

Dôležitosť presného určenia zásob biomasy stromov v lesoch stále narastá. V minulosti sa hodnotila predovšetkým speňažiteľná biomasa, o ktorú bol najväčší záujem a na jej hodnotenie bol vyvinutý široký rámec metód (Alemdag 1984; Petráš, Pajtík 1991; Henry et al. 2011). So zreteľom na klimatickú zmenu vedci začali posudzovať všetky stromové komponenty, jednak z hľadiska ich energetického využitia, ako aj vzhľadom na uhlíkové zásoby (napr. Nabuurs et al. 2002). To vyvolalo potrebu vyvinúť a zlepšiť technológie pre rýchle a štatisticky reprezentatívne hodnotenie aj inej ako kmeňovej biomasy. Jednou z najúčinnejších ciest na dosiahnutie tohto cieľa je použitie alometrických rovníc na báze hrúbky a výšky stromu. Produkcia biomasy a jej alokácia v rámci jednotlivých komponentov stromu (korene, kmeň, konáre a listy) je pri väčších a starších stromoch iné ako pri mladých stromoch. Preto už existujúce rovnice na hodnotenie biomasy dospelých stromov a porastov nie sú všeobecne použiteľné pre mladé stromy. Vzniká tak potreba konštrukcie nových modelov zameraných na vyčíslenie biomasy všetkých komponentov mladých stromov pre jednotlivé druhy drevín. To pomôže pri výpočte zásob biomasy v obnovovaných mladých porastoch, ktorých výmera v posledných rokoch výrazne vzrástla.

2 CIELE PRÁCE

2.1 Konštrukcia alometrických vzťahov a BCEF

Primárnym cieľom dizertačnej práce je konštrukcia regresných modelov slúžiacich na výpočet hmotnosti vyjadrenej v sušine jednotlivých stromových komponentov (tzn. kmeň, konáre, listy, korene) pre mladé porasty hlavných drevín, ako sú: buk lesný (*Fagus sylvatica* L.), dub zimný (*Quercus petraea* (Mattusch.) Liebl.), ale aj ďalších druhov ako sú: jaseň štíhly (*Fraxinus excelsior* L.), javor horský (*Acer pseudoplatanus* L.), jarabina vtáčia (*Sorbus aucuparia* L.) a vŕba rakytová *(Salix caprea* L.*)*. Následným cieľom dizertačnej práce je odvodenie expanzno-konverzných faktorov biomasy (biomass conversion and expansion factors; BCEF) pre uvedené dreviny a ich medzidruhové porovnanie.

2.2 Alokácia biomasy, listová plocha a rastové javy

Ďalším významným poslaním práce je vedecká implementácia regresných modelov pre výpočet niektorých produkčno-ekologických javov, napr. rastovej účinnosti (growth efficiency; GE), čistej primárnej produkcie (net primary production; NPP), indexu listovej plochy (leaf area index; LAI), pomeru sušiny listov k sušine celej rastliny (leaf mass ratio; LMR), pomeru listovej plochy k sušine celej rastliny (leaf area ratio; LAR) a podobne, či už na úrovni jedinca alebo porastu. Uvedené indikátory sa mali porovnať medzi dvomi hospodársky najvýznamnejšími drevinami, konkrétne bukom obyčajným a smrekom obyčajným. Takýmto spôsobom zistiť potenciálne kontrasty v produkčno-ekologických vlastnostiach medzi týmto opadavým a neopadavým druhom, resp. aj rôzny „uhlíkový režim“.

2.3 Ohryz jeleňou zverou a potravinový potenciál

Záverečným (aplikačným) cieľom práce je otestovať možnosti uplatnenia regresných modelov na zistenie reálneho ohryzu v mladých lesných porastoch, ako aj implementácie alometrických vzťahov na odhad potravinového potenciálu pre prežúvavú raticovú zver (t.j. odhryz konárov a listov, prípadne obhryz kôry).

Ide o priekopnícky cieľ objektívneho zistenia množstva sušiny reálne skonzumovanej stromovej biomasy lesnou zverou na základe zistených stôp po odhryze (pahýle odhryznutých konárov) a po obhryze (chýbajúca kôra na kmeni). Čiastkovým cieľom práce je na dopočítanie chýbajúcich stromových komponentov použiť regresné modely na úrovni konára, resp. kmeňa, ako aj na úrovni stromu a porastu. Ďalším cieľom je namodelovanie potenciálne skonzumovateľného množstva biomasy konárov (zimný odhryz), resp. konárov plus listov (letný odhryz), ako aj kôry na kmeni (obhryz) na rôznych úrovniach, t.j. časť stromu (konár, kmeň), celý strom, resp. lesný porast.

3 ROZBOR PROBLEMATIKY

3.1 Konštrukcia alometrických vzťahov a BCEF

Pri výpočtoch zásob biomasy býval v minulosti stredobodom záujmu predovšetkým speňažiteľný objem (na Slovensku ho reprezentuje zásoba hrubiny bez kôry). Tento tvorí hlavne kmeň, na určenie ktorého sa vyvinul celý rad metód (Hakkila 1989; Husch, Beers, Kershaw 2003). Avšak od čias, keď sa zistilo, že alokácia biomasy hrá dôležitú úlohu v uhlíkovom cykle v lesnom ekosystéme (Litton et al. 2007) začala narastať potreba vývoja a zdokonaľovania metód na rýchle a spoľahlivé hodnotenie nekmeňovej lesnej biomasy (Lehtonen 2005; Pregitzer, Euskirchen 2004). Modely zostrojené pre väčšie, staršie stromy nie sú všeobecne použiteľné pre mladé stromy, preto treba odvodiť aj vzorce na výpočet biomasy jedincov v iniciálnych rastových štádiách (Wirth et al. 2004). Nevhodnosť použitia modelov pre staršie stromy zapríčiňujú rozdielne zákonitosti alokácie biomasy v mladých a starých porastoch, ktorá je často veľmi výrazná. Lehtonen et al. (2004) poukázali na to, že pomer jednotlivých komponentov biomasy stromu silne závisí od veku (alebo veľkosti) a odráža vplyv rôzneho obhospodarovania a rastovej stratégie odlišných druhov drevín. Pajtík et al. (2008) zdôraznili vzrastajúcu dôležitosť modelov biomasy pre malé stromy v súvislosti s významným zväčšením plôch mladých porastov v ostatných rokoch vplyvom klimatických zmien a sprievodných negatívnych fenoménov (najmä: víchrice, suché obdobia a lesné požiare). Ďalším argumentom je smerovanie k preferencii rôznovekých lesných porastov (t.j. s výskytom určitého podielu malých stromov), ktoré prebieha v mnohých európskych krajinách.

Výpočet zásob jednotlivých komponentov biomasy stromu sa spravidla vykonáva pomocou jednej z týchto základných metód:

1) regresných rovníc (biomass equations; BE)
2) faktorov biomasy (biomass factors; BF).

Prednosťou regresných rovníc na výpočet biomasy je to, že sa zväčša zakladajú na širšom súbore dát ako faktory biomasy, ako aj, že vychádzajú z ľahko dostupných stromových parametrov (hrúbka, výška). Pritom regresné rovnice zahŕňajú diferencie v štruktúre porastov a sú ľahko použiteľné v národných inventarizáciách uhlíkových zásob. Prednosťou faktorov biomasy je ich jednoduchosť a všeobecnejšie použitie. Táto výhoda sa však pri mladých porastoch stráca, pretože sa odvádzajú z objemu kmeňa (pri dospelých stromoch jeden z najdostupnejších údajov, pri mladých to neplatí). Ďalšou nevýhodou je, že sa v mladom veku hodnota faktorov biomasy významne mení, naopak, v dospelosti je viac-menej stabilizovaná a môže sa použiť ako jedna „defaultná“ hodnota.

Používanie faktorov biomasy v jednotlivých krajinách sa líši, ale vo všeobecnosti sa používajú pri konverzii objemu (kmeňa, speňažiteľného objemu, celkového objemu, ročného čistého prírastku) na iný požadovaný objem alebo na suchú hmotnosť jednotlivých častí biomasy, resp. na celkovú biomasu (či zásobu uhlíka). V prípade použitia prepočtu na rovnakú jednotku (napr. objemu kmeňa na celkový objem stromu, sušina kmeňa na sušinu lístia) sa jedná o expanzné faktory (BEF), pri konverzii jedného typu jednotiek na iný (napr. objemu na hmotnosť) hovoríme o konverzno-expanzných faktoroch (BCEF).

Doteraz sa konštrukcia faktorov biomasy pre lesné dreviny v Európe primárne zameriavala na smrek obyčajný (*Picea abies* L. Karst.) a borovicu lesnú (*Pinus* *sylvestris* L.), pozri napr. Lehtonen a kol. (2004, 2007) a Neumann, Jandl (2005). Práce týkajúce sa iných druhov drevín, napr. buka lesného (*Fagus sylvatica* L.), dubov (*Quercus* sp.) alebo brezy plstnatej *(Betula pubescens Ehrh.)* sú zriedkavejšie (Ciencala et al. 2008; Van Camp et al. 2005; Lehtonen et al. 2004). Ich spoločnou vlastnosťou je, že sa zaoberajú iba dospelými stromami a chýbajú špecifické údaje pre malé (mladé) stromy. Problematike stanovenia zásob biomasy v mladých porastoch sa pozornosť začala venovať iba pred pár rokmi. Dutca et al. (2010) odvodili BCEF pre mladé porasty smreka pestované na nelesných stanovištiach východných Karpát, Blujdea et al. (2012) vytvorili alometrické rovnice na výpočet biomasy mladých listnatých stromov na plantážach v Rumunsku. V podmienkach Slovenska Pajtík et al. (2008, 2011) zostrojili regresné rovnice a odvodili BCEF pre porasty smreka, borovice, buka a duba I. vekového stupňa. V posledných rokoch boli doplnené rovnice pre mladé porasty jaseňa štíhleho (*Fraxinus excelsior* L.) a javora horského (*Acer pseudoplatanus* L.*;* pozri Konôpka et al. 2012, 2015), smrekovca opadavého (*Larix decidua* Mill.; viď Pajtík et al. 2015), vŕby rakytovej (*Salix caprea* L.) a jarabiny obyčajnej (*Sorbus aucuparia* L.; Pajtík et al. 2015).

Regresné rovnice biomasy pre jednotlivé druhy drevín sa začali častejšie objavovať v ekologickej a lesníckej literatúre v päťdesiatych rokoch minulého storočia ako odozva na požiadavku hodnotenia biomasy. Odhady biomasy sú nevyhnutnou podmienkou pre štúdium produkcie lesa, výživových cyklov, energetického využitia biomasy, uhlíkových zásob a sekvestrácie uhlíka v lesoch. Prvými štúdiami vzniknutými na základe potreby určiť produkciu biomasy rozličných druhov drevín boli práce Burgera (1945, 1953) týkajúce sa smrekovca a smreka vo Švajčiarsku. Následne výskumníci začali zameriavať pozornosť na zisťovanie suchej hmotnosti jednotlivých stromových komponentov (napr. kmeň, kôra, konáre, listy, korene), najmä tých, ktoré mali väčšiu dôležitosť pre lesnícke spoločnosti. Ekologické a fyziologické práce tej doby ukázali záujem vedcov prispieť k rozvoju jednoduchých metód na stanovenie biomasy, obzvlášť na kvantifikáciu lístia (Kittredge 1944; Ovington 1957). Mnohé lesnícke štúdie rozvíjajú regresné rovnice pre špecifické geografické oblasti a druhy drevín. Rovnice biomasy stromu, rovnako ako aj jeho komponentov sú zvyčajne založené na vzťahu k hrúbke stromu (vo výške 1,3 m) alebo výške stromu (h), prípadne na vzájomnej kombinácii týchto nezávislých premenných (napr. Satoo, Madgwick 1982; Khan, Faruque 2010; Ter-Mikaelian, Korzukhin 1997; Vahedi et al. 2014). Niekedy sa ako nezávislá premenná používa aj dĺžka koruny (CL), šírka koruny (CW), pomer dĺžky koruny ku výške stromu (CL/h), pomer šírky a dĺžky koruny (CW/CL) alebo štíhlostný koeficient (h/DBH) (napr. Ledermann, Neuman 2006; Cienciala et al. 2008; Eckmüllner 2006; Hochbichler et al. 2006). Ak sa jedná o rovnice na výpočet biomasy stanovišťa používajú sa stanovištné premenné (počet stromov na hektár ($N.ha^{-1}$), kruhová základňa (G), horná výška (H_0), vek (t) alebo nadmorská výška stanovišťa (Z)). Počet štúdií o hodnotení lesnej biomasy v posledných desaťročiach vzrastal, berúc do úvahy dôležitosť začlenenia širokého počtu druhov drevín a rozličných stanovištných štruktúr (Zeide 1987). Zianis et al. (2005) vytvorili prehľad rovníc na výpočet biomasy a objemových rovníc pre lesné dreviny Európy, do ktorého zahrnul 607 rovníc, z ktorých väčšina pochádza zo strednej a severnej Európy. Väčšina týchto štúdií sa okrem kvantifikácie zaoberá aj globálnejšími aspektmi, ako napr. využitím dreva (na celulózu, palivové drevo, atď.) a aplikáciou získaných poznatkov vo výskume (napr. v štúdiách uhlíkového cyklu a pri bilancii živín v lesných ekosystémoch).

Viacerí autori (Kozak 1970; Cunia, Briggs 1984; Bi 2004) upozornili na to, že veľa publikovaných rovníc biomasy nie je stanovených najefektívnejšie, pretože nezahrňujú aditivitu medzi rovnicami komponentov. To znamená, že rovnice pre každý komponent sú stanovované oddelene bez toho, aby bol zohľadnený faktor: 1) vlastnej korelácie medzi komponentmi biomasy meranými na rovnakých vzorníkoch, 2) logického obmedzenia medzi sumou predikovanej biomasy stromových komponentov a predikciou pre celý strom (Parresol 1999). Chýbanie aditivity znamená nesúlad v predikovaných hodnotách vypočítaných sčítaním rovníc stromových komponentov a predikovaných hodnôt z rovnice na výpočet celkovej biomasy stromu. Na elimináciu tejto nezrovnateľnosti bolo navrhnutých niekoľko modelov a metód výpočtu (Chyienda, Kozak 1984; Cunia, Briggs 1985).

Významnú rolu medzi regresnými funkciami zaberajú alometrické rovnice. Alometria je štúdium premenlivých proporcií rozmerov organizmu, spojených so zmenou ich veľkostí, a to buď v rámci individuálneho rastu (ontogenetická alometria), alebo v porovnaní s príbuznými organizmami rôznych veľkostí (fylogenetická alometria). Tento pojem sa často používa aj vo význame nerovnomernosť rastu (vývoja) ako protiklad k pojmu izometria – rovnomernosť rastu. Alometria rastu je vyjadrovaná pomocou alometrickej rovnice, ktorej základný tvar je:

$$Y = a.X^b \qquad (1)$$

Jedným z prvých, ktorí aplikovali túto rovnicu v lesníctve bol Kittredge (1944) a časom sa stala najčastejšie používanou metódou v štúdiách o biomase (napr. Marklund 1987;

Neumann, Jandl 2005; Gschwantner, Schadauer 2006; Ledermann, Neumann 2006). Príčinou tejto obľúbenosti je určite fakt, že je veľmi flexibilná a môže sa ľahko rozšíriť na viacnásobnú mocninovú funkciu tvaru:

$$Y = a_0.X_1^{b_1}.X_2^{b_2}.X_3^{b_3}....X_n^{b_n}.\theta \tag{2}$$

kde Y je závislá premenná, X_1 - X_n sú nezávislé vysvetľujúce premenné, $a_0 - b_n$ sú koeficienty modelu a θ je chyba (multiplicative error term). Často sa používa logaritmický tvar rovnice, pretože umožňuje použiť lineárnu regresiu na odhad parametrov. Okrem toho, logaritmická transformácia kompenzuje tendenciu zrýchľovania rastu závislej premennej s veľkosťou stromu (heteroskedasticitu rezíduí, ktorá je pri takomto type údajov vždy prítomná), a tak uspokojujúco spĺňa predpoklad konštantnej variancie. Z tohto dôvodu môžeme rovnicu napísať ako:

$$\ln Y = b_0 + b_1.\ln X_1 + b_2.\ln X_2 + b_3.\ln X_3 + ... + \ln X_n + \varepsilon \tag{3}$$

kde $b_0 = \ln a_0$, a $\varepsilon = \ln \theta$ je chyba (additive error term). Logaritmická transformácia závislej premennej spôsobuje systematickú odchýlku (bias), ktorá sa objavuje pri spätnej transformácii z logaritmického tvaru na tvar pôvodný (Baskerville 1972; Ledermann, Neumann 2006). Preto, keď sú rovnice retransformované musí byť urobená korekcia na logaritmický bias. Na túto korekciu sa používa korekčný faktor CF označovaný aj ako λ. Prvými autormi zaoberajúcimi sa výpočtom korekčného faktora v logaritmicky transformovaných alometrických rovniciach boli Finney (1941) a Baskerville (1972). Bohužiaľ, formulácia korekčného faktora bola v tých časoch často nesprávna. Na elimináciu biasu slúži vynásobenie korekčným faktorom, ktorý je počítaný zo štandardnej chyby odhadu (standard error of estimate – SEE) regresie. SEE je vypočítané podľa vzorca:

$$SEE = \sqrt{\frac{\sum(\ln y_i - \hat{\ln} y_i)^2}{DF}} \tag{4}$$

kde $\ln y_i$ je hodnota závislej premennej, $\hat{\ln}\, y_i$ je prislúchajúca predpovedaná hodnota vypočítaná z rovnice a DF je počet stupňov voľnosti (degrees of freedom), ktoré sú vypočítané ako N-p, kde N je počet pozorovaní a p je počet parametrov rovnice.

Sprugel (1983) upozornil na nesprávne odvodenie SEE niektorých autorov (Whittaker, Woodwell 1968; Snedecor, Cochran 1967), ktorý v menovateli používali hodnotu $N - 1$.

Korekčný faktor sa teda pomocou SEE vypočíta takto:

$$CF = \exp(SEE^2 / 2) \tag{5}$$

Ale aplikácia tohto korekčného faktora vyžaduje logaritmicko-normálne rozdelenie závisle premennej *Y*, inak dochádza k nadhodnocovaniu (Marklund 1987). Z tohto dôvodu nepoužívame tento korekčný faktor, ale radšej využívame metódu predstavenú Marklundom (1987), ktorý počíta korekčný faktor podľa nasledujúcej rovnice:

$$\lambda = \frac{\sum_{i=1}^{n} Y_i}{\sum_{i=1}^{n} e^{\ln \hat{Y}_i}} \text{, kde } n \text{ je počet stromov} \tag{6}$$

Ledermann, Neumann (2006) odporúčajú použiť tento vzorec pri výpočte celkovej stanovištnej biomasy, v prípade výpočtu biomasy na úrovni jednotlivého stromu odporúčajú použiť vzorec:

$$\overline{\lambda} = \frac{1}{n} \sum_{i=1}^{n} \frac{Y_i}{e^{\ln \hat{Y}_i}} \tag{7}$$

Podrobne sa problematike výpočtu rôznych druhov korekčných faktorov používaných pri logaritmickej transformácii mocninových funkcií a ich vzájomnému porovnaniu venuje vo svojej práci Clifford et al. (2013).

Použitie linearizovaného modelu však vyžaduje získať naspäť netransformované hodnoty biomasy. Na to sa využije retransformácia:

$$Y = e^{(b_0 + b_1 . \ln X_1 + b_2 . \ln X_2 + b_3 . \ln X_3 + ... + b_n . \ln X_n)} . \lambda \tag{8}$$

V posledných rokoch sa s rozvojom nelineárnych regresných metód vynorila otázka, či nie je výhodnejšie používať alometrickú rovnicu v jej mocninovom tvare a vyhnúť sa jej logaritmickej transformácii. Linearizácia dovoľuje použiť pevne stanovené metódy regresnej analýzy a proces výpočtu je jednoduchší, zvlášť ak je zahrnutých viacero nezávislých premenných. Avšak nevýhodou tohto prístupu je, že logaritmická transformácia deformuje originálne dáta a musí byť použitý korekčný faktor na jej retransformáciu. Cienciala et al. (2006) skúmali efekt linearizácie pri tvorbe regresných rovníc na výpočet nadzemnej biomasy, biomasy kmeňa a biomasy živých vetiev borovice. Zistili, že priemerná predikovaná biomasa z nelineárnej regresie sa vždy lepšie zhoduje s nameranými hodnotami ako pri linearizovanej regresii. Ostatné regresné štatistiky, menovite štandardná chyba odhadu (SEE), koeficient determinácie (R^2) a priemerný štvorec rezíduí (MSR) boli nepatrne lepšie pri linearizovaných rovniciach v prípade výpočtu nadzemnej biomasy pomocou dvojparametrovej rovnice. Na druhej strane, nelineárny prístup ukázal lepšie štatistiky pre komplexnejšie rovnice so štyrmi a piatimi parametrami. Naopak Lai et al. (2013) zistili pri tvorbe modelov na výpočet biomasy koreňov na základe hrúbky stromu, že lineárna regresia logaritmicky transformovaných dát je presnejšia ako nelineárna regresia. Naviac došli k dôležitému poznatku, že nevhodne použitá nelineárna regresia vedie k hrubým nepresnostiam pri určení stanovištnej biomasy, najmä pri stanovištiach s dominanciou malých stromov. Aj Mascaro et al. (2013) na otázku, či je logaritmická transformácia v alometrii nevyhnutná odpovedajú: „Desať, sto, tisíckrát áno.“ Keďže sa názory na tieto dva metodické prístupy rôznia, problematike treba venovať vedeckú pozornosť aj naďalej.

Zásoba biomasy lesných drevín sa môže počítať nielen pomocou regresných rovníc, ale aj s využitím faktorov biomasy (biomass factors; BF). Tieto konvertujú, alebo ak je to potrebné, zväčšujú či zmenšujú množstvo biomasy podľa vzorca:

$$B = P * BF \tag{9}$$

kde B je biomasa (v čerstvom alebo suchom stave v kg alebo m^3), P dostupný stromový alebo stanovištný parameter (napr. objem stromu v m^3) a BF je vhodný faktor biomasy, ktorý môže zahŕňať konverznú alebo expanznú zložku.

BF v ich najjednoduchšej forme ako expanzné faktory (BEF) sa používajú na rozšírenie dostupných dát o stromovej kmeňovej biomase na odhad biomasy celého stromu. Avšak Tobin, Nieuwenhuis (2007) zdôraznili, že možno najlepšou cestou použitia BF je integrácia expanzných a konverzných komponentov do jedného faktoru. Takéto konverzno-expanzné faktory biomasy (BCEF) potom konvertujú všeobecne dostupné dáta objemu kmeňa priamo na sušinu stromovej biomasy alebo sušinu biomasy jednotlivých komponentov (Schroeder et al. 1997; Fang et al. 2001; Lehtonen et al. 2004) alebo prípadne na obsah uhlíka podľa vzťahu:

$$BCEF_i = \frac{W_i}{V} \tag{10}$$

kde W_i je suchá hmotnosť zložky stromu i, V je objem kmeňa a i je stromová zložka (listy, vetvy, kmeň, mŕtve vetvy, kôra, peň, hrubé korene, jemné korene alebo celý strom). BCEF kmeňa zároveň vyjadruje jeho objemovú hmotnosť. Môžu byť sformulované buď pre jednu (najčastejšie hrúbka $d_{1,3}$) alebo niekoľko nezávislých premenných (napr. hrúbka, výška, vek), a to buď na regionálnej alebo globálnej úrovni, na úrovni stromovej alebo porastovej, reprezentujúce jednu drevinu alebo súbor drevín určitej oblasti (napr. boreálny les). Ideálne by bolo, ak by tieto faktory boli špecifické pre jednotlivé druhy drevín a zahŕňali by aj vplyv veku a stanovištných podmienok, pretože všetky tieto aspekty majú vplyv na množstvo a distribúciu biomasy stromu (Satoo, Madgwick 1982; Levy et al. 2004). V skutočnosti nie sú takéto špecifické BCEF dostupné pre väčšinu druhov drevín, z čoho vyplýva používanie takzvaných „defaultných“ hodnôt. Tieto hodnoty zvyčajne predstavujú priemer z dostupných pozorovaní (IPCC 2006).

Ak sa na vyjadrenie suchej hmotnosti W_i použije alometrická rovnica základného tvaru, ktorá je vhodná aj na vyjadrenie objemu V, môžeme predchádzajúcu rovnicu napísať v tvare:

$$BCEF_i = \frac{a_1.X^{b_1}}{a_2.X^{b_2}} = a.X^b \text{, kde } a = \frac{a_1}{a_2} \text{ a } b = b_1 - b_2 \qquad (11)$$

a na vyjadrenie BCEF opäť použiť základnú alometrickú rovnicu a vyššie popísaný postup, ktorý sa zhoduje s výpočtom sušiny jednotlivých zložiek biomasy.

3.2 Alokácia biomasy, listová plocha a rastové javy

Alokácia biomasy v rastlinných organizmoch závisí od druhu, ontogenézy a vplyvu okolitého prostredia, predovšetkým intenzity osvetlenia, obsahu CO_2 v ovzduší a dostupnosti živín a vody. Jednou z možností vyjadrenia alokácie sú rôzne pomery sušiny jednotlivých častí rastliny. Najčastejšie používaným pomerom je root:shoot ratio (R/S) (Leuschner et al. 2007; Mokany et al. 2006; Sanquetta et al. 2011; Magalhães, Seifert 2015; Levy et al. 2004) vyjadrujúce pomer podzemnej a nadzemnej časti rastliny. Poznatky o pomere R/S sú veľmi dôležité, pretože slúžia na odvodenie zásob podzemnej biomasy, ktorá je dôležitým komponentom uhlíkových zásob v terestrických ekosystémoch. Zatiaľ čo zákonitosti distribúcie nadzemnej biomasy sú známe a primerane preskúmané, poznatky o podzemnej biomase sú dosť obmedzené (Mc Naughton et al. 1998), hoci sú zásadné na zlepšenie našich vedomostí o alokácii uhlíka a jeho zásobách v terestrických ekosystémoch (Cairns et al. 1997). Konôpka et al. (2011) pomocou regresných rovníc vytvorili model pre odhad podzemnej biomasy pre smrečiny rastúce v podmienkach Slovenska. Model na úrovni porastu vyjadruje pomer medzi podzemnou biomasou a hrubinou nadzemnej biomasy s ohľadom na základné porastové charakteristiky (t.j. vek, priemerná hrúbka, resp. výška).

Alokácia biomasy môže byť vyjadrená aj pomocou frakcií, ktoré vyjadrujú biomasu jednotlivých komponentov relatívne k celkovej biomase rastliny (frakcia lístia, frakcia kmeňa, frakcia konárov, frakcia koreňov). Poorter, Nagel (2000) odporúčajú používať termín „frakcia“ radšej ako všeobecne zaužívaný pojem „pomer“, pretože je okamžite jasné, že suma všetkých frakcií sa rovná hodnote 1. Výhodou použitia frakcie biomasy pred R/S hodnotami je to, že frakcie jednotlivých komponentov sú integrálnou súčasťou rastových analýz a výpočtu uhlíkových zásob (Garnier 1991; Poorter, Pothmann 1992). Pajtík (2008, 2011), Priwitzer et al. (2009) a Konôpka (2015) používajú najčastejšie pojem „podiel“ jednotlivých komponentov (napr. podiel listov, kmeňa, atď.) a vyjadrujú ho relatívne v % sušiny z celkovej sušiny stromu.

Ďalšou formou na vyjadrenie alokácie sú koeficienty alokácie biomasy, ktoré vyjadrujú rastovú stratégiu a definujú sa ako pomer medzi prírastkom komponentu biomasy stromu (kmeň, listy, konáre, korene) a prírastkom biomasy kmeňa. S rastom stromu dochádza k zmene veku, veľkosti a tvaru stromu a mení sa aj príspevok jednotlivých komponentov biomasy na celkový prírastok stromu (Bartelink, 1988). Rozdiel v produkcii biomasy a jej alokácii medzi mladými a dospelými stromami je často značný. Prírastok biomasy celého stromu sa môže vyjadriť ako suma prírastkov jednotlivých komponentov:

$$\Delta B_t = \Delta B_s + \Delta B_f + \Delta B_b + \Delta B_r \tag{12}$$

kde ΔB_t je prírastok biomasy celého stromu, ΔB_s je prírastok biomasy kmeňa, ΔB_f je prírastok biomasy listov, ΔB_b je prírastok biomasy vetiev a ΔB_r je prírastok biomasy koreňov.

Pretože prírastok biomasy kmeňa (ΔB_s) je najčastejšie používaný a meraný druh prírastku v lesníctve, ΔB_f , ΔB_b a ΔB_r sa môžu vyjadriť ako:

$$\Delta B_f = BAC_f . \Delta B_s \tag{13}$$

$$\Delta B_b = BAC_b . \Delta B_s \tag{14}$$

$$\Delta B_r = BAC_r . \Delta B_s \tag{15}$$

kde BAC_i je koeficient alokácie biomasy, BAC_f pre listy, BAC_b pre vetvy a BAC_r pre korene.

Inými slovami, koeficienty BAC_i vyjadrujú pomer prírastku biomasy jednotlivých komponentov (ΔB_f , ΔB_b a ΔB_r) k prírastku biomasy kmeňa (ΔB_s).

Pomer medzi biomasou listov a prírastkom biomasy silno súvisí s produktivitou stromu. Tento pomer je často označovaný ako rastová účinnosť (growth efficiency – GE) (napr. Gersonde, O’Hara 2005) a môže byť vyjadrený ako prírastok biomasy kmeňa na jednotku listovej plochy alebo biomasy listov. V súčasnosti sa veľmi zriedkavo vyskytujú medzidruhové porovnania GE, ktoré by mohli pomôcť vysvetliť ekologické požiadavky a rastové stratégie jednotlivých druhov drevín (Konôpka et al. 2010; Jack, Sheffield, McConville 2002).

V produkčnej ekológii sa používa pojem čistá primárna produkcia (anglický termín Net Primary Productvity, NPP). Ide o energiu naakumulovanú rastlinami fotosyntézou po odčítaní časti energie spotrebovanej na respiráciu. Vyjadrené inými slovami, NPP zahŕňa biomasu (resp. množstvo uhlíka) kmeňa, vetiev, asimilačných orgánov a koreňov vytvorenú počas určitého časového obdobia, zvyčajne jedného roku. Niektorí autori (napr. Pangle et al. 2009; Yuste et al. 2005) v predošlých prácach konštatovali výrazné medzidruhové rozdiely v príspevku jednotlivých komponentov k NPP. Tieto medzidruhové rozdiely možno chápať v kontexte odlišnej rastovej stratégie drevín, resp. medzidruhových kontrastov v „organizovaní“ biochemických cyklov, vrátane obehu a fixácii uhlíka.

Index listovej plochy (LAI; leaf area index) je parameter, ktorý dáva jedinečnú charakteristiku porastu najmä z hľadiska jeho produkčného potenciálu a ukazovateľa schopnosti prijímať CO_2 a iné plyny, transpirovať vodnú paru a podobne (Leuschner et al. 2006). Ovplyvňuje tiež primárnu produkciu (Long, Smith 1990) a intercepciu zrážok (Herbert, Fownes 1999). Z tohto dôvodu je často podstatným parametrom vstupujúcim do mnohých produkčných a bilančných modelov (produkcia biomasy, toky CO_2, O_3, biogénnych emisií prchavých organických látok (BVOC), vodná bilancia porastu a pod.).

V lesníctve je LAI často definovaný ako povrch jednej strany zelených listov na jednotku plochy pre listnaté porasty (Watson 1947). Zatiaľ čo definícia a meranie listovej plochy je pri listnatých drevinách jednoznačné, pre ihličnaté porasty je stanovenie LAI zložitejšie a bývajú používané tri nasledovné definície:

- celkový povrch ihlíc na jednotku plochy,
- celkový povrch ihlíc na jednotku plochy delený dvoma,
- premietnutá plocha ihlíc na jednotku plochy.

Posledná definícia sa v súčasnosti čoraz častejšie využíva i pri stanovovaní LAI pre listnaté porasty, vzhľadom k tomu, že vyššie spomenutá definícia pre listnaté porasty sa dá využiť iba za predpokladu, že všetky listy v poraste sú v horizontálnej polohe, čo väčšinou nie je splnené. V súčasnosti väčšina metód používaných na stanovovanie LAI (nedeštruktívne metódy) vychádza z premietnutej plochy asimilačných orgánov na jednotku zemského povrchu. Často sa označuje aj ako PLA (projected leaf area). Pri optických metódach na stanovenie LAI sa stretávame s pojmom LAI_e, efektívny index listovej plochy, čo je vlastne premietnutá plocha všetkých vegetačných súčastí (listy, stonky, konáre...).

LAI môže byť stanovená pomocou priamych alebo nepriamych metód. Priame metódy merania LAI sa zakladajú na zisťovaní listovej plochy buď meraním (napr. skenovaním) alebo odvodením pomocou špecifických vzťahov medzi veľkosťou plochy listov a sušinou ich biomasy (napr. pomocou špecifickej listovej plochy SLA). Sušina biomasy listov zozbieraných na ploche o známej výmere sa prepočíta na LAI vynásobením pomocou SLA. Je veľmi dôležité správne odobrať listy na určenie pomeru listovej plochy k sušine ich biomasy, pretože ten sa mení v závislosti od druhu dreviny, stanovišťa, na ktorom drevina rastie, ale aj podľa polohy v korune a osvetlenia listu (Bréda 2003; Niinemets 2010), ako aj v závislosti od veku a veľkosti dreviny (Steele et al. 1990; Niinements, Kull 1995). Sušinu biomasy listov pri priamych metódach zisťujeme buď vyťažením stromov a odvážením (deštruktívna metóda), alebo pomocou alometrických vzťahov, resp. zberom opadu (Nizinsky, Saugier 1988; Dufrêne, Bréda 1995) (nedeštruktívne metódy). Priame metódy poskytujú referenčné hodnoty pre kalibráciu a hodnotenie nepriamych metód. Nepriame metódy odvodenia LAI sú nedeštruktívne a sú založené na optickom meraní na základe teórie radiačného prenosu (Anderson 1971; Ross 1981).

3.3 Ohryz jeleňou zverou a potravinový potenciál

Poškodzovanie lesných porastov prežúvavou raticovou zverou súvisí predovšetkým s jej potravnou ekológiou, a teda s príjmom potravy. Potravná ekológia jelenej zveri bola na území bývalého Československa predmetom štúdia viacerých prác (napr. Finďo et al. 1993; Fišer, Lochman 1969; Prokešová et al. 2004). Z nich jednoznačne vyplýva, že lesné dreviny sú významnou zložkou potravy jelenej zveri a ich podiel v závislosti od oblastí, resp. typu prostredia (biotopu), dosahuje 50 až 80 %. Zver spása jednotlivé časti drevín v priebehu roka s rôznou intenzitou, závislou najmä od fenologickej fázy drevín a od zmien v dostupnosti ostatnej zložky potravy. Tohoročné mladé nové výhonky spása zver po celý rok. Lístie najmä koncom jari a v lete a začiatkom jesene, v zime naopak ihličie a konáre s púčikmi. Listy jaseňa konzumuje zver aj po ich opadnutí a často ich vyhrabáva spod snehu. Miera poškodzovania jednotlivých druhov drevín úzko súvisí s ich obľúbenosťou, resp. chuťovými a nutričnými vlastnosťami (Pfeffer 1961). Vo všeobecnosti patria k najobľúbenejším drevinám jedľa biela, javory, jarabina vtáčia, niektoré druhy vŕb a jaseň štíhly (Katreniak 1972; Finďo et al. 1993; Ammer 1996; Motta 1996). Preto sú tieto druhy považované za kriticky ohrozené odhryzom a obhryzom od nárastu až po žrďoviny a tenké kmeňoviny (Finďo, Petráš 2007).

Početnosť populácie jelenej zveri u nás počas ostatných 15 rokov výrazne narástla. Kým napríklad jarné kmeňové stavy (JKS) jelenej zveri boli v roku 1998 necelých 32 tisíc kusov, v roku 2005 to už bolo takmer 40 tisíc a v roku 2012 až 59 tisíc kusov. To znamená, že za sledované obdobie sa populácia jelenej zveri takmer zdvojnásobila. Zároveň treba konštatovať paradoxnú situáciu v lesnom hospodárstve (spôsobenú ekonomickou a sčasti snáď aj stavovskou krízou), a to postupné znižovanie nákladov na starostlivosť a ochranu lesných porastov, vrátane redukcie rozsahu ochrany drevín pred ohryzom zverou (Konôpka, J. et al. 2012).

Naša pozornosť sa sústredila na zhodnotenie poškodenia mladých porastov jarabiny v oblasti s vysokou hustotou jelenej zveri a na kvantifikáciu množstva dendromasy zožratej jeleňou zverou, ako aj potravinového potenciálu (sušiny) v mladých porastoch jarabiny a vŕby rakytovej. Práce nadväzujú na predchádzajúci výskum, ktorý sa zaoberal poškodzovaním mladých porastov jaseňa a javora jeleňou zverou (Konôpka, B. et al. 2014; Konôpka, B. et al. 2015). Vŕba rakytová a jarabina nie sú dôležité dreviny pre priemyselné využitie hlavne kvôli ich nepravidelnému tvaru kmeňa, ktorý sa výrazne rozvetvuje a často vytvára zhluky viacerých kmeňov, a tiež kvôli málo kvalitným vlastnostiam dreva. Avšak sú to prípravné dreviny so špecifickými ekologickými požiadavkami, čo im umožňuje zaberať menej vhodné pokalamitné plochy. Ich prítomnosť zlepšuje pôdne podmienky a mikroklímu, čím vytvára priaznivé podmienky na podporu rastu iných druhov drevín (Myking et al. 2013). Tieto dreviny sú tiež obľúbenou potravou pre celý rad herbivorov vrátane jeleňa lesného *(Cervus elaphus* L.*)*. Obidve dreviny môžu predstavovať vhodnú biologickú reguláciu na zmiernenie škôd zverou na hospodárskych drevinách.

3.4 Validácia modelov

Validácia je overenie platnosti prostredníctvom poskytnutia objektívnych dôkazov, že požiadavky na špecifické zamýšľané použitie alebo na špecifickú aplikáciu boli splnené. Spoľahlivosť modelu je možné validovať pomocou metódy krížovej validácie. Krížová validácia (cross-validation) je technika na zisťovanie miery ovplyvnenia nezávislej vzorky dát predošlou analýzou. Model pracuje s množinou vstupných dát, rozdelenou na podmnožinu známych dát, ktorá slúži ako trénovacia množina a podmnožinu neznámych dát, ktorá je označovaná ako testovacia. Klasifikátor trénuje model na trénovacej množine a pomocou testovacej množiny testuje presnosť tohto modelu. Tento proces sa opakuje viackrát, zakaždým s inou podmnožinou tvoriacou trénovaciu a testovaciu množinu. Jedným z typov krížovej validácie je k-fold cross-validation, kde vstupná množina dát je rozdelená do k podmnožín a proces sa opakuje k-krát. Pre každý proces je použitá jedna z k podmnožín ako testovacia a ďalšie k - 1 podmnožiny sú spojené do trénovacej množiny. Výhodou je, že každá množina je testovaná presne raz a použitá ako trénovacia podmnožina k - 1 krát. Nevýhodou tejto metódy je opakované vykonávanie algoritmu k-krát, takže výpočet evaluácie bude vyžadovať väčšie množstvo času.

K-fold cross-validácia sa výborne hodí na testovanie údajov nameraných na rôznych lokalitách, ako je to napríklad pri súbore dát o biomase drevín z rôznych oblastí. Vtedy je množina dát rozdelená do podmnožín podľa lokalít (hodnota k zodpovedá počtu lokalít). Odchýlka testovanej množiny od trénovacej sa stanoví buď v absolútnych alebo relatívnych hodnotách pomocou priemerných hodnôt štvorcov rezíduí (RMSE – root mean square error) medzi hodnotami predikovanými modelom vytvoreným z hodnôt trénovacej podmnožiny a aktuálnymi hodnotami testovacej množiny. Namiesto k-fold cross-validácie možno tiež použiť leave-one-out cross-validáciu. Ako už názov metódy napovedá, leave-one-out cross-validácia funguje tak, že z celého setu dát vyberie jednu vzorku pre validáciu a zvyšok pre trénovanie. Táto metóda je časovo aj výpočtovo najnáročnejšia, avšak dáva najlepšie výsledky.

Podrobne je teória krížovej validácie regresných modelov popísaná v prácach Picarda, Cooka (1984), Kohaviho (1995) a Varmu a Simona (2006).

4 METODIKA PRÁCE

4.1 Postup pri konštrukcii alometrických vzťahov a BCEF

Pre každú sledovanú drevinu bolo vybraných desať porastov v štádiu od náletov po mladiny, ktoré vznikli z prirodzenej obnovy a reprezentovali priemernú bonitu danej dreviny na Slovensku, pričom podiel vybranej dreviny v jednotlivých porastoch sa pohyboval v plošnom vyjadrení v rozmedzí 90 – 100 %. V každom poraste sa vybrali 3 plochy kruhového tvaru, ktoré reprezentovali celý porast. Ich polomer bol variabilný podľa hustoty porastu a bol zvolený tak, aby sa na kruhovej ploche nachádzalo minimálne 30 stromov, čo je počet vhodný na štatistické zhodnotenie s dostatočnou spoľahlivosťou. Na týchto plochách sa zistil počet jedincov a na všetkých jedincoch sa odmerala hrúbka v koreňovom krčku d_0 (dve na sebe kolmé merania) a výška. Tieto údaje slúžili pri výpočte počtu stromov na hektár a zásoby na hektár.

Na každej ploche sme vykopali 20-25 vzorníkov zastupujúcich hrúbkové a výškové rozpätie jedincov na celej ploche. Na zaistenie dobrého pokrytia rozdelenia podľa veľkosti sme zostrojili 10 rovnakých výškových tried špecifických pre každý porast, a potom náhodne vybrali a vykopali 2 až 3 vzorníky pre každú výškovú triedu. Úmyselne boli vybrané stromy rastúce v typických podmienkach porastu. Solitérne stromy boli vylúčené. Stromy boli odobrané na konci rastovej sezóny, keď rast všetkých komponentov bol ukončený. Vykopané boli všetky korene hrubšie ako 2 mm. Vzorníky sa rozseparovali na korene, kmeň, konáre, listy a kôru kmeňa. Priamo v teréne sa pred vykopaním vzorníka odmerala posuvným meradlom hrúbka v koreňovom krčku s presnosťou na desatinu milimetra v dvoch na seba kolmých smeroch a výška stromu s presnosťou na centimetre. Potom sa vzorky zabalili do označených papierových vriec a transportovali do laboratórií na ďalšie spracovanie.

Každá vzorka sa uložila v suchej, vetranej miestnosti po dobu jedného mesiaca. Potom sa vysušila v elektrickej sušičke pri teplote 105 ºC do konštantnej hmotnosti

Kmeň sa rozdelil na sekcie tak, aby sa skladal aspoň z 3-4 sekcií. Meranie sekcií sa uskutočnilo pred sušením, takže hodnota objemu je uvedená v čerstvom stave. Objem sekcie kmeňa sa vypočítal pomocou Newtonovho vzorca:

$$V = \frac{L(A_b + 4A_m + A_s)}{6} \tag{16}$$

kde V je objem kmeňa, L je dĺžka sekcie, A_b je plocha prierezu na širšom konci sekcie, A_m je plocha prierezu v strede sekcie a A_s je plocha prierezu na tenšom konci sekcie. Celkový objem kmeňa sa potom vypočítal ako suma objemov všetkých sekcií.

Newtonov vzorec sa pri výpočte objemu časti kmeňa (výrezy, sekcie) považuje za najpresnejší a najflexibilnejší, pretože je vhodný nielen pre výpočet objemu valcových a kužeľových tvarov, ale aj pre paraboloid a neloid (Wiant et al. 1992; Harmon, Sexton 1996; Woldendorp et al. 2002). Vypočítané hodnoty boli validované pomocou pyknometra (valec naplnený kvapalinou určený na meranie objemu telies) a rozdiely medzi vypočítaným a odmeraným objemom boli medzi -2 a +5 %. Pretože takéto stanovenie objemu je vhodné iba v laboratórnych podmienkach, v lesníckej praxi sa objem kmeňa zvyčajne počíta na základe jedného alebo dvoch ľahko merateľných parametrov. Najviac rovníc na vyjadrenie objemu kmeňa je takých, kde je nezávislou premennou hrúbka $d_{1,3}$ a výška stromu. Pretože rovnice s nezávislou premennou $d_{1,3}$ nie sú použiteľné v mladých porastoch ($d_{1,3}$ je nemerateľné alebo blízke nule), na vyjadrenie objemu kmeňa sme zostrojili tri alometrické rovnice, kde v prvom prípade bola nezávislou premennou hrúbka na báze kmeňa (d_0, označovaná aj ako DAB – diameter at base, alebo RCD – root collar diameter), v druhom prípade výška stromu (h) a v treťom prípade obidve tieto premenné (d_0, h). Objem kmeňa sa stanovil v čerstvom (mokrom) stave po vykopaní vzorníkov a to jednak ako objem kmeňa s kôrou a po olúpaní kôry bol vypočítaný aj objem kmeňa bez kôry.

V našom prípade je závislou premennou zásoba biomasy jednotlivých komponentov stromu vyjadrená v hmotnostných jednotkách. Vzhľadom na malé rozmery stromov nebude možné použiť ako nezávisle premennú hrúbku $d_{1,3}$. Namiesto nej sa použije hrúbka v koreňovom krčku d_0. Napriek tomu, že sa vo všeobecnosti málo používajú modely, kde je výška jedinou nezávislou premennou, využili sme aj tento model, pretože výška je v najmladších vývojových štádiách ľahšie merateľná ako hrúbka d_0 a pomocou nej je možné spojiť modely dospelých porastov s modelmi iniciálnych štádií. Testovali sme tri funkcie, kde nezávislými premennými boli postupne hrúbka d_0, výška h a ich vzájomná kombinácia.

$$W_i = e^{(b_0 + b_1 . \ln d_0)} . \lambda \tag{17}$$

$$W_i = e^{(b_0 + b_1 . \ln h)} . \lambda \tag{18}$$

$$W_i = e^{(b_0 + b_1 . \ln d_0 + b_2 . \ln h)} . \lambda \tag{19}$$

kde

W_i = produkcia biomasy (g sušiny vyjadrená na úrovni stromu)

d_0 = hrúbka koreňového krčka (mm)

h = výška stromu (m)

b_0, b_1, b_2 = parametre

BCEF boli odvodené na základe rovníc 10 a 11, keď po ich úprave vznikli nasledujúce rovnice:

$$BCEF = e^{(b_0 + b_1 . \ln d_0)} . \lambda \tag{20}$$

$$BCEF = e^{(b_0 + b_1 . \ln h)} . \lambda \tag{21}$$

$$BCEF = e^{(b_0 + b_1 . \ln d_0 + b_2 . \ln h)} . \lambda \tag{22}$$

Tieto rovnice sú rovnakého tvaru ako rovnice na vyjadrenie biomasy jednotlivých komponentov stromu (17-19) a obsahujú aj rovnaké nezávislé premenné (hrúbku na báze kmeňa, výšku stromu, alebo ich vzájomnú kombináciu).

4.2 Výpočet rastovej účinnosti, indexu listovej plochy a čistej primárnej produkcie

Pri výpočte rastovej účinnosti sme použili alometrické rovnice z regresného modelu na výpočet zásob biomasy. Rastová účinnosť je definovaná ako produkcia biomasy na jednotku biomasy listov:

$$GE_i = \frac{\Delta B_i}{B_f} \tag{23}$$

kde ΔB_i je prírastok komponentu *i* a B_f je listová biomasa.

Rastová účinnosť GE bola odvodená pomocou nasledujúcich vzorcov:

$$GE_i = \frac{(e^{(b_{i0}+b_{i1}\ln(DAB_{B_f}+\Delta DAB))}\lambda)-(e^{(b_{i0}+b_{i1}\ln DAB_{B_f})}\lambda)}{B_f} \tag{24}$$

$$GE_i = \frac{(e^{(b_{i0}+b_{i1}\ln(h_{B_f}+\Delta h))}\lambda)-(e^{(b_{i0}+b_{i1}\ln h_{B_f})}\lambda)}{B_f} \tag{25}$$

$$GE_i = \frac{(e^{(b_{i0}+b_{i1}\ln(DAB_{B_f}+\Delta DAB)+b_{i2}\ln(h_{B_f}+\Delta h_{B_f})}\lambda)-(e^{(b_{i0}+b_{i1}\ln DAB_{B_f}+b_{i2}\ln h_{B_f})}\lambda)}{B_f} \tag{26}$$

Rastová účinnosť sa alternatívne môže odvodiť na báze biomasy asimilačných orgánov alebo listovej plochy. Za účelom použitia druhej spomenutej metódy sme odobrali listy zo všetkých vybratých výskumných porastov. Listy boli získané z minimálne 40 jedincov pochádzajúcich z každého biosociologického postavenia (t.j. 10 kusov predrastavých, 10 úrovňových, 10 vrastavých a 10 potlačených). Po oskenovaní listov sa odvodila ich plocha pomocou programu LeafArea (voľne dostupná verzia z internetu). Následne sa vysušili a odvážili. Z plochy a hmotnosti listu sa odvodila špecifická listová plocha (specific leaf area; SLA, t.j. plocha listu na hmotnostnú jednotku). SLA sa využila na konvertovanie údajov z biomasy listov na ich plochu. Na základe výšky a hrúbky stromov (resp. aj biosociologického postavenia) sa skonštruovali alometrické vzťahy na vyjadrenie listovej plochy na úrovni jedinca a porastu.

Modely na výpočet indexu listovej plochy (LAI) na vybraných plochách boli skonštruované na základe údajov o hrúbke d_0 jednotlivých stromov, sušiny listov každého stromu a SLA. Sušina listov bola vyjadrená pomocou vyššie popísaných alometrických rovníc. SLA bola odvodená regresným modelom z empiricky nameraných hodnôt listovej plochy jednotlivého listu (LA_f) a jeho príslušnej sušiny (w_f):

$$SLA_f = \frac{LA_f}{w_f}, \tag{27}$$

Pretože hodnoty SLA_f závisia od osvetlenia koruny (Johansson 1996), boli na konštrukciu modelu použité iba listy so strednej časti koruny stromu. Pre každý odobraný list boli zaznamenané hodnoty hrúbky d_0 stromu, na ktorom rástli. Po oskenovaní listov a následnom vysušení a odvážení bolo pre každý list vypočítané SLA. Hodnoty SLA v závislosti od hrúbky d_0 boli vyrovnané alometrickou rovnicou, pričom bola použitá metóda najmenších štvorcov. Na základe existujúcich alometrických rovníc na výpočet sušiny listov a SLA je možné vypočítať celkovú listovú plochu stromu podľa vzťahu:

$$LA = w.SLA, \tag{28}$$

kde *w* je sušina všetkých listov stromu a *SLA* je hodnota na úrovni stromu

Keďže sušina listov je vyjadrená známou alometrickou rovnicou tvaru $y = e^{(b_0 + b_1 \ln d_0)}\lambda_1$ a SLA je tiež vyjadrené rovnicou rovnakého tvaru $y = e^{(b_2 + b_3 \ln d_0)}\lambda_2$, po dosadení dostaneme:

$$LA = (e^{(b_0 + b_1 \ln d_0)}\lambda_1)(e^{(b_2 + b_3 \ln d_0)}\lambda_2) = e^{(a_0 + a_1 \ln d_0)}\lambda \text{, kde } a_0 = b_0 + b_2, \tag{29}$$

$a_1 = b_1 + b_3$ a $\lambda = \lambda_1 \lambda_2$

Výpočet LAI na úrovni jednotlivých subplôch bol vykonaný nasledujúcim spôsobom:

- pre každý strom na subploche bola na základe d_0 vypočítaná listová plocha LA všetkých jeho listov,
- suma plôch listov jednotlivých stromov rastúcich na subploche tvorí plochu všetkých listov na subploche (tu sme zobrali do úvahy predpoklad, že plocha listov stromov rastúcich na okraji subplochy, ktoré sa nachádzajú mimo subplochy, je zhodná s plochou listov stromov, ktoré rastú mimo subplochy, ale svojou korunou zasahujú dovnútra),
- LAI bol vyjadrený ako podiel sumy plôch listov a výmery subplochy:

$$LAI_j = \frac{\sum LA_{ij}}{S_j}, \tag{30}$$

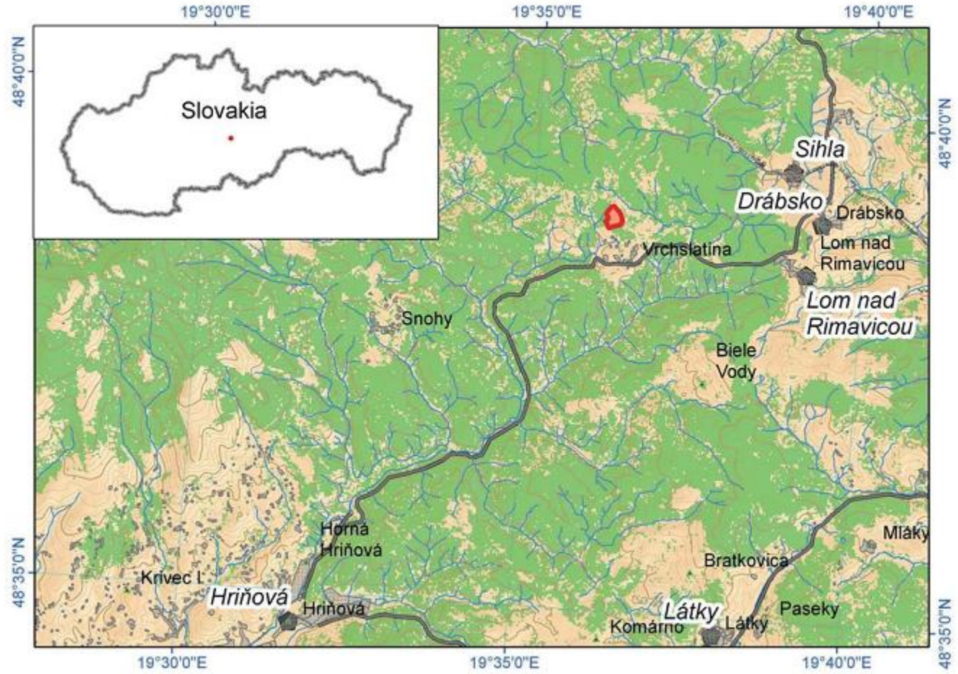
kde LA_{ij} je listová plocha i-teho stromu na j-tej subploche a S_j je výmera j-tej subplochy

Čistú primárnu produkciu (NPP) nadzemnej časti stromu sme pre frakciu kmeň s kôrou a konáre vyjadrili ako rozdiel v sušine biomasy týchto komponentov na začiatku rokov $i+1$ a i:

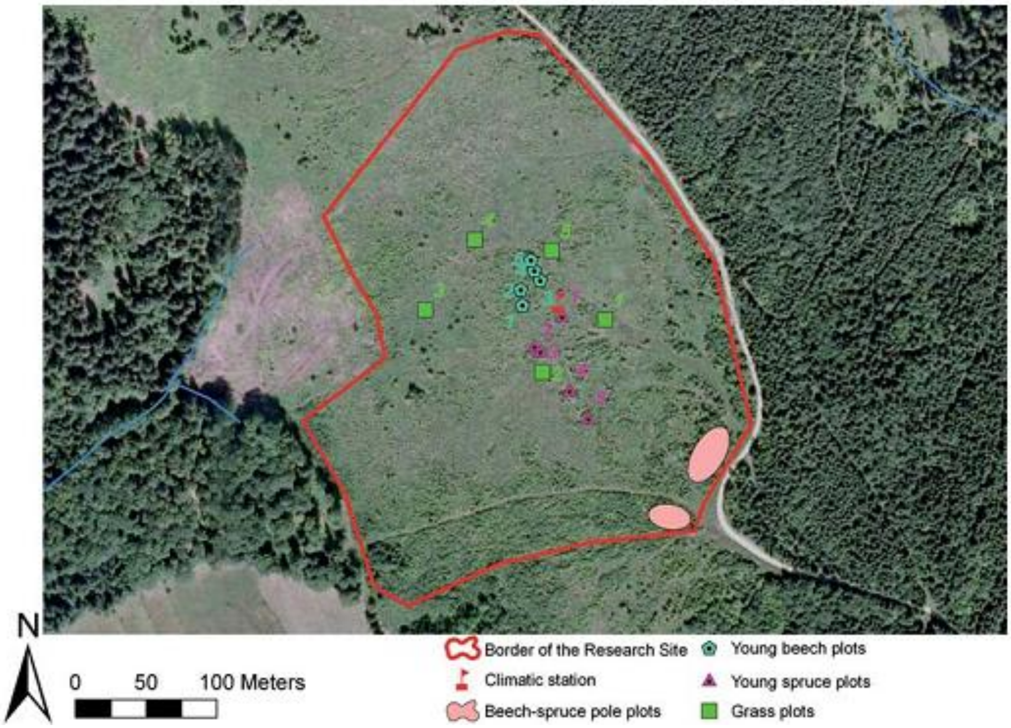
$$NPP_i = W_{i+1} - W_i \tag{31}$$

kde NPP_i je čistá primárna produkcia danej frakcie v roku i,
W_{i+1} je sušina príslušnej frakcie v roku $i+1$
a W_i je sušina príslušnej frakcie v roku i
Hodnoty W_i a W_{i+1} boli vyjadrené na základe hrúbky na báze kmeňa a výšky v rokoch i a $i+1$ pomocou vzorcov 17-19.
NPP_i pre frakciu listov buka sme vyjadrili ako zásobu sušiny tejto frakcie v roku i pomocou vzorcov 17-19. Pri frakcii ihličia smreka, ktoré obsahuje niekoľko ročníkov, bol v rokoch kedy sme počítali NPP na vyťažených 40 vzorníkoch smreka (po 10 z každého sociologického postavenia) odobratý posledný ročník ihličia a odvodené alometrické rovnice na výpočet jeho hmotnosti na základe hrúbky na báze kmeňa a výšky stromu.

Merania slúžiace na vyhodnotenie GE, LAI a NPP buka a smreka sme uskutočnili vo výskumnom objekte Vrchslatina, ktorý sa nachádza v južnej časti Veporských vrchov v nadmorskej výške 960 m (48°38´55″ N, 19°36´07″ E). Detailný popis výskumného objektu uvádza Konôpka et al. (2013d). Zobrazenie polohy výskumného objektu Vrchslatina a letecká snímka tohto objektu je na obr. 1 a 2.



Obr. 1. Zobrazenie polohy výskumného objektu Vrchslatina



Obr. 2. Letecká snímka na objekt Vrchslatina s náčrtom výskumných plôch. Štvorce reprezentujú plochy pre sledovanie mladých bučín, trojuholníky pre sledovanie mladých smrečín.

4.3 Kvantifikácia ohryzu jeleňou zverou a potravinového potenciálu

Údaje namerané na výskumných plochách a vzorníky na nich vykopané neboli pri drevinách jarabina vtáčia a vŕba rakytová využité iba na konštrukciu alometrických rovníc na výpočet biomasy jednotlivých komponentov stromu, ale tiež na konštrukciu modelov na výpočet potravinového potenciálu týchto drevín pre jeleniu zver. Preto boli na odobraných vzorníkoch okrem hrúbky v koreňovom krčku d_0, hrúbky v prsnej výške $d_{1,3}$ a výšky stromu h, odmerané aj hodnoty hrúbky vo výške 1,8 m $d_{1,8}$ a hodnoty výšky, v ktorej má strom hrúbku 10 mm h_{10}. Tieto potom slúžili ako nezávislé premenné v modeloch. Okrem toho sa na stromoch zaznamenalo prípadné poškodenie obhryzom, resp. odhryzom. Pri obhryze bola odmeraná plocha všetkých obhryzov. Použila sa na to transparentná šablóna so štvorcovou sieťou (rôzne farby označovali štvorce s rozmermi 1 x 1 mm, 10 x 10 mm a 100 x 100 mm). Zistila sa minimálna a maximálna vzdialenosť obhryzu od úrovne pôdy. Pri odhryze sa zmerala jeho vzdialenosť od zeme a hrúbka bočného konára, alebo terminálu v mieste odhryzu (tzn. na báze odhryznutého konára). Vzorníky sa rozdelili na jednotlivé komponenty podobne ako pri tvorbe modelov na výpočet biomasy, navyše sa však rozdelili listy a konáre do dvoch skupín. Prvú tvorili tie, ktoré môžu byť potenciálne zožrateľné jeleňou zverou (nachádzajúce sa do výšky 200 cm od zeme, pričom priemer konárov je menší ako 10 mm) a druhú tvorili zvyšné, nedostupné pre jeleniu zver. Komponenty stromu boli vysušené pri teplote 95 °C na konštantnú hmotnosť, a potom odvážené s presnosťou na 0,05 g. Tieto údaje boli použité na konštrukciu alometrických rovníc pre stromové komponenty. Na konštrukciu modelov bolo použitých 93 vzorníkov jarabiny o hrúbke d_0 5-80 mm a 100 vzorníkov rakyty o hrúbke d_0 4-70 mm.

Biomasa bola počítaná na troch úrovniach: úroveň konára (BL), úroveň stromu (TL) a úroveň porastu (SL). Zožrateľná biomasa (B_e) na úrovni konára bola stanovená oddelene pre dve kategórie: konáre bez listov (zimný odhryz, B_{eb}) a konáre s listami (letný odhryz, B_{eb+ef}). Do rovníc vstupovala ako nezávislá premenná hrúbka konára v mieste odhryzu:

$$B_{eb}(BL) = b_1 d_b^{b_2} \tag{32}$$

$$B_{eb+ef}(BL) = b_1 d_b^{b_2} \tag{33}$$

Regresná rovnica rovnakého typu bola použitá aj na odvodenie špecifickej plošnej hmotnosti kôry (w_s) na základe hrúbky d_0:

$$w_s = b_1 d_0^{b_2} \quad (34)$$

Alometrické rovnice na výpočet sušiny jednotlivých stromových komponentov boli vytvorené pre dve nezávislé premenné: hrúbku d_0 a/alebo výšku h.

$$B(TL) = e^{(b_1 + b_2 \ln d_0 + b_3 \ln h)} \lambda, \quad (35)$$

kde b_1, b sú regresné koeficienty a λ je korekčný faktor.

Zožrateľná sušina (B_e) na úrovni stromu (TL) sa kvantifikovala pre nasledujúce komponenty: konáre, listy, terminálny výhonok a kôru kmeňa. Potenciálne zožrateľná biomasa konárov (B_{eb}) a listov (B_{ef}) bola vypočítaná podľa nasledujúcej rovnice:

$$B_e(TL) = B.r, \quad (36)$$

kde r (r_b alebo r_f) je pomer zožrateľných konárov alebo listov k celkovej biomase konárov alebo listov. Tento pomer bol vypočítaný z hmotnosti sušiny zožrateľnej a nezožrateľnej frakcie pre každý vzorník. Na modelovanie tohto pomeru na základe hrúbky d_0 bola použitá beta regresia (Ferrari, Cribari-Neto 2004; Simas et al. 2010). Tento typ regresie sa používa na modelovanie kontinuálnych premenných a predpokladá, že hodnoty sú v štandardných jednotkových intervaloch. Testovali sme niekoľko funkcií a na základe hodnôt AIC kritéria (Akaike 1974) bola ako najlepšia vybraná funkcia tvaru:

$$r = 1\text{-exp}\ (\text{-exp}(b_1 + b_2 d_0)) \quad (37)$$

Pri modelovaní zožrateľnej biomasy terminálnej časti kmeňa sme vychádzali z predpokladu, že odhryz je limitovaný výškou kmeňa približne 2 m a hrúbkou kmeňa okolo 10 mm. Z toho potom vyplýva, že ak je strom na báze kmeňa tenší ako 10 mm je celý kmeň potenciálne zožrateľný a sušina biomasy zožrateľnej terminálnej časti kmeňa sa rovná sušine biomasy kmeňa vypočítanej pomocou alometrickej rovnice. Ak je hrúbka bázy kmeňa väčšia ako 10 mm, množstvo biomasy zožrateľnej časti kmeňa sa už nezväčšuje, ale zostáva konštantné za predpokladu, že objem kmeňa s hrúbkou na báze 10 mm je zhodný s objemom terminálu s hrúbkou v mieste odhryzu rovnou 10 mm:

$$B_{es}(TL) = B_s(TL) \quad (38)$$

pre $d_0 \leq 10$ mm

alebo $B_{es}(TL) = B_{s(10)}(TL) = 21{,}17$ g $\quad (39)$

pre d_0 >10 mm a $d_0 \leq d_{h=2}$,kde $d_{h=2}$ je hrúbka prislúchajúca výške 2 m.

Pri modelovaní zožrateľnej biomasy kôry stromu sme vychádzali z predpokladu, že jeleň neobhrýza stromy, ktoré majú na báze hrúbku menšiu ako 20 mm a obhryz dosahuje do výšky v ktorej má strom hrúbku d_k=10 mm, maximálne však 1.80 m. Sušina zožrateľnej biomasy kôry kmeňa (B_{ebark}) bola potom pre jednotlivé vzorníky vypočítaná podľa vzorca:

$$B_{ebark}(TL) = S * w_s \,, \tag{40}$$

kde S je plocha zožrateľnej kôry kmeňa, w_s je špecifická plošná hmotnosť kôry.

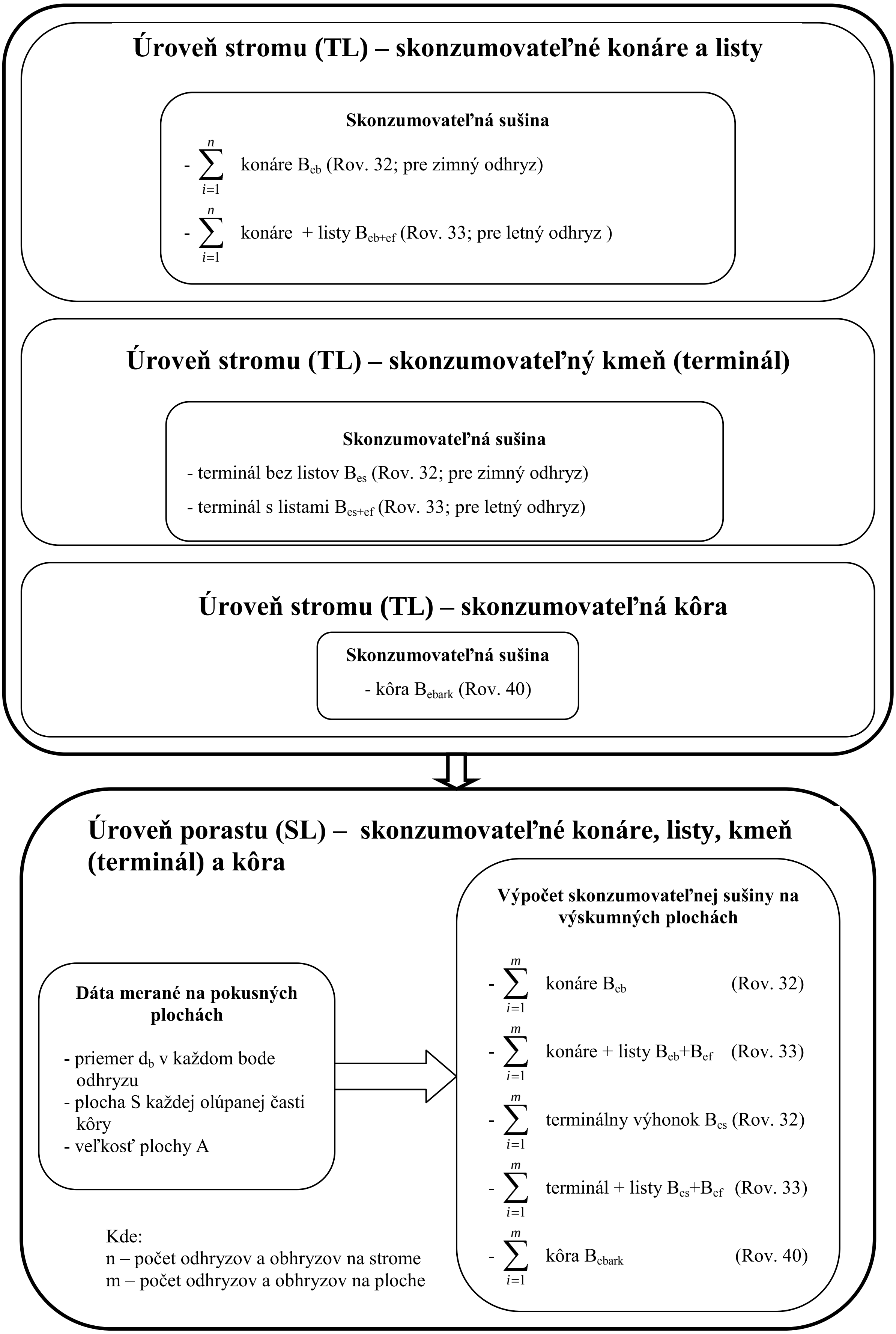
Pri výpočte plochy S sa použil vzorec na stanovenie povrchu plášťa zrezaného rotačného kužeľa s polomerom dolnej podstavy $r_{0.0}$, s polomerom hornej podstavy $r_{1.8}$ a výškou 1.80 m. Vypočítané hodnoty B_{ebark} boli následne vyrovnané regresnou funkciou tvaru (36), kde nezávisle premennou je iba d_0:

$$B_{ebark}(TL) = b_1 d_0^{b_2} \,, \text{ pre } d_0 \geq 20 \,\text{mm} \tag{41}$$

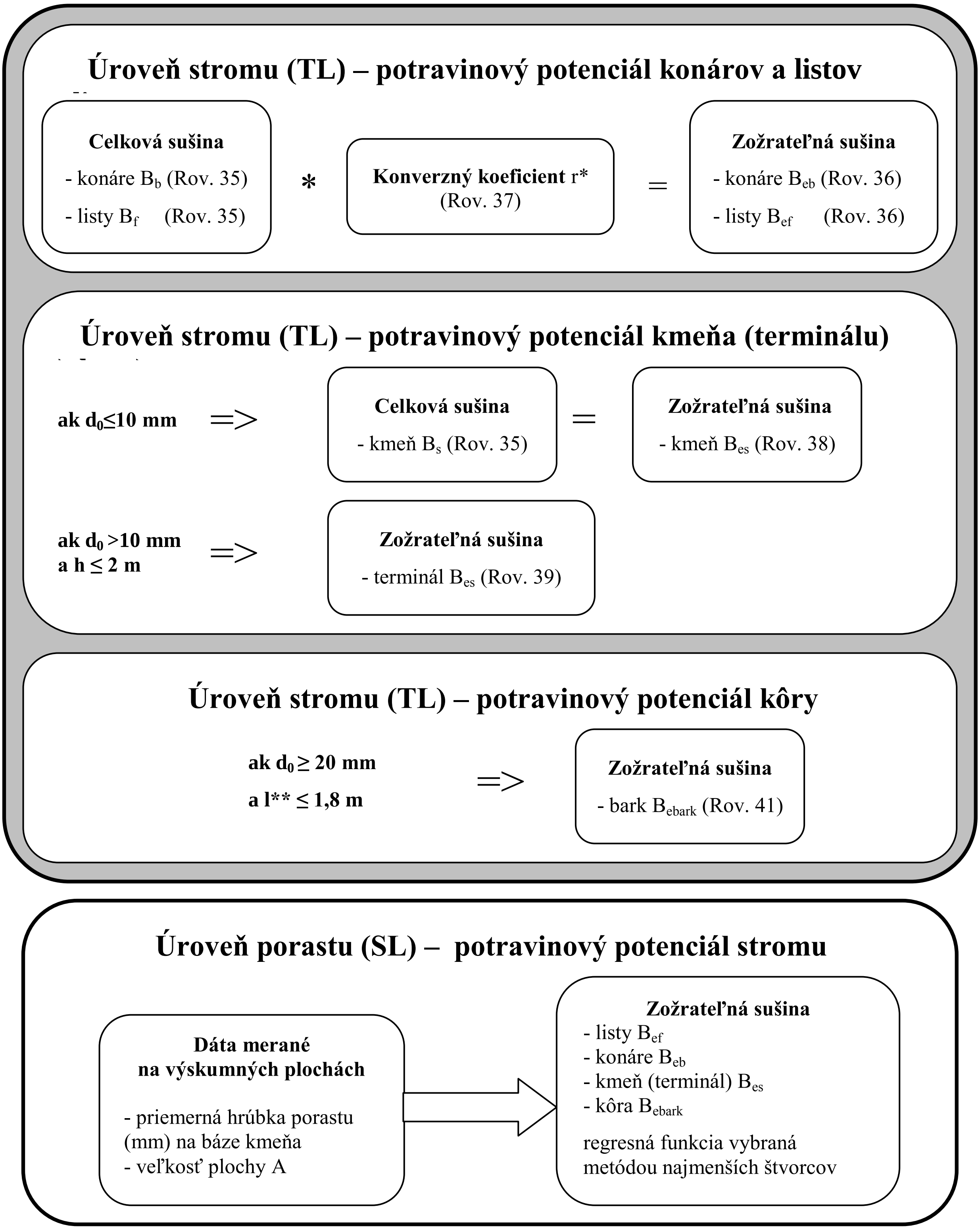
kde b_1, b_2 sú regresné koeficienty.

Modely na úrovni stromu (TL) boli implementované na 20 výskumných plôch za účelom vyčíslenia množstva biomasy jednotlivých komponentov, ktoré boli reálne skonzumované jeleňou zverou. Navyše modely boli využité na vyhodnotenie potenciálne zožrateľnej biomasy jednotlivých komponentov na úrovni porastu. Aktuálne zožraté množstvo biomasy spolu s potenciálne zožrateľným bolo prepočítané na 100 m^2 plochy a zápoj 50 %. Pri tvorbe modelov na úrovni porastu, kde nezávislou premennou bola stredná hrúbka porastu d_0, boli testované viaceré regresné funkcie a pomocou metódy najmenších štvorcov vybrané tie, ktoré najlepšie aproximovali empiricky namerané hodnoty.

V priložených schémach sa zobrazuje návrh postupu pre odhad reálne skonzumovanej biomasy podľa stromových komponentov jeleňou zverou, jednak na úrovni stromu, ako aj porastu (Obr. 3). Ďalej postup výpočtu potravinového potenciálu pre jeleniu zver na úrovni stromu a porastu (Obr. 4).



Obr. 3. Schéma postupu pre odhad reálne skonzumovanej biomasy podľa stromových komponentov na úrovni stromu a porastu



Poznámky:

** - konverzný koeficient r vyjadruje pomer zožrateľnej biomasy k celkovej biomase. Koeficient bol odvodený pomocou β funkcie.*

*** - kôra kmeňa prístupná pre zver je definovaná maximálnou vzdialenosťou 1,80 m od zeme.*

Obr. 4. Schéma výpočtu potravinového potenciálu jarabiny podľa komponentov na úrovni porastu. Kroky označené sivým pozadím (úroveň stromu) nie sú pre užívateľa nevyhnutne potrebné (model na úrovni porastu je priamo aplikovateľný).

5 VÝSLEDKY

Primárnym (východiskovým) výstupom vedeckej práce autora bolo odvodenie alometrických vzťahov a BCEF pre mladé jedince týchto listnatých drevín: buk obyčajný, dub zimný, jaseň štíhly, javor horský, jarabina vtáčia a vŕba rakytová. Prehľad modelov pre biomasu celých stromov, nadzemnej časti spolu, konárov, listov, kmeňa s kôrou a koreňov sa uvádza samostatne pre každú drevinu v Prílohách 1 až 6. Prílohy obsahujú alometrické rovnice pre tri nezávislé premenné (hrúbku na báze kmeňa, výšku stromu a ich vzájomnú kombináciu). Rovnice na výpočet BCEFov neuvádzame z dôvodu, že sú ťažšie uplatniteľné, pretože pri ich aplikácii v praxi zvyčajne absentujú rovnice na výpočet objemu kmeňa, ktorý BCEF konvertujú na sušinu biomasy.

Zároveň sa tieto modely pre niektoré dreviny implementovali do publikačných výstupov v podobe vedeckých článkov. Konkrétne sa využili v publikácii: „Biomass functions and expansion factors for young trees of European ash and Sycamore maple in the Inner Western Carpathians“ (pre javor horský a jaseň štíhly; viď. podkapitola 5.1), „Above-ground net primary productivity in young stands of beech and spruce“ (pre buk obyčajný; viď. podkapitola 5.2), „Foliage and fine roots in terms of growth efficiency – a comparison between European beech and Norway spruce at early growth stages“ (pre buk obyčajný; viď. podkapitola 5.2), „Specific leaf area and leaf area index in developing stands of *Fagus sylvatica* L. and *Picea abies* Karst. (pre buk obyčajný, viď podkapitola 5.2), „Modelling forage potential for red deer: A case study in post-disturbance young stands of rowan“ (pre jarabinu vtáčiu; viď. podkapitola 5.3) a „Quantifying edible biomass on young Salix caprea and Sorbus aucuparia trees for Cervus elaphus: estimates by regression models“ (pre vŕbu rakytovú a jarabinu vtáčiu; viď. podkapitola 5.3).

V ďalšom texte kapitoly Výsledky sa uvádza šesť pôvodných vedeckých prác zoskupených do troch hlavných okruhov (podkapitol). Konkrétne oblasť „Konštrukcia alometrických vzťahov, BCEF a alokácia biomasy“ reprezentuje jedna práca (podkapitola 5.1), oblasť „Čistá primárna produkcia, listová plocha a rastová efektívnosť tri práce (podkapitola 5.2) a oblasť „Ohryz jeleňou zverou a potravinový potenciál“ dve práce (podkapitola 5.3).

5.1 Konštrukcia alometrických vzťahov, BCEF a alokácia biomasy

Funkcie biomasy a expanzné faktory pre mladé stromy jaseňa štíhleho a javora horského vo Vnútorných Západných Karpatoch

Abstrakt

Modely na výpočet biomasy stromu sú dôležité nielen pre výpočet celkovej biomasy stromu, ale tiež pre výpočet biomasy jej jednotlivých komponentov. Vyvinuli sme alometrické rovnice a konverzno-expanzné faktory (BCEF) pre mladé porasty jaseňa štíhleho *(Fraxinus excelsior L.)* a javora horského *(Acer pseudoplatanus L.)*. Dáta reprezentujú po 100 vzorníkov z každej dreviny z oblasti stredného Slovenska. Na každom vzorníku bola odmeraná hrúbka na báze kmeňa, výška a stanovil sa jeho objem. Vzorníky boli rozseparované na jednotlivé stromové komponenty: korene, kmeň, konáre a listy, potom nasledovalo ich vysušenie a odváženie. Modely na výpočet biomasy sa skonštruovali na základe hrúbky na báze kmeňa a/alebo výšky, ktoré vystupujú v modeloch ako nezávislé premenné. Štruktúru biomasy jaseňa a javora sme porovnali so štruktúrou biomasy buka lesného *(Fagus sylvatica L.)*, ktorá bola vyjadrená na základe dát získaných v predošlom období z tej istej oblasti. Zatiaľ čo sme zaznamenali relatívne malé rozdiely v celkovej biomase jednotlivých druhov stromov, medzidruhové rozdiely v množstve biomasy sledovaných komponentov stromu boli výraznejšie. Najväčšie rozdiely sme zistili v percentuálnom podiele frakcie kmeňa a frakcie konárov buka v porovnaní s jaseňom a javorom. Podiel jednotlivých komponentov závisí od veľkosti stromu. Tieto zmeny sú pravdepodobne následkom rastovej stratégie od ranných k neskorším rastovým štádiám. Podiel kmeňa a konárov na celkovej biomase stromu narastá s veľkosťou stromu, zatiaľ čo podiel listov a koreňov klesá. Napríklad najmenšie stromčeky majú pomer koreňov k nadzemnej biomase (root/shoot ratio) blízky hodnote 1,0, ale u stromov s hrúbkou na báze kmeňa okolo 70 mm dosahuje tento pomer hodnotu 0,2. Ukázali sme medzidruhové rozdiely medzi alometrickými rovnicami a BCEF skonštruovanými pre jaseň a javor. Zároveň sme porovnali naše alometrické modely s inými regresnými modelmi pre tieto dreviny, ktoré boli zostrojené v Nemecku a Veľkej Británii.

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Biomass functions and expansion factors for young trees of European ash and Sycamore maple in the Inner Western Carpathians

Biomassefunktionen und Expansionsfaktoren für junge Europäische Eschen und Bergahorne in den Inneren Westlichen Karpaten

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Keywords: Biomass model, biomass structure, tree components, tree height, stem diameter
Schlüsselworte: Biomassemodelle, Biomassestruktur, Baumkomponenten, Baumhöhe, Stammdurchmesser

Summary

Forest tree biomass models are important, not only for estimating total tree biomass but also for estimating biomass structure by components. Thus, we developed allometric equations, biomass conversion and expansion factors (BCEF) for young European ash (*Fraxinus excelsior*) and Sycamore maple (*Acer pseudoplatanus*). New data, including 100 sample of each tree species, were collected from central Slovakia. Stem diameter, volume and length were measured and individual tree components; roots, stem, branches and foliage were dried and weighed. Biomass models were constructed using diameter at stem base and/or tree height as independent variables and biomass structure in ash and maple were compared with existing European beech (*Fagus sylvatica*) data obtained previously from the same region. While relatively few interspecific differences were recorded in whole tree biomass, there is evidence of structural diversity in component biomass. The main differences were found in percentages of stem and branch biomass with beech results contrasting with ash and

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maple. Contributions of tree components to structural biomass change relative to tree size. These changes are possibly a consequence of progressive growth strategy from early to later tree growth stages. Proportions of stem and branches to whole tree biomass increase with tree size, while foliage and roots decrease. For instance, the smallest trees have a root to shoot ratio of nearly 1.0 while trees with a stem diameter of 70 mm demonstrate proportions of around 0.2. We showed differences between allometric equations and BCEF in both European ash and Sycamore maple. Moreover, our allometric models were compared with other models from Germany and UK.

Zusammenfassung

Forstliche Biomassemodelle für Bäume sind nicht nur bedeutsam für die Bestimmung der gesamten Biomasse eines Baumes, sondern auch für die Kompartimentsstruktur der Biomasse. Daher entwickelten wir allometrische Gleichungen und Umwandlungs- und Expansionsfaktoren der Biomasse (biomass conversion and expansion factors - BCEF) für junge Europäische Eschen (*Fraxinus excelsior*) und Bergahorne (*Acer pseudoplatanus*). Neue, für jede Baumart 100 Proben umfassende Daten wurden in der Zentralslowakei aufgenommen. Stammdurchmesser, Volumen und Länge wurden gemessen und die individuellen Baumkomponenten Wurzel, Stamm, Zweige und Belaubung wurden getrocknet und gewogen. Biomassemodelle wurden aufbauend auf die unabhängigen Variablen des Durchmessers am Stammfuß und/oder der Baumhöhe konstruiert. Die Biomassestruktur von Esche und Ahorn wurde mit existierenden Daten der Europäischen Buche (*Fagus sylvatica*) in derselben Region verglichen. Während relativ wenige interspezifische Differenzen bei der Biomasse des Gesamtbaumes festgestellt wurden, gibt es Anzeichen für strukturelle Differenzen in den Komponenten der Biomasse. The Hauptgegensätze ergaben sich bei den Anteilen der Biomasse von Stamm und Zweigen zwischen den Ergebnissen von Buche verglichen mit denen von Esche und Ahorn. Die Beiträge der Baumkomponenten zur strukturellen Biomasse ändern sich relativ zur Baumgröße. Diese Änderungen begleiten progressive Wachstumsstrategien von frühen zu späteren Wachstumsstufen der Bäume. Anteile des Stammes und der Zweige an der Biomasse des Gesamtbaumes steigen mit Baumgröße, während die Anteile von Belaubung und Wurzeln sinken. Zum Beispiel hat der kleinste Baum eine Relation von Wurzel zu Sproß von 1,0 während Bäume mit Stammdurchmesser von 70 mm Anteile von 0,2 aufweisen. Wir zeigten Unterschiede zwischen allometrischen Gleichungen und Konversion- und Expansionsfaktoren der Biomasse für beide Europäische Esche und Bergahorn. Darüber hinaus wurden unsere allometrischen Modelle mit anderen aus Deutschland und Großbritannien verglichen.

1. Introduction

The importance of carbon sequestration in forest ecosystems as a complex measure to mitigate climate change is an established concept (e.g. Vogt, 1991; Dixon, 1994). On a global scale, European forests are an important carbon sink, currently accumulating biomass. They are also significant soil carbon stores highlighting their importance for carbon store in the future (Janssens et al., 2003; Karjalainen et al., 2003). In central Europe, the amount of carbon stored in tree biomass exceeds soil carbon storage (Brunner and Godbold, 2007). At the same time, the quantity of carbon fixed in forest biomass is more dynamic than that in the forest soils. Thus, accurate estimates of forest tree biomass are important to develop a clear understanding of biomass carbon storage. Traditionally, only biomass estimates of merchantable wood; stem and coarse branches with diameter over 7 cm (in some countries over 5 cm), were conducted in forestry practice and subsequently a wide range of methods were developed for its inventory. However, biomass allocation among tree components influence the residence time of carbon fixation and therefore plays a critical role in the carbon cycle in forest ecosystems (e.g. Helmisaari et al., 2002; Konôpka et al., 2013). Two basic tree component groups are considered important for biomass carbon storage: long-term fixed carbon storage (e.g. stem, branches and coarse roots) that contain carbon for decades or longer; and short-term carbon storage (e.g. foliage and fine roots) that store carbon for months to a few years maximum (e.g. Yuste et al., 2005). Consequently, there is an urgent need to improve the existing methods for reliable assessments of non-stem components on both the tree and stand levels (Lehtonen, 2005).

In general, during the past couple of decades, focus has centered on tree biomass models with particular emphasis based on allometric equations or biomass expansion factors (e.g. West, 2009). Allometric equations or biomass functions express biomass calculations of various parts of individual trees based on measurable characteristics (e.g. stem diameter or tree height). Biomass expansion factors are used to expand the available tree stem biomass data to estimate the total tree biomass or specific tree component. Integrating biomass expansions and conversion components (Tobin and Nieuwenhuis, 2007) into one biomass factor expressed as a biomass conversion and expansion factor (BCEF) converts the most commonly available data on stem volume directly to whole tree or component biomass (Schroeder et al., 1997) and this can be further up-scaled to the forest stand level (e.g. Jalkanen et al., 2005; Šmelko et al., 2011). At the same time, the choice of method and the sample material might have a strong impact on the biomass/carbon results (Thurnher et al., 2013).

A lack of research focusing on young trees identifies the requirement to find allometric relations to enable biomass calculations for juvenile carbon storage potential (Wirth et al., 2004; Pajtík et al., 2008, 2011). This is further supported by the fact that the tree biomass component proportions are height (age) dependant and reflect different growth strategies in young and old stages (Claesson et al., 2001; Lehtonen et al., 2004). Similarly, Wirth et al. (2004) further suggested that it is necessary to establish biomass models for small trees as the existing models for large tress are non-transferable due to contrasting biomass allocation patterns.

The Good Practice Guidance for land use; Land Use Change and Forestry (IPCC, 2003) suggests direct field measurements in young stands because current biomass models originate from large trees only. Pajtík et al. (2008) stressed the importance of biomass models for small trees due to a rise in the area covered by even-aged young forests in the last decade as a consequence of afforestation and salvage cuttings. Further, recent changes in the forestry policy towards preference from even-aged monocultures to mixed-age forests can be documented in most of the European countries and in practice increases the percentage of young trees within forest stands.

In Slovakia the contribution of "other" broadleaved species (the term expresses all broadleaves excepting the main commercial species; European beech, Pedunculate oak, Sessile oak and Common hornbeam) to standing stock in young stands is much higher than in older stands (Konôpka et al., 2012b). For instance, the National Forest Inventory (NFI) in Slovakia performed in 2005 – 2006 (unpublished data) showed that Sycamore maple (*Acer pseudoplatanus*) represented approx. 8.2% of the entire forest cover when considering the first age class (up to 20 years). On the other hand, this species made up only 3.0% and 1.5% in the stands aged 40 – 80 years and over 100 years, respectively. European ash (*Fraxinus excelsior*) made up ca. 3.2%, 2.0% and 0.6% of the forest cover considering stands with ages 0 – 20, 40 – 80, and over 100 years, respectively. The percentage cover of these tree species decrease gradually with stand age, most probably due to interspecific competition, intentional forest management (thinning) and external factors such as red deer (*Cervus elaphus*) browsing.

After reviewing literature (e.g. Zianis et al., 2005; Muukkonen, 2007; Teobaldelli et al., 2009) we can state that only few studies have previously focused on biomass models in European ash and Sycamore maple. For instance in Slovakia, Petráš and Pajtík (1991) constructed models for stem and coarse branch volume in European ash, Albert et al. (2014) in Germany and Bunce (1968) in UK developed models for biomass allocation of aboveground woody parts (i.e. stem and branches) in both European ash and Sycamore maple. Hence, biomass models expressing all tree compartments and total tree biomass are lacking for both species.

The specific aims of this paper are summarized as follows:

1. Construct both allometric equations as well as BCEF for tree components in young European ash and Sycamore maple
2. Demonstrate the differences between allometric equations and BCEF in young European ash and Sycamore maple
3. Compare our biomass models for European ash and Sycamore maple to models for European beech from our previous work (Pajtík et al. 2011).

2. Material and Methods

2.1 Site and stand description

Our research focused on the forested mountain area of the Slovak Central Mountains which belongs to the sub-province of the Inner Western Carpathians. The mountains are volcanic in origin and the predominantly andesitic bedrock is covered by Cambisol. The forest composition is dominated by European beech with a mixture of other broadleaf species at lower altitudes such as Common hornbeam, European ash and Sycamore maple. In higher altitudes, coniferous species such as Norway spruce (*Picea abies*), Silver fir (*Abies alba*) and isolated populations of European larch (*Larix decidua*) are present.

A preliminary screening of forest stands containing European ash or Sycamore maple was conducted using a forest database (Programs of Forest Management by Stand Units in Slovakia; available on: http://gis.nlcsk.org/lgis/) with specific information on tree species composition and age class (defined within a 10 year interval). The main criteria was to select forest stands with a minimum composition of 80% of the target tree species (ash or maple) and a stand age of up to 20 years. The final selection of 20 forest stands (10 x ash and 10 x maple; Figure 1; Table 1 and 2) were identified for their exclusively natural regeneration. The altitudinal range was between 710 m – 950 m a.s.l. for ash stands and 700 m – 980 m a.s.l. for maple forest stands. The area thus belonged to two altitudinal vegetation zones categorised by the native dominant forest tree species; beech and fir-beech. In this region the total mean annual precipitations is 950 mm and average annual temperature 5.5˚C.

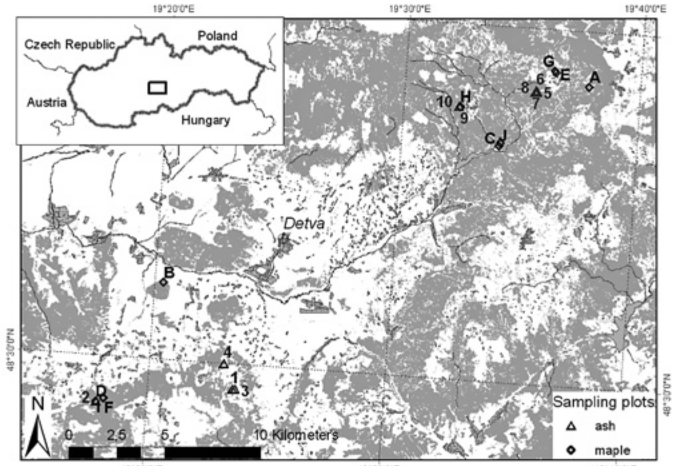

Fig. 1: Localization of the sampling plots for European ash (codes 1-10) and Sycamore maple (codes A-J)

Table 1: Basic characteristics of stand properties in research plots used for study of European ash

Plot code	Canopy cover (%)	Percentage of ash (%)	Number of trees* per 100 m²	Mean stem diameter d_0* (mm)	Lorey's height* (m)	Age* (years)
1	45	90	358	14.7	0.80	2
2	35	90	390	15.5	0.96	3
3	55	100	454	15.6	1.03	3
4	70	100	920	15.8	1.22	3
5	60	100	222	27.9	2.05	5
6	40	100	183	36.8	2.94	6
7	85	100	207	36.1	4.17	6
8	75	100	223	39.7	4.20	7
9	90	100	239	31.3	4.25	5
10	90	100	366	32.5	4.59	6

Explanatory note: * characteristics for ash trees

Table 2: Basic characteristics of stand properties in research plots used for study of Sycamore maple

Plot code	Canopy cover (%)	Percentage of maple (%)	Number of trees* per 100 m²	Mean stem diameter d_0* (mm)	Lorey's height* (m)	Age* (years)
A	40	100	1047	5.5	0.30	1
B	45	90	679	12.3	0.94	2
C	70	80	271	22.1	1.53	4
D	50	80	358	25.5	2.40	4
E	35	100	271	27.8	2.79	5
F	30	95	280	21.1	3.81	4
G	95	100	430	36.0	4.80	6
H	80	85	188	39.5	5.81	7
I	90	90	305	38.4	6.09	7
J	70	95	158	46.6	6.86	8

Explanatory note: * characteristics for maple trees

2.2 Tree measurements and sampling

Circle-like plots with radius of between 1 and 2 m were established in each of the 20 selected stands during the second half of the growing season in 2012 and 2013. The size of each plot was determined with regards to stand density to include approximately 40 trees for further analysis. Tree height, diameter at stem base (diameter d_0), diameter at breast height (dbh) and number of individual trees (ash, maple or other species) were recorded on each plot and divided into five height classes of equal interval. Then, ten trees were identified and sampled to represent each of the five height classes (two trees per class) for both ash and maple. A total of 200 trees, 100 individual trees of each species, were excavated including roots with a diameter of over 1 mm. By using a handsaw and garden shears the trees were separated into roots, stem and branches with foliage. The borderline between roots and stem was the ground level (marked prior to tree excavation) and to separate stem and branches the branch base was identified (i.e. the area of each branch closest to the stem surface). The samples of roots, stems and branches with foliage were packed and transported to the laboratory.

In the laboratory, diameters d_0 and dbh were measured in two perpendicular directions and tree height was recorded. Stems were divided into approximately 50 cm-long sections and if trees were under 150 cm in height they were divided into three equal sections. Three diameters were measured on each section; the middle point and the diameter at both ends. The volume of each section was calculated according to Newton's formula (e.g. West, 2009):

$$V = \frac{L(A_b + 4A_m + A_s)}{6} \tag{1}$$

where V is the volume, L is the section length, A_b the cross-sectional area at the large end of section, A_m the cross-sectional area at midpoint of section and A_s is the cross-sectional area at smallest end of section. The total sum of volumes of all three sections was calculated to represent the total stem volume (over bark).

Table 3: Descriptive statistics of the sampled trees

Species	Tree parameter	Mean	Median	S.D.	S.E.	Min	Max	Lower quartile	Upper quartile	Skewness	Kurtosis
Ash	Diameter d_0 (mm)	23.44	21.45	11.61	1.29	5.35	51.25	13.35	31.75	0.42	-0.73
	Height (m)	2.09	2.09	1.18	0.13	0.19	4.24	1.02	2.96	0.12	-1.17
	ABVG biomass (g)	369.10	204.38	421.27	47.10	2.45	1806.50	41.43	546.15	1.42	1.40
	Total biomass (g)	508.01	292.15	586.19	65.95	5.25	3064.50	65.90	701.30	1.80	3.95
	Stem volume (cm³)	502.06	261.63	571.05	63.45	2.10	2239.89	52.31	771.21	1.33	0.90
Maple	Diameter d_0 (mm)	31.30	27.85	22.09	2.21	5.70	104.50	12.48	43.78	1.01	0.50
	Height (m)	3.36	2.93	2.46	0.25	0.24	9.87	0.85	5.17	0.59	-0.45
	ABVG biomass (g)	1053.05	282.29	1921.50	194.10	3.07	14098.13	27.21	1122.59	3.96	21.81
	Total biomass (g)	1368.72	408.78	2383.58	243.27	5.67	16932.93	59.98	1509.65	3.68	18.95
	Stem volume (cm³)	1750.72	489.56	3188.91	318.89	2.28	23114.93	28.04	1883.24	3.85	20.46

After a few days under room temperature foliage was separated from the branches. Tree components were then oven dried at a temperature of 105˚C until they reached a constant weight. Volume, size and weight measurements were subsequently used for alometric relations and BCEF. Descriptive statistics for the sampled trees are presented separately for ash and maple in Table 3.

2.3 Construction of biomass models

For calculations of biomass, whole tree or specific tree components, the most frequent allometric equation is in the form:

$$Y = aX^{b} \tag{2}$$

where Y is the dependent variable, X is independent variable and a and b are parameters of the biomass model. Due to its flexibility, a variety of applications of this formula have been established, since it can easily be expanded into the following multiple form:

$$Y = a_0.X_1^{b_1}.X_2^{b_2}.X_3^{b_3}.....X_n^{b_n}.\theta \tag{3}$$

where Y is the dependent variable, X_1-X_n are independent variables, a_0-b_n are model coefficients and θ represents the multiplicative error term. We implemented the function in its logarithmic form as it allows for linear regression to be used to estimate the coefficients:

$$\ln Y = b_0 + b_1.\ln X_1 + b_2.\ln X_2 + b_3.\ln X_3 + ... + \ln X_n + \varepsilon \tag{4}$$

where $b_0 = \ln a_0$ and $\varepsilon = \ln \theta$. It is relevant to point out that the logarithmic transformation of the dependent variable does cause a bias which occurs during reverse transformation of the logarithmic form (e.g. Baskerville, 1972). Hence, it is necessary to use a correction factor for re-transformation which is calculated using the method suggested by Marklund (1987) as follows:

$$\lambda = \frac{\sum_{i=1}^{n} Y_i}{\sum_{i=1}^{n} e^{\ln \hat{Y}_i}} \tag{5}$$

where n is the sample size.

Since some trees in the sample set were smaller than 130 cm, we could not use the standard tree mensuration parameter dbh. Instead we implemented diameter d_0 as the independent variable which is considered useful for all tree heights. Moreover, we used tree high as an individual parameter and in combination with diameter d_0 because this characteristic is rather easy to measure in young forest stands.

The predictive power of the following functions was tested:

$$B = e^{\left(b_0 + b_1 \ln d_0\right)} \lambda \tag{6}$$

$$B = e^{\left(b_0 + b_1 \ln h\right)} \lambda \tag{7}$$

$$B = e^{\left(b_0 + b_1 \ln d_0 + b_2 \ln h\right)} \lambda \tag{8}$$

where B is the total dry biomass per tree, d_0 the diameter at stem base, h is the tree height and b_0, b_1, b_2 are the coefficients.

Biomass allocated in a tree can be calculated by regression equations or by using biomass factors. We used BCEF (e.g. Lehtonen et al., 2004) which is expressed as:

$$BCEF_i = \frac{W_i}{V} \tag{9}$$

where W_i is the biomass (dry matter) of a tree component (i.e. roots, stem, branches, foliage, above-ground parts and whole tree) and V is stem volume. In fact, BCEF of the stem is the stem density.

Stem volume was calculated as described above (Equation 1) and the point cloud was fitted through the function (2) transformed in the forms:

$$V = e^{\left(b_0 + b_1 \ln d_0\right)} \lambda \tag{10}$$

$$V = e^{\left(b_0 + b_1 \ln h\right)} \lambda \tag{11}$$

$$V = e^{\left(b_0 + b_1 \ln d_0 + b_2 \ln h\right)} \lambda \tag{12}$$

where V is the stem volume.

For expressing dry weight, Wi, we have used the basic allometric formula (Equation 2) which fits for the calculation of volume, V. We can therefore expand Equation 9 into the form:

$$BCEF_i = \frac{a_1 X^{b_1}}{a_2 X^{b_2}} = aX^b \text{, where } a = \frac{a_1}{a_2} \text{ and } b = b_1 - b_2 \tag{13}$$

and use the allometric equation to calculate the BECFs of all tree biomass components. Therefore, three functions, similar to Equations 6 – 8 were tested:

$$BCEF = e^{(b_0 + b_1 \ln d_0)} \lambda \qquad (14)$$

$$BCEF = e^{(b_0 + b_1 \ln h)} \lambda \qquad (15)$$

$$BCEF = e^{(b_0 + b_1 \ln d_0 + b_2 \ln h)} \lambda \qquad (16)$$

Since stem volume is an exclusive independent variable for calculating tree component biomass by means of BCEF method, we found a simple estimation method where we utilised an equation for the calculation of a cone volume and compared the result with stem volume expressed as a sum of section volumes (Newton's formula). We compared the two volumes for all of the sampled trees; ash, maple and beech data that was implemented from our previous work (see Pajtík et al., 2011) and fitted a linear relationship. All statistical analyses were carried out using the least squares method using Statistica 7.0 (StatSoft, Oklahoma, USA).

3. Results

3.1 Allometric equations

Through combining these results with the previous study focusing on biomass studies in young stands of European beech in the same region (Pajtík et al., 2011), biomass results for three broadleaved species; beech, ash and maple are combined. The main motivation of this research is based on the fact that beech is the regional dominant species and together with ash and maple made up mixture in the stands. Since diameter d_0 is not a common characteristic in forestry practice, we showed the relationship between diameter d_0 and tree height (Fig. 2a) and further between diameter d_0 and dbh (Fig. 2b). Relatively large interspecific differences existed in the relationship between diameter d_0 and tree height. For example, if we consider ash and maple with the same diameter d_0, ash trees were in general shorter while maple trees were tall and slender. In this aspect, beech trees were more closely related to ash than to maple. Formulas for their relationship were calculated as follows:

ash: $h = \frac{d_0^2}{125.858 + 0.395 d_0 + 0.193 d_0^2}$, $R^2 = 0.861$

maple: $h = \frac{d_0^2}{72.728 + 3.890 d_0 + 0.069 d_0^2}$, $R^2 = 0.895$

beech: $h = \frac{d_0^2}{1.166 + 11.157 d_0 + 0.018 d_0^2}$, $R^2 = 0.784$

As for the relationship between diameters d_0 and $d_{1.3}$, a linear relationship was considered suitable for all species:

ash: $d_{1.3} = -3.446 + 0.664d_0$, R² = 0.827

maple: $d_{1.3} = -3.142 + 0.680d_0$, R² = 0.956

beech: $d_{1.3} = -4.878 + 0.654d_0$, R² = 0.808

Interspecific differences for correlation between diameter d_0 and dbh were negligible with maximum values in maple and minimum in beech.

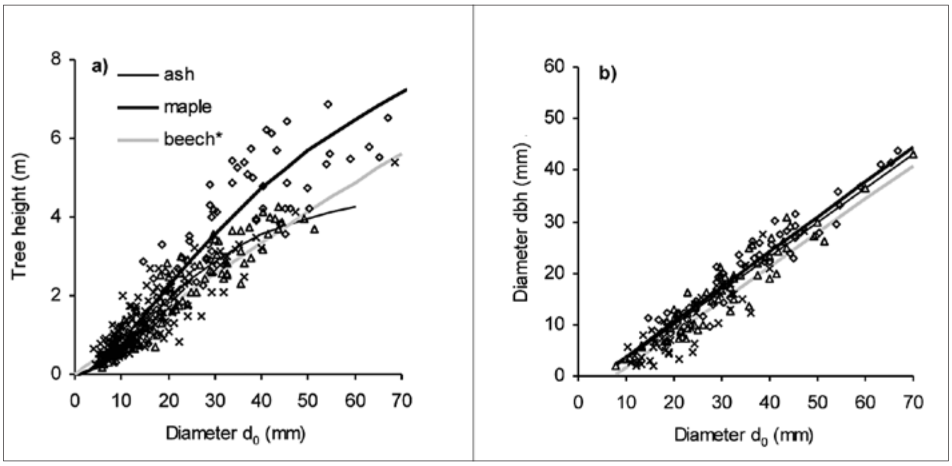

Fig. 2: Relationship between (a) diameter d_0 and tree height and (b) diameter d_0 and dbh in ash (triangles), maple (diamonds) and beech (crosses; *data from Pajtík et al., 2011)

Estimated coefficients and statistic characteristics of allometric equations for ash are presented in Table 4 and for maple in Table 5. It is evident that diameter d_0 is a statistically more suitable variable than tree height for predicting the biomass of all tree components in both species. As for ash trees, while diameter d_0 explained 84 – 95 % of sample variability in particular component quantity, the tree height explains 75 – 94 %. As for maple, the precision of the models were slightly higher with diameter d_0 explained 93 – 98 % of sample variability and tree height explaining 85 – 97 %. Models are even more precise when estimating whole tree biomass. Using diameter d_0 we reached 96% and 98% confidence in ash and maple respectively, and by using tree height we obtained 92% and 94% in ash and maple. Through combining the independent variables, diameter d_0 and tree height, the allometric models are only slightly improved, by between 1 – 2% compared to the model based solely on diameter d_0.

Table 4: Regression coefficients (b_0, b_1, b8), their relative standard errors (S.E.) and p-values; coefficient of determination (R^2); mean squared errors (MSE); logarithmic transformation bias (λ) and standard deviation (S.D.) for equations 6 – 8 (allometric relationships) in ash trees

Eq.	Ash component	b_0	S.E.	P	b_1	S.E.	P	b_2	S.E.	P	R^2	MSE	λ	S.D.
(6)	Stem	-4.374	0.229	<0.001	2.997	0.075	<0.001				0.954	0.140	1.072	0.430
	Branches	-9.108	0.624	<0.001	3.738	0.197	<0.001				0.835	0.562	1.256	0.792
	Leaves	-3.969	0.255	<0.001	2.388	0.083	<0.001				0.912	0.174	1.085	0.435
	Roots	-3.301	0.243	<0.001	2.454	0.079	<0.001				0.925	0.146	1.077	0.452
	ABVG	-3.839	0.209	<0.001	2.925	0.068	<0.001				0.959	0.117	1.057	0.360
	Whole tree	-2.999	0.200	<0.001	2.769	0.065	<0.001				0.959	0.099	1.049	0.332
(7)	Stem	3.523	0.056	<0.001	2.206	0.061	<0.001				0.944	0.171	1.096	0.601
	Branches	0.698	0.168	<0.001	2.785	0.189	<0.001				0.753	0.841	1.433	1.174
	Leaves	2.345	0.070	<0.001	1.721	0.077	<0.001				0.864	0.270	1.129	0.554
	Roots	3.171	0.075	<0.001	1.780	0.084	<0.001				0.853	0.288	1.156	0.719
	ABVG	3.874	0.057	<0.001	2.140	0.062	<0.001				0.938	0.178	1.093	0.522
	Whole tree	4.279	0.062	<0.001	2.048	0.069	<0.001				0.920	0.193	1.100	0.525
(8)	Stem	-0.906	0.372	0.017	1.667	0.139	<0.001	1.052	0.103	<0.001	0.980	0.060	1.038	0.399
	Branches	-6.807	1.152	<0.001	2.830	0.431	<0.001	0.795	0.339	0.022	0.847	0.529	1.244	0.782
	Leaves	-2.219	0.596	<0.001	1.717	0.223	<0.001	0.531	0.165	0.002	0.923	0.156	1.075	0.411
	Roots	-2.043	0.562	<0.001	1.968	0.211	<0.001	0.394	0.160	0.016	0.931	0.137	1.073	0.450
	ABVG	-0.795	0.355	0.028	1.757	0.133	<0.001	0.923	0.099	<0.001	0.981	0.055	1.031	0.315
	Whole tree	-0.589	0.372	0.117	1.838	0.140	<0.001	0.754	0.106	<0.001	0.976	0.060	1.032	0.301

The allometric models show that the quantity of the specific tree components is similar in ash and maple (Fig. 3a, 3b) with slightly higher values in all tree components recorded in ash. Interspecific differences were minimal between ash, maple and beech, when concerning above-ground biomass (Fig. 4a), whole tree biomass (Fig. 4b) and root (below-ground biomass) to shoot (above-ground biomass) ratio (Fig. 4c). In both above-ground biomass and whole tree biomass the largest values were found for ash and lowest for maple with beech values most similar to ash. For root to shoot ratio, all species recorded a decrease with tree size (diameter d_0). While the smallest trees had a root to shoot ratio of nearly 1:1, trees with diameter d_0 of 70 mm recorded values of around 0.2. This indicates that the total tree biomass was composed of approximately 17% below- and 83% above-ground biomass.

Table 5: Regression coefficients (b_0, b_1, b_2), their relative standard errors (S.E.) and p-values; coefficient of determination (R^2); mean squared errors (MSE); logarithmic transformation bias (λ) and standard deviation (S.D.) for equations 6 – 8 (allometric relationships) in maple trees

Eq.	Maple component	b_0	S.E.	P	b_1	S.E.	P	b_2	S.E.	P	R^2	MSE	λ	S.D.
(6)	Stem	-4.169	0.150	<0.001	2.914	0.046	<0.001				0.976	0.112	1.064	0.421
	Branches	-8.107	0.342	<0.001	3.351	0.101	<0.001				0.926	0.443	1.225	0.800
	Leaves	-2.650	0.173	<0.001	1.950	0.053	<0.001				0.933	0.162	1.082	0.473
	Roots	-2.595	0.153	<0.001	2.226	0.047	<0.001				0.960	0.119	1.060	0.370
	ABVG	-3.342	0.127	<0.001	2.755	0.039	<0.001				0.981	0.088	1.044	0.324
	Whole tree	-2.432	0.115	<0.001	2.583	0.035	<0.001				0.983	0.067	1.034	0.276
(7)	Stem	3.194	0.051	<0.001	2.273	0.040	<0.001				0.971	0.149	1.077	0.435
	Branches	0.386	0.135	0.005	2.583	0.101	<0.001				0.882	0.708	1.335	0.959
	Leaves	2.329	0.079	<0.001	1.459	0.062	<0.001				0.853	0.357	1.182	0.705
	Roots	3.109	0.085	<0.001	1.648	0.066	<0.001				0.868	0.391	1.205	0.753
	ABVG	3.632	0.056	<0.001	2.133	0.044	<0.001				0.960	0.1832	1.0942	0.482
	Whole tree	4.140	0.066	<0.001	1.969	0.051	<0.001				0.941	0.234	1.120	0.552
(8)	Stem	-0.832	0.174	<0.001	1.577	0.068	<0.001	1.094	0.053	<0.001	0.996	0.023	1.011	0.153
	Branches	-5.912	0.775	<0.001	2.463	0.301	<0.001	0.741	0.237	0.002	0.934	0.402	1.195	0.709
	Leaves	-2.626	0.466	<0.001	1.941	0.181	<0.001	0.008	0.142	0.956	0.934	0.164	1.082	0.473
	Roots	-2.797	0.404	<0.001	2.307	0.157	<0.001	-0.066	0.122	0.589	0.960	0.120	1.059	0.367
	ABVG	-0.783	0.194	<0.001	1.729	0.075	<0.001	0.840	0.059	<0.001	0.994	0.028	1.014	0.167
	Whole tree	-0.784	0.241	0.002	1.923	0.094	<0.001	0.539	0.073	<0.001	0.989	0.043	1.021	0.218

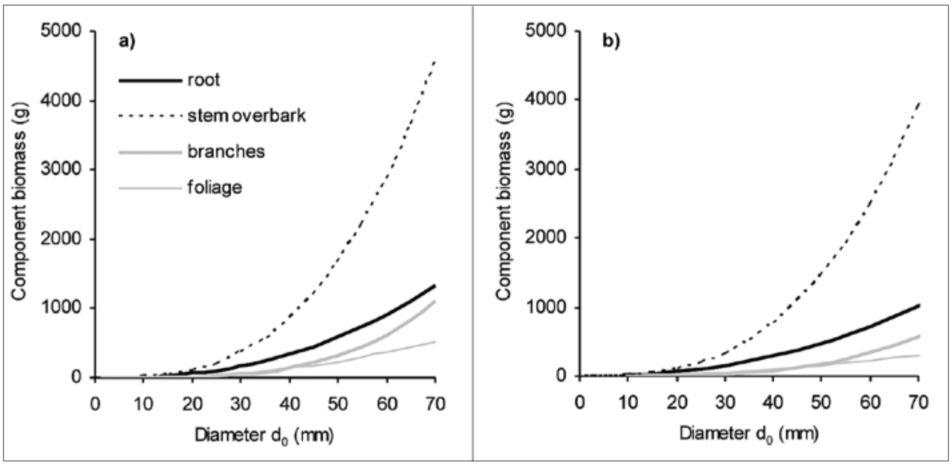

Fig. 3: Biomass of roots, stem (overbark), branches and foliage in (a) ash and (b) maple against diameter d_0

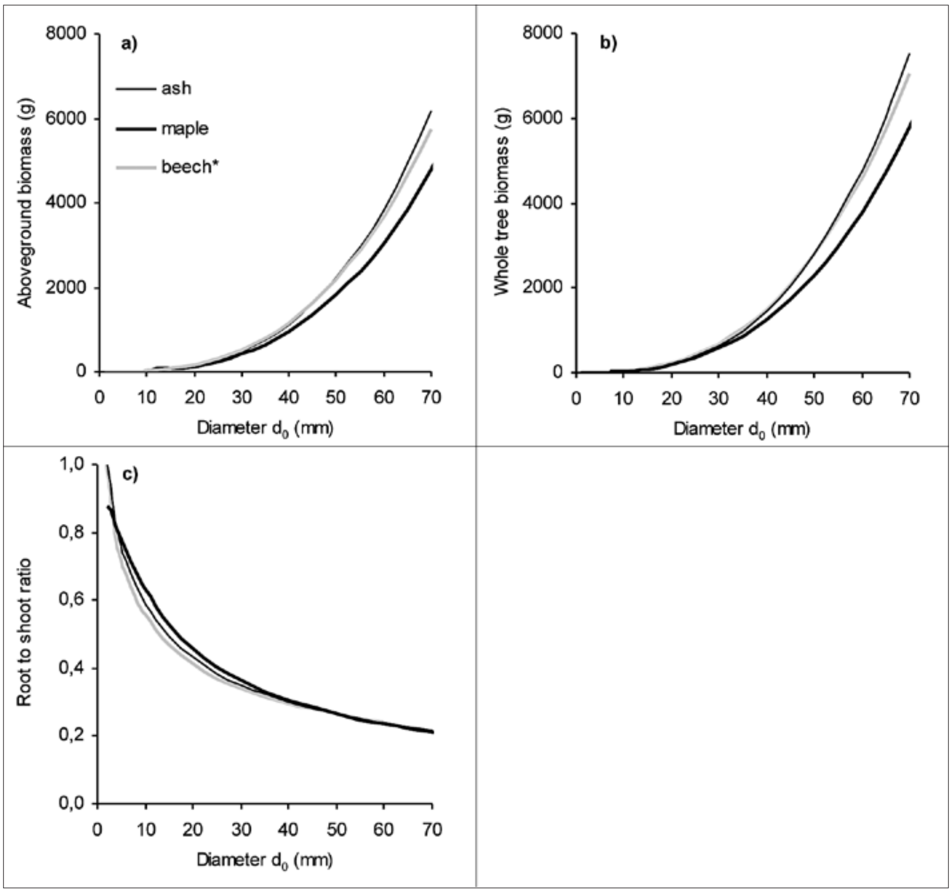

Fig. 4: Ash, maple and beech (a) above-ground biomass (b) whole tree biomass and (c) root to shoot ratio against diameter d_0 (* data from Pajtík et al., 2011)

While relatively little interspecific differences were recorded in whole tree biomass, there is evidence of differences existing in biomass structure (Fig. 5a-d). The largest differences were recorded in the percentage biomass of stem and branches. In these parameters, beech contrasted with ash and maple specifically with beech having a much higher proportion of branch biomass but lower percentage of stem biomass than the other species. If considering the largest trees (diameter d_0 of 70 mm), contribution of beech branches was approx. 23% while in ash and maple branch biomass contribution was 14% and 10% respectively. At the same time, total biomasses of the largest trees were composed by around 49% (beech), 60% (ash) and 67% (maple) of stem biomass.

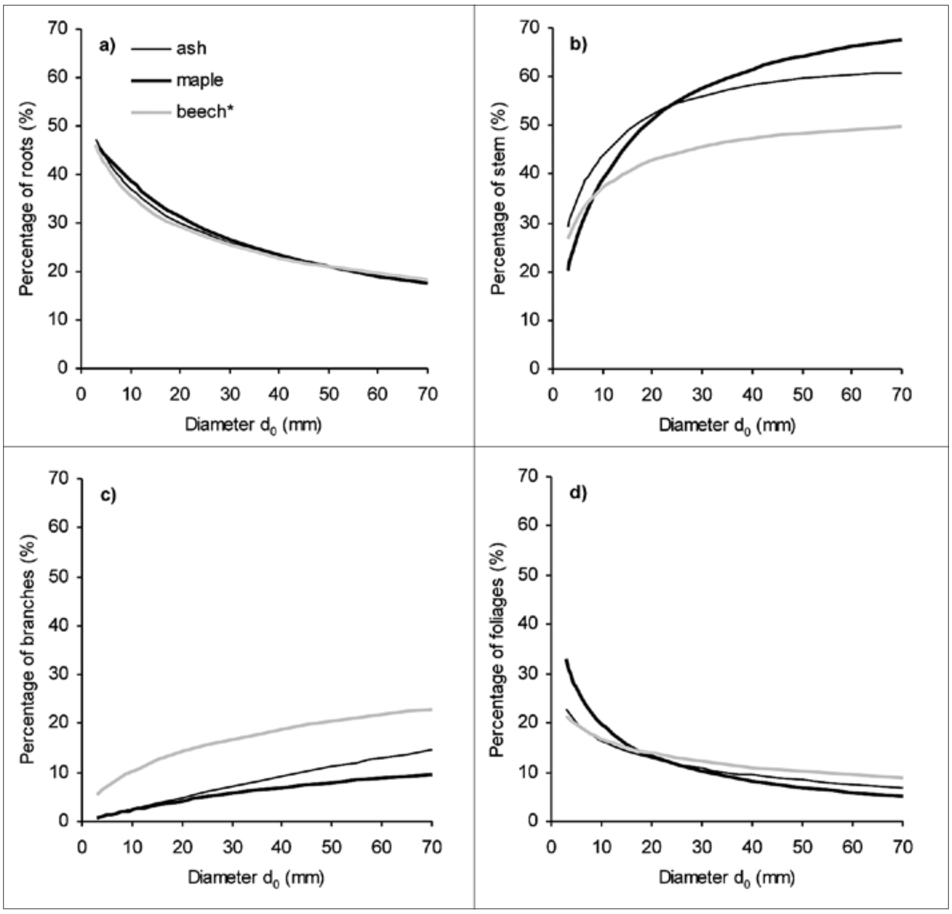

Fig. 5: Contribution of (a) roots, (b) stem, (c) branches and (d) foliage to whole tree biomass against diameter d_0 in ash, maple and beech (* data from Pajtík et al., 2011)

3.2 Biomass expansion and conversion factors

Estimated coefficients and statistic characteristics for stem volume in both ash and maple species are presented in Table 6. The results show that both variables; diameter d_0 and tree height explain sample variability with a very high precision. The highest values; 0.991% in ash and 0.997% in maple for coefficient of determination R^2 was recorded for model results when implementing both diameter d_0 and tree height as independent variables. Estimated coefficients and statistic characteristics for models of BCEFs for ash are in Table 7 and for maple in Table 8. Values of coefficients of determinations are much lower than for allometric models. It is proposed that for these models, both variables should be utilised. Doing so, a very precise model (R^2=0.832) was constructed for whole tree biomass in maple.

Table 6: Regression coefficients (b_0, b_1, b_2), their relative standard errors (S.E.) and p-values; coefficient of determination (R^2); mean squared errors (MSE); logarithmic transformation bias (λ) and standard deviation (S.D.) for equations 10 – 12 (stem volume) in ash and maple trees

Eq.	Species	b_0	S.E.	P	b_1	S.E.	P	b_2	S.E.	P	R^2	MSE	λ	S.D.
(4)	Ash	-4.100	0.230	<0.001	3.093	0.075	<0.001				0.956	0.141	1.071	0.402
	Maple	-3.890	0.169	<0.001	3.028	0.052	<0.001				0.972	0.155	1.080	0.456
(5)	Ash	4.041	0.046	<0.001	2.299	0.051	<0.001				0.963	0.117	1.057	0.351
	Maple	3.747	0.045	<0.001	2.375	0.035	<0.001				0.979	0.119	1.060	0.377
(6)	Ash	0.040	0.252	0.874	1.505	0.094	<0.001	1.257	0.070	<0.001	0.991	0.028	1.014	0.170
	Maple	0.081	0.137	0.553	1.436	0.053	<0.001	1.302	0.042	<0.001	0.997	0.14	1.007	0.118

Table 7: Regression coefficients (b_0, b_1, b_2), their relative standard errors (S.E.) and p-values; coefficient of determination (R^2); mean squared errors (MSE); logarithmic transformation bias (λ) and standard deviation (S.D.) for equations 14 – 16 (BCEF) in ash trees

Eq.	Ash component	b_0	S.E.	P	b_1	S.E.	P	b_2	S.E.	P	R^2	MSE	λ	S.D.
(14)	Stem	-0.324	0.073	<0.001	-0.087	0.024	<0.001				0.147	0.014	1.007	0.120
	Branches	-5.411	0.590	<0.001	0.766	0.186	<0.001				0.192	0.502	1.246	0.865
	Leaves	0.131	0.254	0.607	-0.705	0.083	<0.001				0.478	0.172	1.080	0.408
	Roots	0.702	0.254	0.007	-0.609	0.082	<0.001				0.412	0.159	1.080	0.444
	ABVG	0.270	0.116	0.022	-0.173	0.038	<0.001				0.212	0.036	1.020	0.255
	Whole tree	0.957	0.138	<0.001	-0.282	0.045	<0.001				0.336	0.051	1.027	0.265
(15)	Stem	-0.545	0.016	<0.001	-0.078	0.017	<0.001				0.215	0.013	1.006	0.115
	Branches	-3.310	0.137	<0.001	0.439	0.154	0.006				0.102	0.558	1.272	0.885
	Leaves	-1.696	0.050	<0.001	-0.579	0.055	<0.001				0.588	0.136	1.064	0.363
	Roots	-0.850	0.048	<0.001	-0.544	0.053	<0.001				0.576	0.115	1.058	0.374
	ABVG	-0.168	0.023	<0.001	-0.160	0.026	<0.001				0.333	0.030	1.017	0.233
	Whole tree	0.235	0.027	<0.001	-0.251	0.029	<0.001				0.486	0.039	1.021	0.230
(16)	Stem	-0.785	0.171	<0.001	0.090	0.064	0.164	-0.140	0.048	0.004	0.235	0.013	1.006	0.114
	Branches	-6.886	1.112	<0.001	1.348	0.416	0.002	-0.509	0.327	0.124	0.219	0.492	1.228	0.791
	Leaves	-2.260	0.557	<0.001	0.212	0.209	0.313	-0.726	0.155	<0.001	0.593	0.136	1.063	0.362
	Roots	-2.107	0.498	<0.001	0.475	0.187	0.013	-0.879	0.141	<0.001	0.608	0.107	1.053	0.350
	ABVG	-0.806	0.254	0.002	0.240	0.095	0.014	-0.326	0.070	<0.001	0.384	0.028	1.016	0.222
	Whole tree	-0.528	0.288	0.071	0.287	0.108	0.010	-0.450	0.080	<0.001	0.530	0.036	1.019	0.216

Table 8: Regression coefficients (b_0, b_1, b_2), their standard errors (S.E.) and p-values; coefficient of determination (R^2); mean squared errors (MSE); logarithmic transformation bias (λ) and standard deviation (S.D.) for equations 14 – 16 (BCEF) in maple trees

Eq.	**Maple component**	**b_0**	**S.E.**	**P**	**b_1**	**S.E.**	**P**	**b_2**	**S.E.**	**P**	**R^2**	**MSE**	**λ**	**S.D.**
(14)	Stem	-0.279	0.048	<0.001	-0.113	0.015	<0.001				0.374	0.013	1.006	0.116
	Branches	-4.311	0.335	<0.001	0.349	0.009	<0.001				0.124	0.425	1.207	0.739
	Leaves	1.235	0.235	<0.001	-1.075	0.072	<0.001				0.698	0.299	1.155	0.671
	Roots	1.314	0.232	<0.001	-0.807	0.071	<0.001				0.577	0.275	1.144	0.611
	ABVG	0.544	0.080	<0.001	-0.271	0.025	<0.001				0.557	0.035	1.018	0.195
	Whole tree	1.473	0.128	<0.001	-0.448	0.039	<0.001				0.582	0.084	1.043	0.313
(15)	Stem	-0.553	0.013	<0.001	-0.103	0.010	<0.001				0.502	0.010	1.005	0.102
	Branches	-3.365	0.108	<0.001	0.207	0.081	0.012				0.070	0.452	1.213	0.736
	Leaves	-1.417	0.055	<0.001	-0.916	0.043	<0.001				0.827	0.171	1.093	0.565
	Roots	-0.647	0.053	<0.001	-0.722	0.041	<0.001				0.761	0.155	1.077	0.421
	ABVG	-0.115	0.019	<0.001	-0.242	0.015	<0.001				0.729	0.021	1.011	0.152
	Whole tree	0.384	0.029	<0.001	-0.401	0.023	<0.001				0.770	0.046	1.023	0.226
(16)	Stem	-0.913	0.110	<0.001	0.141	0.043	0.001	-0.208	0.034	<0.001	0.552	0.009	1.005	0.097
	Branches	-5.856	0.780	<0.001	0.974	0.303	0.002	-0.521	0.239	0.032	0.170	0.408	1.199	0.734
	Leaves	-2.702	0.460	<0.001	0.503	0.179	0.006	-1.292	0.140	<0.001	0.841	0.159	1.088	0.569
	Roots	-2.891	0.398	<0.001	0.876	0.154	<0.001	-1.373	0.120	<0.001	0.822	0.117	1.057	0.358
	ABVG	-0.859	0.151	<0.001	0.291	0.059	<0.001	-0.460	0.046	<0.001	0.785	0.017	1.009	0.137
	Whole tree	-0.871	0.215	<0.001	0.490	0.083	<0.001	-0.766	0.065	<0.001	0.832	0.034	1.017	0.197

The results related to BCEFs show a large difference between the tree components in both ash and maple species (Fig. 6a, 6b). Comparing BCEFs with tree size (diameter d_0), values decreased with increasing diameter d_0 which is particularly evident for biomass components, foliage and roots. On the other hand, the opposite was found for tree size (diameter d_0) and branches. In fact, BCEF for stem is equal to density (wood and bark together) thus, it is not surprising that the highest values of stem density in both species were found for the smallest trees (nearly 0.70 g.cm^{-3}) with the lowest values in the largest trees (around 0.50 g.cm^{-3}). Considering all tree species, large differences were found for BCEFs in above-ground (Fig. 7a) and whole tree biomass (Fig. 7b). For BCEF expressing above-ground biomass, maple differed (lower values) from ash and beech. BCEF for whole tree biomass differed in beech (higher values) from those of ash and maple. In all trees, the values of these BCEFs decreased with increasing tree size (diameter d_0) however, the values for trees with diameters of approximately 30 mm changes only moderately.

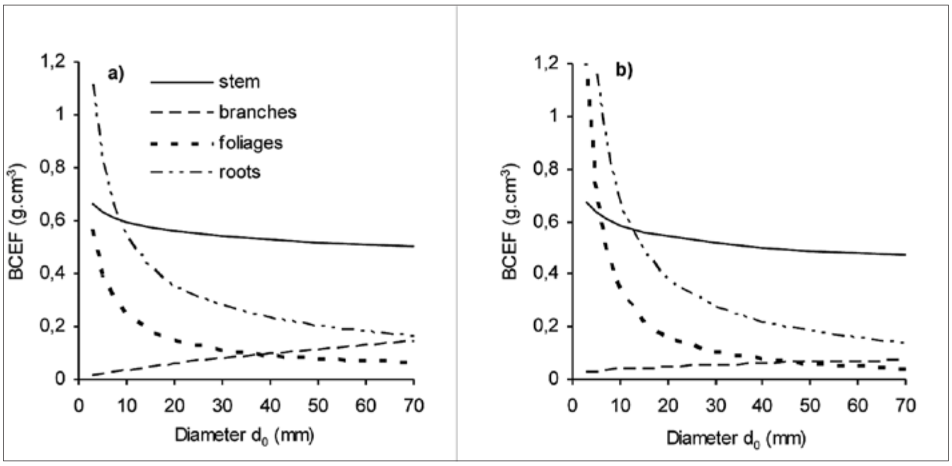

Fig. 6: BCEF for tree compartments in (a) ash and (b) maple against diameter d₀

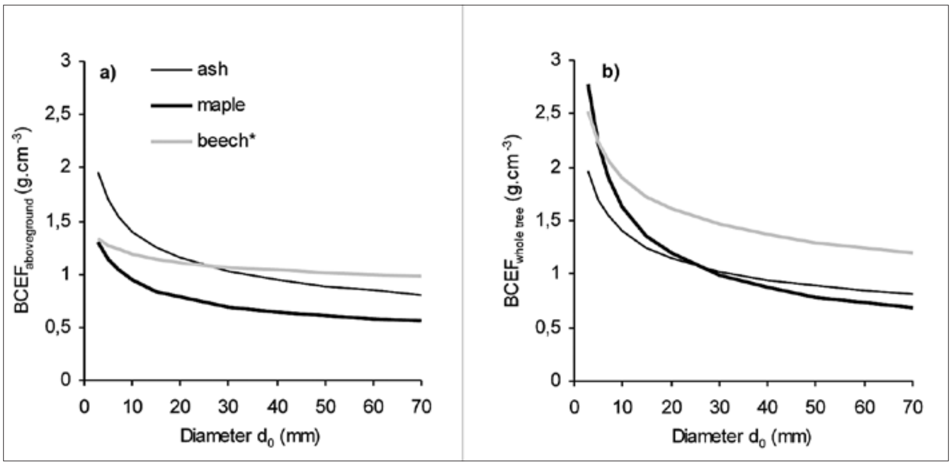

Fig. 7: BCEF for (a) above-ground biomass and (b) whole tree biomass against diameter d₀ in ash, maple and beech (* data from Pajtík et al., 2011)

Comparisons of the two methods, i.e. alometric relation and BCEF, for biomass estimates suggested just moderately different results in both species (Fig. 8a, 8b). As for the precision of the models, BCEF (residual standard deviations for BCEF using modeled and measured stem volume was 237.1 and 149.1, respectively) performed better than alometric relation (252.9) for ash trees. In contrast, alometric relationship (453.11) was more precise than BCEF (594.5 and 549.5, respectively for BCEF using modeled and measured stem volume) for maple trees. Here, the equation for modeling stem volume in ash was $V = 0.257139DAB^{2.31126}$ and in maple was $V = 0.026715DAB^{2.92014}$, where DAB is diameter d_0.

Finally, our alometric models for both species were compared with other available relationships from Germany (Albert et al., 2014) and UK (Bunce, 1968). Unfortunately, these models for European ash and Sycamore maple were expressed for above-ground woody biomass only. The comparison showed that our model outputs recorded "average" values compared to the other models in the case of both tree species (Fig. 9; see also Table 9 and 10). Specifically, while our models and the models from Germany recorded larger above-ground woody biomass compared to dbh in both ash and maple, the models from UK estimated less biomass.

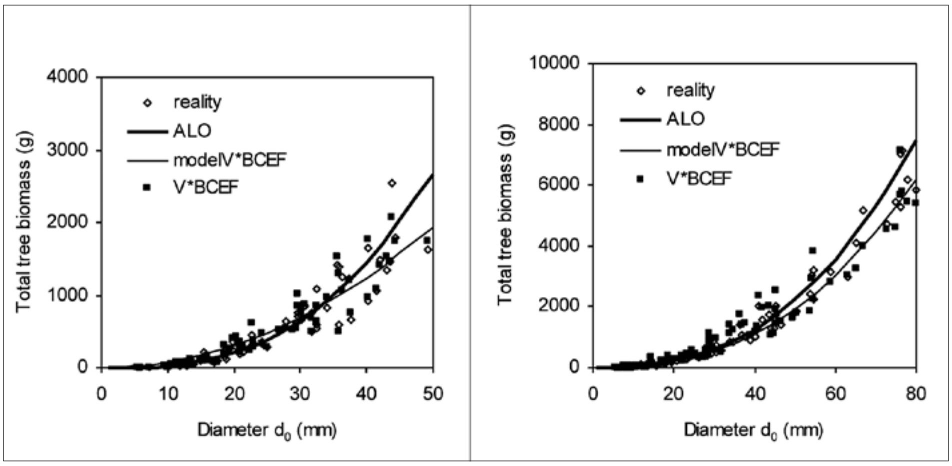

Fig. 8: Comparison of total tree biomass estimated by alometric relation (ALO) and BCEF (as for modeled stem volume - modelV*Bcef and mesaured stem volume – V*BCEF) in (a) ash and (b) maple trees. Open circles represent really weighted tree biomass (reality).

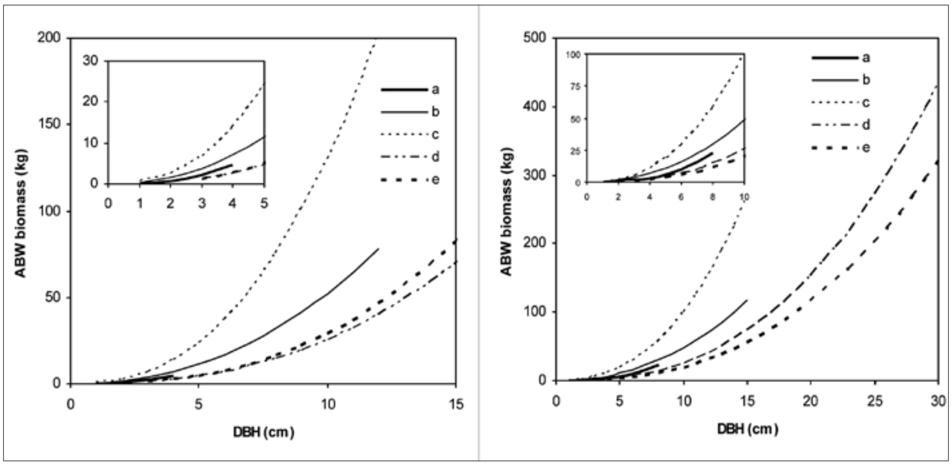

Fig. 9: Comparison of our models with some other alometric models for ash (upper plate) and maple (lower plate) aboveground woody biomass. The letters in the legends represents: a – our model; b and c – models of Albert et al., 2014; d and e – models of Bunce, 1968

Table 9: Comparison of equations for aboveground woody biomass based on dbh as a predictor in European ash (a – our model; b and c – models of Albert et al., 2014; c and d – models of Bunce, 1968)

	n	dbh (cm)	Region	Equation
a	100	0 – 3.5	Slovakia	$ABW = e^{\left(-4.511+3.075*\ln\left(\frac{DBH+3.4462}{0.664}\right)\right)} *1.069$
b	178	0.1 – 12.1	Germany (Liebenburg)	$ABW = 0.2292 * DBH^{2.1799}$
c	21	1.0– 14.8	Germany (Barterode)	$ABW = 0.1757 * DBH^{2.4351}$
d	15	2.9 – 33.0	United Kingdom	$\ln ABW = -2.5 + 2.49 * \ln DBH$
e	15	3.0 – 18.0	United Kingdom	$\ln ABW = -2.5 + 2.55 * \ln DBH$

Table 10: Comparison of equations for aboveground woody biomass based on dbh as a predictor in Sycamore maple (a – our model; b and c – models of Albert et al., 2014; c and d – models of Bunce, 1968)

	n	dbh (cm)	Region	Equation
a	100	0 – 8.0	Slovakia	$ABW = e^{\left(-4.203+2.951*\ln\left(\frac{DBH+3.1418}{0.6798}\right)\right)}*1.063$
b	148	0.1 – 15.5	Germany (Liebenburg)	$ABW = 0.2286*DBH^{2.1639}$
c	20	1.2 – 14.6	Germany (Barterode)	$ABW = 0.1349*DBH^{2.4361}$
d	15	3.5 – 28.0	United Kingdom	$\ln ABW = -2.7+2.58*\ln DBH$
e	10	3.7 – 31.0	United Kingdom	$\ln ABW = -2.8+2.52*\ln DBH$

4. Discussion and conclusion

The results indicate that allometric equations are more suitable for expressing biomass and structural components of small trees than BCEFs. Although, we did not find differences between these two approaches for accuracy of biomass estimates, alometric equations are more practical for implementation than BCEFs in young trees. Specifically, it is simpler to use only stem characteristic (diameter and/or height) as a predictor for allometric relations than stem volume (due to complicated measurement or calculation) for BCEF. On the other hand, we suppose that BCEF is suitable for large trees where the stem volume (predictor) is generally better known than for small trees. Moreover, while the value of BCEF is near constant in large trees (Lehtonen et al. 2004), its value is sensitive to tree dimensions in small trees (Pajtík et al., 2011). The use of stem diameter as the most precise independent variable for alometric equations is supported in previous work (e.g. Johansson, 1999; Hochbichler et al., 2006; Pajtík et al., 2008). As for diameter d_0, practical measurement might be difficult in young, often dense stands and may be further complicated by deformations on stem bases. Since dbh is applicable exclusively for trees with height over 130 cm, a compromise between model precision and practical measurement can be achieved by using tree height as a variable. This further creates compatibility between small and large tree results.

The results show little interspecific difference between young ash, maple and beech trees in whole tree biomass with regard to diameter d_0. At the same time, minimum interspecific differences exist for root to shoot ratio. Previous work conducted in Slovak forest (Konôpka et al., 2010) indicated a large differences in root to shoot ratio among the four most abundant tree species; European beech, Norway spruce, Scots pine (*Pinus sylvestris*) and Sessile oak. Specifically, substantial differences were observed between the broadleaved (higher value of root to shoot ratio) and coniferous trees (lower value). This sort of information is highly relevant to understand carbon cycling in young stands. Since young stands often grow under high competition stress, they typically record a high mortality rate (e.g. Lutz and Halpern, 2006). At the same time, the proportion of carbon emitted or stored by the above- and belowground biomass, after tree mortality, is determined by the root to shoot ratio. For instance, King et al. (2007) established linear models for root to shoot ratio compared to tree size in a variety of species. However, the focus was on older growth stands than observed during this study. Our results indicate that ash, maple and beech with diameter d_0 between 40 and 70 mm manifest values of root to shoot ratio from between 0.3 and 0.2. These values agree with the results of Harris (1992), who showed that, under normal conditions, root to shoot ratio in most adult trees vary between 0.16 and 0.20.

Large interspecific differences between young ash, maple and beech trees were found for biomass structure, specifically for stem and branch components. Beech has evidently higher proportion of branches than ash and maple, and in contrast, ash and maple manifested higher contributions of stem biomass than beech. These results might have some implication for the understanding of interspecific competition. If we neglect possible interspecific differences in growth rate, especially in height, and also ecological demands, higher competition potential might be predicted for beech with larger proportion of branches (this species occupies a relatively bulky space in canopy layer) than for ash and maple. On the other hand, minimum differences were found in the contribution of foliage to total biomass. This knowledge would be useful for instance in terms of modeling carbon cycling through foliage or growth efficiency, expressing production of biomass in stem or all woody components based on foliage mass unit (Gersonde and O'Hara, 2005). Another implication of foliage and branch quantity or their contribution to whole tree biomass, might be related to feed potential for ruminating ungulate game (e.g. Konôpka et al., 2012a; Pajtík et al., 2015) or competition for light with weed (Ceacero et al., 2014).

Our results show that structure of biomass as a contribution of tree components changes dramatically with tree size with the most significant changes found for smallest trees (diameter d_0 up to approx. 30 mm). These changes perhaps relates to alternating changing growth strategy from early (primary intention to occupy sufficient soil space) to later stages (to compete neighbouring trees for light). Proportion of stem on whole tree biomass increased with tree growth is generally acknowledged (e.g. Kozlowski and Pallardy, 1997). In young ash, maple and beech trees, contrasting tendencies with increasing size were recorded, increasing for branches and decreasing for foliage. This phenomenon is also evident in Norway spruce stands at least until the development of a closed canopy (Kantola and Mäkelä, 2006). At this stage the level of branch contribution to whole tree biomass stabilizes and percentage of foliage continues to decrease. This is most probably related to limited light resources under closed canopy conditions and as a consequence the constraints for foliage survival.

There is the potential for future studies on European ash and Sycamore maple to focus on biomass models for larger trees. At the same time, the models should include all tree components in the above-ground and below-ground parts of trees, especially for the purpose of biomass/carbon stock estimates in forest stands. The biomass models for the most frequent tree species can be implemented in combination with data from the NFI (in Slovakia, the first NFI was in 2005 – 2006 and the second will be in 2015 – 2016; see Šmelko et al., 2014). Since all trees with height over 0.1 m are registered in NFI in Slovakia, our biomass models for small ash and maple trees can be incorporated. Thus, after the second NFI and the potential construction of models for the full range of tree dimensions, not only biomass/carbon stock, but also biomass production can be estimated on the national level.

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5.2 Čistá primárna produkcia, listová plocha a rastová účinnosť

Čistá primárna produkcia nadzemnej biomasy v mladých porastoch buka a smreka

Abstrakt

Jedným z predpokladaných následkov klimatickej zmeny a neodmysliteľným sprievodným úkazom je postupná modifikácia drevinového zloženia v lesných ekosystémoch (napr. rozšírenie odolnejších druhov na úkor druhov menej rezistentných). Klimatická zmena je sprevádzaná zvyšovaním teploty a nedostatkom zrážok a môže predstavovať vážnu hrozbu obzvlášť pre smrekové stanovištia v európskej časti mierneho pásma. Buk lesný je jedným z možných druhov lesných drevín, ktoré môžu potenciálne nahradiť ohrozený smrek. V tomto príspevku sme pomocou využitia kontinuálnych meraní a deštruktívneho odberu celých stromov pozorovali zásobu nadzemnej biomasy porastu (tj. kmeňa, konárov a listov) a jej ročnú čistú primárnu produkciu (NPP) v mladých porastoch buka a smreka z prirodzenej obnovy. Úmyselne sme vybrali stanovište, kde zmena klimatických podmienok lepšie vyhovuje ekologickým požiadavkám buka ako smreka (ktorý je dominantným druhom v sledovanej oblasti). Zaznamenali sme iba malé rozdiely v zásobe kmeňov buka a smreka ak bola zásoba vyjadrená v tonách na hektár. Pri vyjadrení zásoby v metroch kubických na hektár sú zásoby smreka väčšie, čo je spôsobené rozdielnou objemovou hustotou dreva týchto dvoch druhov drevín. Najväčšie rozdiely medzi drevinami sa pozorovali v zásobe asimilačných orgánov. Pri smreku je táto zásoba trikrát väčšia ako pri buku. Pritom buk alokuje viac uhľohydrátov v kmeni ako smrek. Na druhej strane sme vypočítali takmer rovnakú produkciu listov a konárov pri obidvoch sledovaných drevinách.

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ABOVE-GROUND NET PRIMARY PRODUCTIVITY IN YOUNG STANDS OF BEECH AND SPRUCE

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One of the expected consequences of climate change and its inherent phenomena to forest ecosystems is the gradual modification of their tree species composition (i.e. expansion of resistant species instead of less resistant ones). Climate change accompanied with increasing temperatures and a lack of precipitations may present a threat especially to spruce stands in the European part of the temperate zone. European beech is one of the possible forest tree species which might replace the potentially endangered spruce. In this paper, we observed, by using a combination of continual measurements and destructive whole-tree sampling, standing stocks of above-ground biomass (i.e. stem, branches, and foliage) and its annual net primary productivity (NPP) in naturally regenerated young stands of beech and spruce. We intentionally selected a site where the changing climate conditions are better suited to the ecological demands of beech rather than spruce (the species is dominant in the observed area). We recorded only small differences in the standing stock of stems of the beech, if based on tons per ha. However, this is in favor of spruce if based on cubic meters per ha. The largest difference between the species was found for the standing stock of foliage, spruce retained three times the biomass of beech. Also, beech allocated more carbohydrates to stem than spruce. On the other hand, we estimated nearly the same production of foliages and branches in both stands.

Keywords: *Fagus sylvatica, Picea abies, net primary productivity, above-ground biomass, standing stock, tree compartments*

1. Introduction

Since forests store approximately 80% of the total terrestrial aboveground carbon (Six *et al.,* 2002) they would play a principal role in the mitigation of the climate change process (Jandl *et al.,* 2007). For instance, Janssens *et al*. (2003) estimated that in European conditions, forests absorb about 10% of emissions with agricultural land being a source and forests a sink of CO_2. At the same time, Brunner & Godbold (2007) stated that the temperate of forests in Central Europe stored about 110 t C per ha in tree biomass and 65 t C per ha in the soil (without roots). This means that nearly 2/3 of a forest ecosystems' C pool was fixed in tree biomass. At the same time, circa 3/4 of biomass is located in the aboveground compartments and 1/4 in the root system (Brunner & Godbold, 2007). In general, an essential part of tree biomass is obviously found in the stem (West, 2010). However, this assumption relates mostly to middle-age and old forest stands. Rather different biomass partitioning patterns exit in small trees. Specifically, young stages of tree growth typically have a rather high portion of carbohydrates invested into branches and foliages sometimes even prevailing over the quantity in the stem (Kozlowski & Pallardy, 1997).

Distinct changes in tree biomass allocation to the particular compartments with an increasing stand size (age) in young stages of European beech and Norway spruce were shown by Konôpka *et al.* (2010). The paper indicated that while the contribution of stem to total aboveground biomass increased, the contribution to branches and foliages decreased with increasing stand size. In general, aboveground tree compartments, as for carbon fixation span, can be separated into two groups: those with a fast turnover (foliages) and those with a slow turnover (stem and branches). Hence, changes in the proportion of compartments with contrasting carbon sequestration times can be assumed as well. Implicitly, the role of forest stands in carbon cycling and fixation should be analyzed and interpreted with respect (besides some other factors) to growth stage, eventual size and age.

One of the most efficient and rather simple ways to express tree biomass quantity and its structure by the compartments is using allometric equations based on easily measurable tree characteristics, often diameter and/or height (West, 2009). While plenty of papers show allometric equations for old European beech and Norway spruce stands (Cienciala *et al.,* 2005; Wirth *et al.,* 2004; Fehrmann & Kleinn, 2006; Seidl *et al.,* 2010) only a few authors focus on their young growth stages (e.g. Claesson *et al.,* 2001; Pajtík *et al.,* 2011a). At the same time, equations for tree compartment biomass estimated for large and older trees are not generally applicable to young trees (Wirth *et al.,* 2004).

Our previous paper (Konôpka *et al.,* 2010) indicated a certain tendency of biomass allocation patterns with regard to tree size. However, changes in biomass partitioning patterns were based on estimative height increments focusing at tree level. Consequently, we decided to make a step forward in this field and demonstrate in this current paper how the structure of aboveground standing biomass changes inter-annually in young stands of European beech and Norway spruce – both grown at the same site. Here, our calculations were based on empiric material of real stand growth (height and diameter increments of trees in the stands) in the specific years of observation. At the same time, a partial aim of the work was to construct stand-specific allometric equations for the aboveground compartments, i.e. stem, branches and foliages. A further mission of this paper was to estimate aboveground net primary productivity (NPP) and its structure in the particular years of our study.

2. Materials and methods

2.1. Site description

The site "Vrchslatina" is located in the southern part of the Veporske vrchy massif at cca 960 m above sea level (48° 38′ 55′′ N, 19° 36′ 07′′ E). A more detailed description of the research site is given in Konôpka *et al.* (2013b). Since NPP and biomass allocation may be effected by climatic conditions, we measured temperature and precipitation at the site. Monthly means for 2009 – 2012 as well as monthly means for a reference periods from 1961 to 1990 are shown in the paper of Konôpka *et al.* (2013b). On this site, we selected two neighbouring stands of pure European beech and pure Norway spruce, both naturally regenerated after a stand clearance with ages between circa 12 – 14 years. Both stands were approximately 0.7 ha in size making up compact clumps (groups of trees) of varying density with a few scattered gaps dominated by *Calamagrostis epigejos* (L.). The specific clumps were mostly composed exclusively by either beech or spruce trees.

In April 2009, we established 5 plots in beech and also 5 plots in the spruce stand. The plots were circular and placed to avoid atypical spots (e.g. gaps, stand ages and so on). The plots had a radius of between 0.7 and 1.0 m, their size depended on stand density and was adjusted to include cca 30 – 50 individuals of beech or spruce. Every year since 2009, we measured basic characteristics of the trees, specifically: diameter at stem base (d_0), diameter at breast height ($d_{1.3}$) and tree height. The measurements were done outside the growing season (either very early spring or late autumn). The diameters were measured by means of digital callipers with a precision of 0.1 mm – on a stem base for all trees, and 130 cm from the ground level for those which exceeded this height. Tree heights were measured by a wooden meter – for trees up to a height of 2 m with a precision of 1 cm, for higher ones with a precision of 5 cm. Then, mean diameters, mean heights and mean stem volume were calculated as weighted arithmetic mean from plot average numbers weighted by plot sizes. To calculate the mean height we used the Lorey procedure. To the express stem volume of trees the approach as in our previous paper was used (Pajtík *et al.*, 2011a). Then, mean stem volume was calculated as an average from stem volumes for all trees on the plots.

Quantities of biomass (expressed as dry weight) for foliages, branches and stem of the specific aboveground tree compartments were expressed by these allometric equations:

$$W_i = e^{(b_0 + b_1 \,.\, \ln d_0)} \,.\, \lambda \qquad [1]$$

$$W_i = e^{(b_0 + b_1 \,.\, \ln h)} \,.\, \lambda \qquad [2]$$

$$W_i = e^{(b_0 + b_1 \,.\, \ln d_0 + b_2 \,.\, \ln h)} \,.\, \lambda \qquad [3]$$

where W_i is biomass for compartment *i* (foliages, branches, stem, woody parts together, entire aboveground part),

d_0 is diameter at the stem base, h is tree height, b_0, b_1 a b_2 are coefficient, λ is logarithmic transformation bias.

To construct the allometric equations which express the biomass of aboveground tree compartments using diameter and/or height as independent variables, 80 spruces (20 individuals for each specific bio-sociological position, i.e. dominant, co-dominant, sub-dominant and suppressed) and 60 beeches (15 individuals for each specific bio-sociological position) were cut at the site in September 2009. Thus, we were able to make site- and stand-specific equations.

By a combination of data on tree diameters and heights with allometric equations, standing stock of the specific tree compartments on a hectare base was calculated. In this way, standing biomass stock of live trees in April of the current year as well as the quantity of trees which died in the period between Aprils of the consecutive years were estimated. Detailed descriptions of tree sampling, laboratory procedures, construction of allometric equations and estimations of tree standing biomass on a stand level are shown in the papers of Pajtík *et al.* (2008) and Konôpka *et al.* (2010).

In this paper, biomass for the above-ground tree compartments is calculated through the equation [3], it means that both tree diameter and height are used as independent variables. Hence, biomass of stem, branches and foliages were estimated. However, for needle biomass in spruces, a different approach has to be used. In fact, the biomass of needles was composed prevailingly of four sets (separated by year of birth) and a very small amount of five-year-old needles. First, we estimated needle mass of the spruces expressed as a status in April 2010. This amount was determined from an allometric model, i.e. by using sample trees taken in September 2009, minus the mass of needles accumulated in litter collectors (see also Konôpka *et al.,* 2013b) in the period between September 2009 and April 2010. If this “starting” needle amount is marked as B_{2010}, then, biomass of spruce needles in the specific years is calculated by means of the algorithms:

$$B_{2009} = B_{2010} - b_{2009} + L_{2009} \qquad [4]$$

$$B_{2011} = B_{2010} - b_{2010} + L_{2010} \qquad [5]$$

$$B_{2012} = B_{2011} - b_{2011} + L_{2011} \qquad [6]$$

where B_i is total needle stock in April of year (i), b_i is stock of needles born in the current year (i), L_i is quantity of needle litter collected between April of previous year (i) and April of consecutive year (i+1).

The stock of needles born in specific years (b_i), 2010 and 2011, was determined from felled sample trees. In both years, we felled 40 spruces (10 pieces of each bio-sociological status), the needle sets born in the said years were separated, oven-dried and weighed. An allometric model for the needles was constructed according to equation [3].

To estimate the litter of needles, three open collectors sized 27 × 27 cm were placed on each plot in April 2009. Then, litter was harvested from the collectors in circa 6-weeks intervals. The mass of needles found after certain periods in the collectors reflected a loss of needles between two occasions. In beech foliages, the sum of litters harvested during one growing season was used as a reference value of figures obtained via allometric equations on a stand level.

Finally, total above-ground biomass and production was calculated as a sum of all compartments (stem, branches and foliages) on a tree level. Then, values of above-ground biomass and production were expressed on the plot levels (by summarizing all trees recorded on the plots) and up-scaled on a hectare base.

All mathematical and statistical operations were performed using the Statistica 10.0 program.

3. Results and discussion

The measurements proved large inter-annual differences in the basic stand characteristics of both beech and spruce (Table 1). While a number of trees diminished, tree size increased considerably.

Histograms of tree distribution by diameter and height classes are shown in Figure 1. Spruce has shown

Table 1. Basic stand characteristics of the beech and spruce in the springs of 2009 – 2012

Stand characteristics	**European beech**			
	April 2009	**April 2010**	**April 2011**	**April 2012**
Number of trees [ths. ha^{-1}]	157	150	136	125
Mean tree height [cm]	225	272	323	373
Mean diameter d_0 [cm]	1.89	2.13	2.43	2.67
Average stem volume [cm^3]	233.1	313.2	452.2	594.9
Stand characteristics	**Norway spruce**			
	April 2009	**April 2010**	**April 2011**	**April 2012**
Number of trees [ths. ha^{-1}]	176	154	134	98
Mean tree height [cm]	172	212	242	301
Mean diameter d_0 [cm]	1.88	2.29	2.71	3.23
Average stem volume [cm^3]	224.6	336.0	495.8	860.4

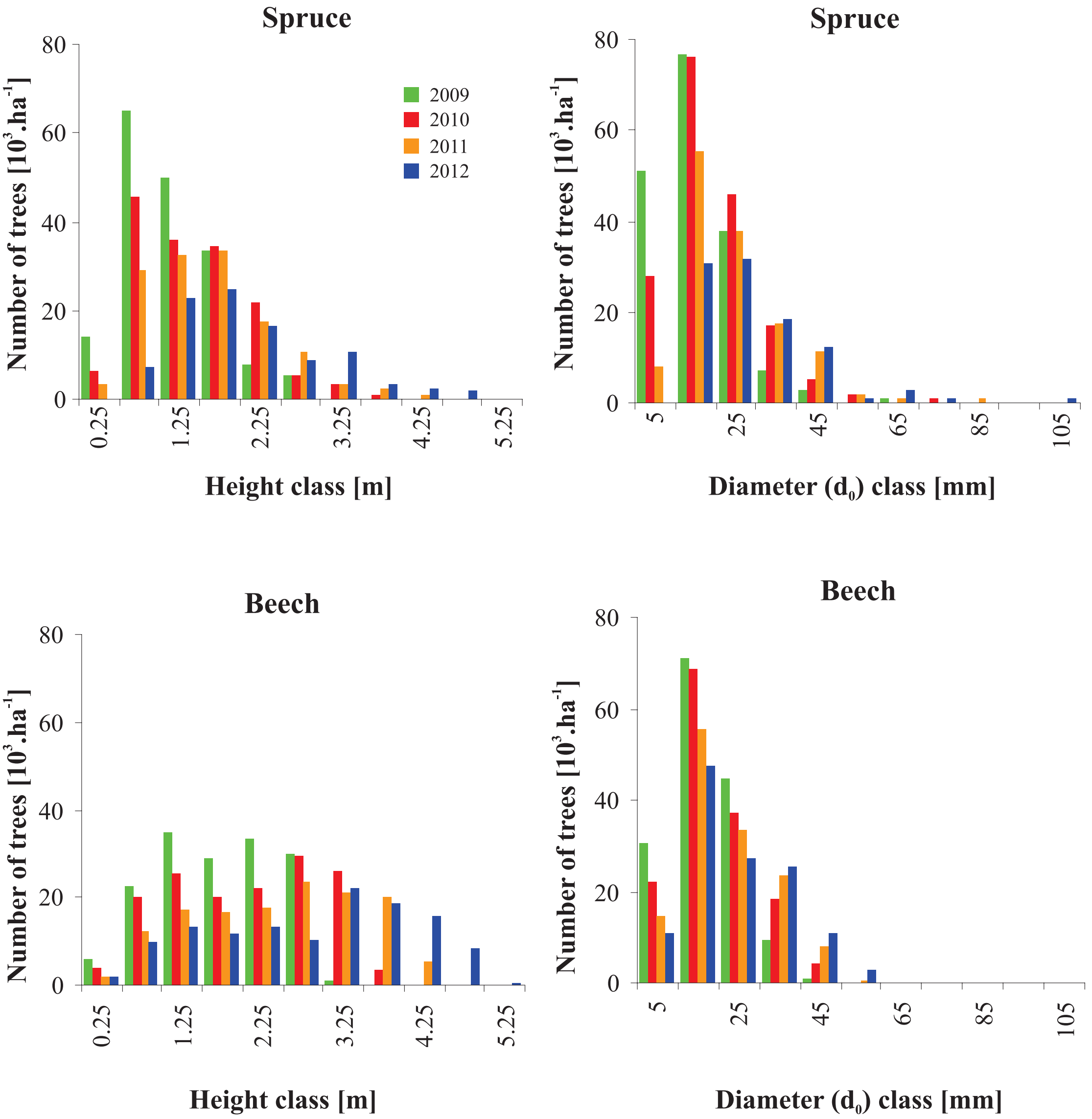

Fig. 1. Diameter and height histograms of Norway spruce and European beech found in experimental plots in April in 2009, 2010, 2011 and 2012

a slightly left-sided distribution of heights in 2009 and 2011 and a normal distribution in 2010 and 2012 (Kolmogorov-Smirnov test). Heights of spruces in the stands manifested a normal distribution in all years. As for the beech stand, heights showed up normal distribution in 2009 and 2011, but a slightly left-sided distribution in 2010 and 2012. Heights of beech manifested normal distribution in all years except for 2012 which showed a slightly right-sided distribution. Coefficients of skewness showed positive values, only the beech height distribution had negative values, indicating that most values are situated more to the right than average figures.

The number of trees per hectare in the beech stand declined in the years 2009 – 2012 by 20.4%, the mean tree height, diameter and stem volume increased by 65.7%, 41.3% and 155.2%, respectively. The inter-annual increments of the mean tree height were between 47 – 51 cm, and the mean tree diameters were 0.24 – 0.30 cm. These increments of the mean tree parameters did not depend exclusively on growth intensity but also on the number and size of trees that died in the specific years.

As for the spruce stands, a number of the trees per hectare decreased in the entire period of observation by 44.3%, mean tree height, diameter and stem volume increased by 75.0%, 71.8% and 283.1%, respectively. The inter-annual increase of the mean tree heights were from 30 to 59 cm and mean tree diameters from 0.42 to 0.52 cm. Differences in mean tree diameters between the beeches and spruces in the first three years were low (up to 10%). On the other hand in 2012, the differences were as much as 44.6% in favor of the beeches due to the high mortality of suppressed and co-dominant spruces. This mortality influenced the height and diameter frequency distribution considerably.

Table 2. Basic statistical characteristics for allometric equations expressing biomass of aboveground tree compartments

Tree species	Tree compartment	b_0 (S. E.) P	b_1 (S. E.) P	b_2 (S. E.) P	R^2	MSE	λ	S. D.
Norway spruce	Stem	0.695 (0.269) 0.012	1.100 (0.101) < 0.001	1.380 (0.115) < 0.001	0.990	0.027	1.014	0.192
	Branches	-1.963 (0.541) < 0.001	1.824 (0.204) < 0.001	0.831 (0.230) < 0.001	0.967	0.108	1.051	0.327
	Needles	-1.888 (0.521) < 0.001	1.977 (0.196) < 0.001	0.533 (0.221) 0.018	0.967	0.100	1.049	0.337
	Needles 2009	-3.629 (0.943) < 0.001	2.025 (0.355) < 0.001	0.610 (0.400) 0.132	0.906	0.328	1.150	0.592
	Needles 2010	-3.543 (1.388) 0.015	1.799 (0.533) 0.002	1.420 (0.574) 0.018	0.919	0.249	1.116	0.583
	Needles 2011	-4.084 (0.578) < 0.001	2.065 (0.259) < 0.001	0.826 (0.361) 0.028	0.972	0.090	1.041	0.296
European beech	Stem	-1.763 (0.216) < 0.001	1.905 (0.093) < 0.001	1.069 (0.093) < 0.001	0.989	0.024	1.011	0.152
	Branches	-6.581 (0.577) < 0.001	3.265 (0.249) < 0.001	0.174 (0.248) 0.485	0.947	0.170	1.076	0.413
	Foliages	-5.943 (0.439) < 0.001	2.783 (0.190) < 0.001	0.332 (0.189) 0.083	0.962	0.098	1.045	0.305

Table 3. Biomass standing stock by tree compartments in tons per hectare (in April of current year)

Tree compartment	Beech				Spruce			
	2009	2010	2011	2012	2009	2010	2011	2012
Stem	17.439	25.219	35.058	44.716	13.838	19.766	25.420	31.418
Stem*	36.597	46.980	61.499	74.363	39.530	51.744	66.437	84.319
Branches	5.526	8.151	11.867	15.125	7.689	11.483	15.558	19.028
Foliages	0.000	0.000	0.000	0.000	13.611	15.306	17.873	19.418

** expressed on volumetric base (m^3.ha^{-1}).*

Table 4. Annual biomass production by tree compartments in tons per hectare a year

Tree compartment	Beech			Spruce		
	2009	2010	2011	2009	2010	2011
Stem (A)	7.785	10.175	10.107	6.165	6.408	7.039
Stem*	10.390	14.971	13.468	12.683	16.422	20.526
Branches (B)	2.626	3.802	3.378	3.901	4.487	3.992
Foliages (C)	3.803^{+}	4.847^{+}	6.025^{+}	4.031	5.421	5.650
Aboveground biomass (A+B+C)	14.214	18.870	19.569	14.097	16.316	16.681

** expressed on volumetric base (m^3.ha^{-1}), $^{+}$ calculated through allometric equation.*

By using allometric equations (see Table 2 for their parameters) we were able to calculate the standing stock of the specific tree compartments at the beginning of the growing seasons in 2009 – 2012 (Table 3). The stem standing stock grew in the beech stand between 2009 and 2012 from 17.4 to 44.7 t.ha^{-1} (i.e. 2.6 fold) and in the spruce stand from 13.8 to 31.4 t.ha^{-1} (2.3 fold). There was a sharper increase of stem standing stock in the beech than in the spruce stand, even though in the case of stem volume it was the reverse. This happened for two reasons; the first reason was large tree mortality in the spruce stand and the second there was a higher value of wood density in the beech. A similar situation is assumed also for the standing stock of branches as well as total aboveground woody biomass. In all the years of observation, the standing stock of branch biomass was higher in the spruce than the beech stands. Particularly in 2012, the branch biomass standing stocks were 19.4 t.ha^{-1} and 15.1 t.ha^{-1} in the spruce and beech, respectively. The standing stock of foliages could not be compared between the beech and spruce stands because the beech leaves were not developed yet, thus, we used an inter-species comparison in the productions (Table 4). We assume that the values in the spruces might be over-estimated in terms of litter amount occurrence during the development of the current year's needles. Between the years 2009 – 2011, the standing stock of leaf biomass increased from 3.8 t.ha^{-1}, however, standing stock of the spruce needle biomass was much larger (between 13.6 t.ha^{-1} and 17.9 t.ha^{-1}).

Biomass allocation in the specific tree compartments can be expressed in a variety of ways. Most frequently these two approaches are used: 1) by contribution of the tree compartments to the total standing biomass (Yuste *et al*., 2005; Slot *et al*., 2012; Konôpka *et al*., 2013), or ii) through an allometric method in which the amount of a certain tree compartment is expressed to the biomass of

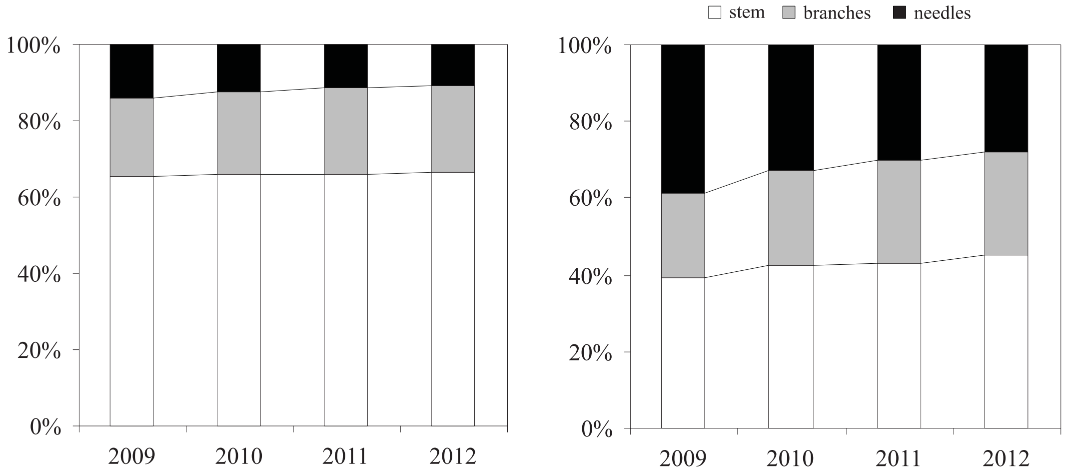

Fig. 2. Contribution of the specific tree compartments to total aboveground biomass in beech (left plate) and spruce (right plate)

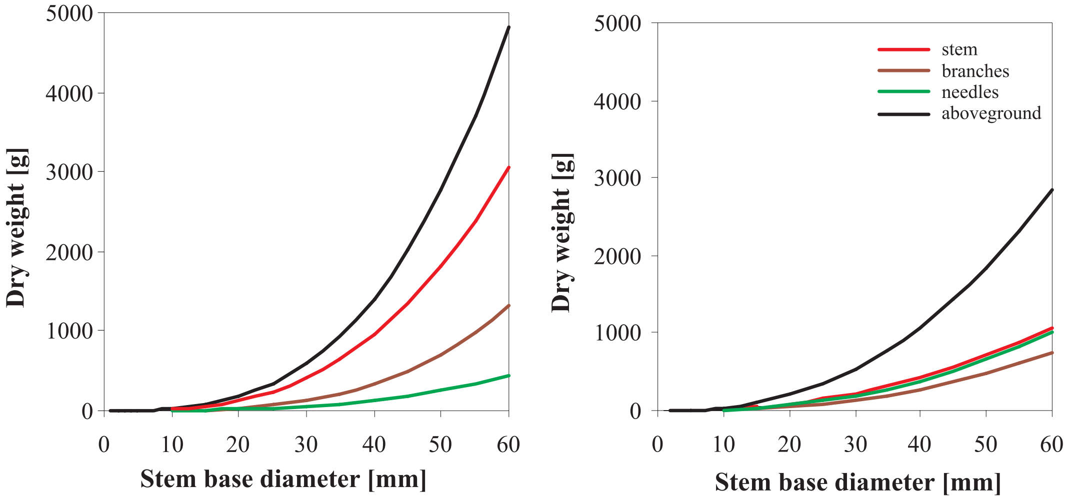

Fig. 3. Dependence of biomass by compartments on tree diameter d_0 in beech (left plate) and spruce (right plate)

another compartment (Enquist&Niklas, 2002; Poorter *et al*., 2011), ultimately this is based on basic tree characteristics – diameter and/or height (Pajtík *et al*., 2008; Enquist&Niklas, 2002). To derive this relationship, a logarithmic transformation of traditional allometric equation is used (Huxley, 1932; Gould, 1966). Our paper shows results obtained via both approaches. If we compare the contribution of the specific tree compartments to the total above-ground standing stock (Figure 2), large inter-annual differences are evident for stem and foliages. While in the year 2009 the needle biomass of the spruce made up 38.7% of aboveground standing stock, the beech leaves contributed only to 14.2%. The contribution of the foliages gradually decreased over time, and in 2012 the spruce needles made up 27.8% and the beech leaves 10.8% of aboveground biomass standing stock. In 2009, the share of the stems contributed to the aboveground biomass by 65.1% in the beech and 39.4% in the spruce stands. This share gradually increased during the years of observation. In fact, a gradual increase of stem contribution, and decrease of foliage contribution to total tree biomass in young stands of beech and spruce and also oak and pine with tree (stand) size are shown in our previous works (Pajtík *et al*., 2008; Priwitzer *et al*., 2009; Pajtík *et al*., 2011a, b).

The proportions of branches to the aboveground biomass were similar in both species. In 2009, the proportions were 20.6% in the beech stand and 21.9% in the spruce stand, these gradually increased in the period of observation. Biomass allocation among the tree compartments with respect to tree diameter d_0 is given in the Figure 3. The biomass was calculated by means of classic allometric equations, which were logarithmically transformed and then retransformed to the form [1] (Marklund, 1987). Coefficients of the equations are in Table 2.

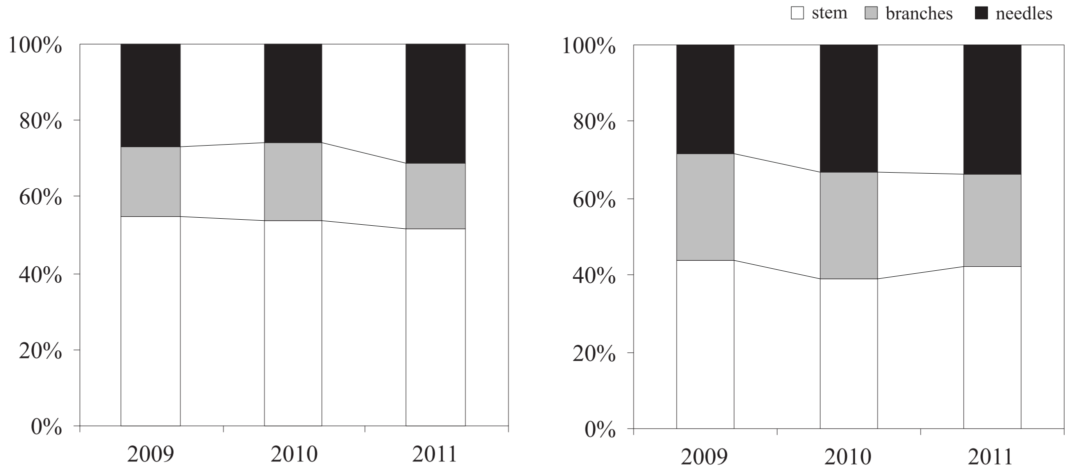

Fig. 4. Contribution of the specific tree compartments to aboveground net primary productivity in beech (left plate) and spruce (right plate)

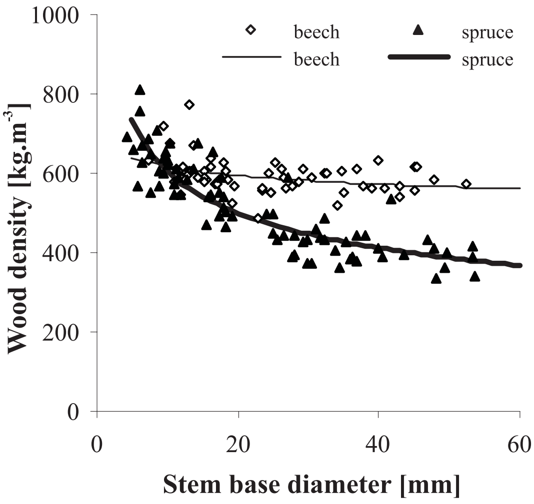

Fig. 5. Specific weight of beech and spruce stems with regard to tree diameter d_0

The largest contribution to the above-ground NPP in both tree species was found to be stems, followed by foliages and branches. Production of the compartments in the specific years was similar in both tree species (Table 4, Figure 4). Annual aboveground NPP increased from 14.2 $t.ha^{-1}$ to 19.6 $t.ha^{-1}$ in the beech, and from 14.1 $t.ha^{-1}$ to 16.7 $t.ha^{-1}$ in the spruce stand. However, in the case of volumetric expression of stem production, larger figures are shown for the beech than spruce stand. This is a consequence of the different wood densities of the species (Figure 5) and also contrasting developments in the number of trees. In general, it is usual for young spruce stands from natural regeneration to experience sharp decreases in the number of trees; this is caused by low light intensity under the canopy (Pajtík *et al.*, 2008; Dutca *et al.*, 2010). Thus, the above-ground NPP in the spruce only slightly increased during 2011 in spite of large diameter increments (see also Bošeľa *et al.*, 2013). On the other hand, a small increase of the NPP in the beech during 2011 was related to small diameter and height increments (also Bošeľa *et al.*, 2013). Inter-special differences in foliage quantities are much larger for standing stock than in NPP, because the production only covers the current year spruce needles. Besides certain inter-annual differences in NPP, rather large differences were recorded for losses on tree compartments (Table 5).

Figure 6 demonstrates a comparison of aboveground NPP by compartments between the species and the years. The largest inter-species differences are for the stem biomass this was significantly larger in the beech than spruce stands especially in 2010 and 2011. Branch

Table 5. Inter-annual losses on tree compartments in tons per hectare a year

Tree compartment	Beech			Spruce		
	2009	2010	2011	2009	2010	2011
Stem	0.005	0.336	0.449	0.237	0.754	1.041
Stem*	0.007	0.452	0.604	0.469	1.729	2.644
Branches	0.001	0.086	0.120	0.107	0.412	0.522
Foliages	3.216$^+$	4.120$^+$	4.787$^+$	2.336	2.854	4.105

** expressed on volumetric base ($m^3.ha^{-1}$), $^+$ data originating from litter collectors.*

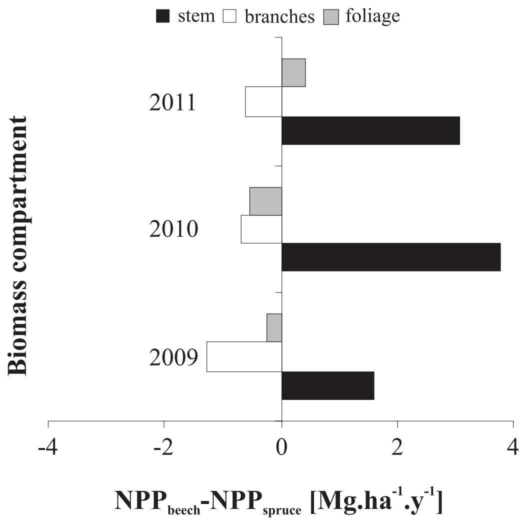

Fig. 6. Differences in NPP of the aboveground tree compartments between European beech and Norway spruce (years 2009 – 2011). Positive values are in favor of beech, negative ones in favor of spruce

productions were larger in the spruce than beech stands; on the other hand, foliage productions were rather similar in both tree species. Here, we would like to point out contrasting strategies of foliage turnover between the species. These features govern a higher role for beech foliages in carbon cycling than in the case of the spruce needle.

4. Conclusion

We studied the above-ground biomass standing stock and production by tree compartments in young beech and spruce stands grown under the same site conditions. The beech stand manifested relatively low tree mortality and maintained high tree density. Here, subdominant trees tried to reach the main crown layer and many suppressed trees survived in the under-layer. Most beech trees were high and slim with a high height to diameter ratio. On the other hand, the spruce stand was standard with a high share of tree mortality which suppressed; subdominant trees lacked light. The live trees invested carbohydrates to stem thickening, thus, they were lower but thicker than those in the beech stand.

Contrasting figures between the stands were found for the standing stock of stems with regard to different bases (volumetric versus biomass). A larger aboveground NPP was recorded in the beech than in the spruce stand; this is partly related to the higher wood density of beech. Large inter-species differences existed in the standing stocks of foliages, spruce manifested an amount threefold larger than beech. However, the reverse situation is expected for interspecies differences if we focus on the role of foliages in carbon cycling (evergreen against deciduous species).

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Resumé

V tejto práci sme pomocou kombinácií kontinuálnych meraní a deštruktívnych odberov vzorníkov sledovali a porovnali zásobu nadzemnej biomasy a ročnú primárnu produkciu (NPP) v prirodzene obnovených mladých porastoch buka a smreka. Na vybranej lokalite predpokladáme, že zmenené klimatické podmienky budú lepšie vyhovovať buku pred v súčasnosti prevládajúcim smrekom. Lokalita Vrchslatina sa nachádza v južnej časti Veporských vrchov v nadmorskej výške 977 m nad morom (48° 38′ 50′′ N, 19° 36′ 07′′ E). Priemerné ročné zrážky sa pohybujú okolo 900 mm, priemerná ročná teplota je 5,2 °C.

Na sledovanej lokalite sme pozorovali odlišný priebeh rastu buka a smreka. Pri buku bola pozorovaná menšia medziročná mortalita, udržiaval sa až prehustený zápoj, v ktorom sa aj podúrovňové stromy snažili dostať do úrovne. Toto sa prejavilo na tvare kmeňov, ktoré sú tenké a vysoké. Štíhlostný koeficient sa pri stromoch so strednou hrúbkou a strednou výškou postupne zvyšoval od 1,19 do 1,40. Pri smreku dochádza k vyššej mortalite, vrastavé a podúrovňové stromy odumierajú z dôvodu nedostatku svetla. Stromy rastú viac do hrúbky, čo sa odráža aj na štíhlostnom koeficiente, ktorý bol po celé obdobie viac-menej konštantný a pohyboval sa v rozpätí 0,89 až 0,93 (tab. 1). Zásoby kmeňa sú pri smreku v jednotlivých rokoch o 3 – 10 $m^3.ha^{-1}$ väčšie ako pri buku (tab. 3). Po prepočítaní na sušinu je vplyvom rozdielnej objemovej hmotnosti (obr. 5) celková zásoba sušiny drevných častí (kmeň a konáre) väčšia pri buku (tab. 3). Najväčší rozdiel medzi drevinami je v zásobe asimilačných orgánov, ktorá je pri smreku viac než trojnásobná (tab. 3 a 4). Počas rastu dochádza pri obidvoch drevinách k zvyšovaniu podielu kmeňa a znižovaniu podielu asimilačných orgánov (obr. 2). Hlavný medzidruhový rozdiel pri pomerne vyrovnaných hektárových zásobách je v rozdelení nadzemnej biomasy medzi komponenty, kde buk alokuje do kmeňa viac asimilátov ako smrek (obr. 2 – 4).

Pri porovnaní ročnej NPP asimilačných orgánov a konárov neboli zistené žiadne signifikantné rozdiely medzi sledovanými drevinami (obr. 6). Ukázali sme, že zásoby nadzemnej biomasy ako aj NPP buka a smreka boli v mladých plnozakmenených porastoch z prirodzeného zmladenia na danom stanovišti podobné (tab. 3 a 4).

Špecifická listová plocha a index listovej plochy v mladých porastoch buka a smreka

Abstrakt

Buk lesný *(Fagus sylvatica L.)* a smrek obyčajný *(Picea abies (L.) Karst.)* patria medzi ekologicky a ekonomicky najdôležitejšie lesné dreviny v Európe. Tieto dva druhy sa vyskytujú spoločne na mnohých územiach Európy čo vedie k ich vzájomnej konkurencii. Sledovali sme prispôsobenie sa asimilačných orgánov zatieneniu, index listovej plochy LAI stanovišťa a prírastok stromov v dvoch čistých porastoch buka a smreka pochádzajúcich z prirodzenej obnovy s plným zápojom. Zistili sme, že individuálna veľkosť listu je omnoho menej variabilná u smreka ako u buka. Jednotlivá veľkosť listu resp. ihlice bola väčšia v hornej časti koruny ako v spodnej u obidvoch drevín. Opačný vzťah sa zaznamenal pre špecifickú listovú plochu (SLA), kde najvyššie hodnoty SLA boli namerané v najnižšej (zatienenej) časti koruny Nezistili sa významné rozdiely v indexe listovej plochy medzi dvomi porastmi, avšak LAI medziročne stúpal z 10,8 na 14,6 $m^2.m^{-2}$ v období od 2009 do 2011. Dominantné stromy oboch drevín boli výkonnejšie pri konverzii biomasy listov, resp. plochy listov na produkciu biomasy kmeňa, aj keď zmena tohto vzťahu s vekom bola špecifická pre jednotlivé dreviny. Celkovo sme zistili širšiu plasticitu listov vo vzťahu ku svetelným podmienkam pri buku než pri smreku, čo ukazuje na väčšiu kapacitu využitia voľného priestoru v poraste.

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Specific leaf area and leaf area index in developing stands of *Fagus sylvatica* L. and *Picea abies* Karst.

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ABSTRACT

European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* Karst.) are two of the most ecologically and economically important forest tree species in Europe. These two species co-occur in many locations in Europe, leading to direct competition for canopy space. Foliage characteristics of two naturally regenerated pure stands of beech and spruce with fully closed canopies were contrasted to assess the dynamic relationship between foliage adaptability to shading, stand LAI and tree growth. We found that individual leaf size is far more conservative in spruce than in beech. Individual leaf and needle area was larger at the top than at the bottom of the canopy in both species. Inverse relationship was found for specific leaf area (SLA), highest SLA values were found at lowest light availability under the canopy. There was no difference in leaf area index (LAI) between the two stands, however LAI increased from 10.8 to 14.6 $m^2\ m^{-2}$ between 2009 and 2011. Dominant trees of both species were more efficient in converting foliage mass or area to produce stem biomass, although this relationship changed with age and was species-specific. Overall, we found larger foliage plasticity in beech than in spruce in relation to light conditions, indicating larger capacity to exploit niche openings.

1. Introduction

Competition for light and resulting mortality are the most critical processes driving development of young forest stands (King, 1990). As the canopy closes, in particular in stands originating from natural regeneration, tree height relative to neighbours, but also position within a crown dictate light availability to foliage (Niinemets et al., 2001; Richardson et al., 2001). Leaves and needles are the only tissues with the capacity to capture energy and thus drive forest growth. Foliage responds very sensitively to growth conditions within a stand and has been shown to adapt its morphology (Bussotti et al., 2000), structure (Kull et al., 1999) and metabolism (Hallik et al., 2009) in response to light intensity.

Vertical distribution of foliage, but also changes in the size of individual leaves, have both been attributed to relative light conditions within the stand (Johansson, 1996). The relationship between light availability and specific leaf area (SLA, defined as leaf area per unit leaf mass) varies among tree species (Niinemets, 2010). No consensus currently exists as to whether different tree species exhibit greater leaf size plasticity in relation to light availability. Several studies report larger plasticity of leaf morphology in shade-intolerant than in shade-tolerant species (Oguchi et al., 2005; Sanchez-Gomez et al., 2006; Portsmuth and Niinemets, 2007), while others found the reverse (Paz, 2003; Delagrange et al., 2004) or no variation (Paquette et al., 2007). In addition to shade tolerance, SLA in trees is also influenced by tree age and size (Steele et al., 1990; Niinements and Kull, 1995). It is important to point out that tree age, size and irradiation gradient along the canopy are strongly correlated. Older and taller trees are likely to generate deeper canopies, which expose foliage to irradiation levels ranging from full to a fraction of full sunlight (Niinemets, 2010).

Efficient light capture is of crucial importance to trees growing in dense stands with high level of competition for light (Pearcy et al., 2005). Trees maximise capture of available light by developing layered canopies with several strata of overlapping leaves. Defined as the total one-sided foliage area per unit ground area, Leaf Area Index (LAI) controls light interception, but also acts as a determinant of carbon and water exchange between forest canopy and the atmosphere (Leuschner et al., 2006), primary

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production (Long and Smith, 1990) and rainfall interception (Herbert and Fownes, 1999). Whilst the definition and measurement of leaf area is fairly straightforward in broadleaves, three different definitions have been proposed for conifers: total needle surface area, half of the total needle surface area, and projected needle area. The latter definition was used in this paper as it is commonly accepted as the most practical, but also indicative of the needle surface involved in light interception at any one time (Chen et al., 1997). Forest stand LAI is determined by leaf size, total number of leaves per tree, but also by stem density (Leuschner et al., 2006).

Despite a considerable amount of literature describing foliage characteristics and the development of LAI in growing forests, studies investigating the relationship between LAI and foliage and stem biomass allocation are rare. Although LAI plays a key role in the conversion of radiative energy to biomass, little is known about the mechanisms linking light interception and biomass allocation in trees. Description of foliage mass and foliage area, together with data on mass of wood compartments may allow for an investigation of growth efficiency of foliage. Several authors (e.g. Pickup et al., 2005; Shipley, 2006; Milla et al., 2008) used the ratio between leaf and total plant dry plant mass (leaf mass ratio – LMR) or between leaf area and of total plant dry mass (leaf area ratio – LAR) to describe ecological and production interactions. However, none of these studies allow for the description of the dynamic relationship between foliage plasticity, stand LAI and tree growth. Konôpka et al. (2010) and Jack et al. (2002) described growth efficiency in temperate trees, albeit only on the basis of biomass partitioning and did not describe foliage dynamics.

Allometric relations are frequently used to assess biomass partitioning to various pools in forests (Claesson et al., 2001; Wirth et al., 2004; Fehrmann and Kleinn, 2006; Cienciala et al., 2008; Pajtík et al., 2011). In general, biomass contained in a particular tree compartment can be predicted by an allometric equation usually using tree height or diameter (at breast height, *i.e.* DBH) as predictor variables (West et al., 2009). Estimates of foliage biomass in young beech and spruce stands were put forward by Kantor et al. (2009), whilst Xiao and Ceulemans (2004) established allometric equations for foliage at both branch and tree levels in young Scots pine. The latter study attempted to consider the vertical position of a whorl as one of the independent variables predicting foliage biomass. Having said that, biomass allometric equations by definition predict only foliage mass and do not offer any information about foliage area. Since leaf area and its stratification is a key determinant of forest stand productivity, this paper aims to link allometric relations to foliage area and stand LAI. Developing stands of pure *Fagus sylvatica* L. (beech) and pure *Picea abies* Karst. (spruce) with fully closed canopy are contrasted and their growth performance compared.

In particular, this paper links up information on foliage mass and foliage area for two of the most important European forest tree species growing on the same site. There are several levels at which these two species can be contrasted. As a deciduous tree, beech produces all of its foliage in the current year. Spruce, on the other hand, retains its needles for up to 5 years, possibly leading to higher LAI in spruce. Beech is shade-tolerant, while spruce is classified as intermediate in relation to its shade tolerance (Ellenberg and Leuschner, 1996). Lastly, since the selected site is located at the lower elevation limit of spruce in this area of Europe, climate change is expected to favour beech leading to an eventual replacement of spruce by beech at this elevation. Thus this study offers insights into effects of climatic warming on growth performance of forests currently occupying the climatic boundary between the two species. In this study, we hypothesised that (i) spruce has higher LAI than beech, and (ii) dominant trees of both species have higher leaf mass ratio.

2. Materials and methods

2.1. Site description

The experimental site was located in the southern part of Slovak Ore Mountains, 977 m above sea level (48°38′50″ N and 19°36′12″ E). Annual sum of precipitation is close to 900 mm, while mean temperature is 5.2 °C. The soil type has been classified as Humic Cambisol on granodiorit bedrock, with a high stone content and pH (H_2O) of 5.1, 5.2, and 5.3 in the soil depths 0–10, 10–35 and 35–65 cm, respectively. Two neighbouring stands of pure beech and spruce were examined. Both stands originate from natural regeneration following a clearcut of preceding high forest. At the start of measurements presented in this study, both stands featured trees about 12–14 years of age. The beech stand was composed of dense groups of beech trees with a few scattered gaps colonised by *Calamagrostis epigejos* L. The structure of the spruce stand was similar to that of beech, however no grass cover was present due to shading by spruce trees. Detailed description of the site characteristics can be found in Konôpka et al. (2013).

2.2. Size distribution, biomass and foliage sampling

Five circular experimental plots were established in each stand in March 2009. The plots were 100 cm in radius and contained around 40 trees each. The plots were randomly positioned within each stand, but at a distance of at least 5 canopy heights from each other. All trees within each plot (PlotTrees thereafter) were tagged. Height and diameter d_0 (diameter at ground level) of all tagged trees were measured in September of 2009, 2010 and 2011.

During late summer 2011, 40 beech and 40 spruce trees were selected just outside the experimental plots and their foliage sampled from upper, middle and lower crown sections (FolTrees thereafter). Ten trees each were selected from the following four crown classes within the canopy: dominant, co-dominant, intermediate and overtopped (Kraft, 1884). Care was taken to cover the entire diameter distribution found in experimental plots. Then, three leaves were randomly selected and taken from each crown section of beech trees (9 leaves per tree). In spruce, 30 needles were collected from each crown section and in each of the following age cohorts (by year of needle set): 2011, 2010, 2009, 2008 and, rarely, 2007. All foliage samples were scanned on a flatbed scanner (EPSON Expression 10000), oven-dried and weighed. Leaf area of sampled foliage was established by WinFOLIA (Regent Instruments Inc., Quebec). Specific leaf area (SLA) of individual leaves or needles was calculated as a ratio of foliage area and dry mass.

A further 80 beech and 100 spruce trees were selected from each stand for destructive sampling in early September 2011 (BiomTrees thereafter). All tree compartments with the exception of fine roots thinner than 2 mm were harvested. Slightly fewer beech trees were sampled as the population of this species was more uniform in size than spruce. Height and d_0 of all sampled trees were established prior to destructive sampling. Harvested trees were divided into foliage and other (woody) compartments, dried until constant weight and weighed. Out of the 100 harvested spruce trees, 30 were randomly selected to establish the contribution of needle cohorts to total needle mass. All needles found on these trees were collected, divided to 5 cohorts (2011 through 2007), dried and weighed.

Stocking density and size distribution data from experimental plots were used for inter-specific comparisons between beech and spruce stands. Foliage size distribution data formed the basis for characterisation of vertical leaf size profiles of the canopy. Data on biomass compartment and foliage characteristics gathered outside experimental plots were used for biomass model parameterisations.

2.3. Estimations of biomass equations, LA and LAI

Dry weight data of biomass compartments measured in BiomTrees were used to construct biomass equations after Pajtík et al. (2008). The following model was used to estimate dry weights of stems, branches, coarse roots and foliage of individual trees:

$$W_i = e^{(b_0 + b_1 \ln d_0)} \lambda \tag{1}$$

where W_i is dry biomass of a tree component i, d_0 is stem diameter at base, b_0, and b_1 are coefficients to be estimated and λ is logarithmic transformation bias. Site-specific biomass equation parameters are listed in Table 1.

Specific leaf area (SLA) of foliage taken from FolTrees was calculated as the ratio between projected leaf area of foliage sample and its dry mass. Once the relationship between foliage biomass and tree size has been established, total leaf area of an individual tree (LA) dependent on d_0 can be calculated as follows:

$$\mathrm{LA} = \mathrm{SLA}(e^{(b_0 + b_1 \ln d_0)} \lambda) \tag{2}$$

where LA is total leaf area per tree, SLA is specific leaf area in $\mathrm{m}^2\,\mathrm{g}^{-1}$, b_0 and b_1 are site-specific coefficients of leaf biomass Eq. (1), d_0 is stem diameter at the base and λ is logarithmic transformation bias.

In each circular permanent experimental plot, we calculated LAI by dividing the sum of LA of all PlotTrees found within the plot by its area:

$$\mathrm{LAI}_j = \frac{\sum_{i=1}^{n} \mathrm{LA}_{ij}}{S_j} \tag{3}$$

where n is the number of trees within a plot, LA_{ij} is the leaf area of i-th tree on j-th plot, and S_j is the area of the j-th plot. This calculation is fairly straightforward in European beech due to the presence of a single cohort of leaves. In Norway spruce, however, the variation of SLA in needle cohorts was also taken into account. For each needle cohort, LA of needles from all trees present within a permanent plot can be calculated as follows:

$$\mathrm{LA}_k = \sum_{i=1}^{n} (W_i P_k \mathrm{SLA}_k) \tag{4}$$

where n is the number of trees within a plot, W_i is the dry needle biomass of i-th tree, P_k is the proportion of k-th cohort from the total and SLA_k is the specific leaf area of the k-th needle cohort. Mean SLA for the entire vertical profile of the canopy was used for each cohort. Based on an analysis of trees harvested at the site, we established that P_k in spruce is stable and independent of d_0 (Supplementary Fig. S1), therefore mean values of P_k were used across all diameter classes. LA of all spruce trees found within each plot was then obtained by summing up leaf areas of the five needle cohorts.

2.4. Data analysis

All stand-level observations were averaged to plot level ($N = 5$), differences between species were compared by one-way ANOVA and considered significant at $P < 0.05$. All variables were checked for the homogeneity of variance (Levene's test) and normality of distribution (D'Agostino and Pearson Test). Repeated measures ANOVA was used to compare the development of LAI in the two stands over the period of observation. Two-way ANOVA was used to assess the effect of species and canopy position on SLA, followed by Tukey's multiple comparison test. Data were log-transformed where they did not satisfy ANOVA assumptions. Linear or exponential equations were fitted to individual tree data where appropriate, using least squares fit. Model parameters were assessed for differences between species (stem increment per unit leaf mass) or from specific value (needle cohort contribution to total) by extra sum-of-squares F test.

3. Results

Although very similar in age, the two studied ecosystems did differ in several standard forest stand characteristics (Table 2). Beech trees were significantly taller than spruce, while spruce trees had a larger diameter at base, resulting in a significantly larger height/diameter ratio in beech than in spruce. The difference in height to diameter ratio between the two species is evident throughout the diameter size distribution (Supplementary Fig. S2). On the other hand, there was no difference in the number of trees per unit area, mean stem volume and basal area.

Measurements of foliage collected from 40 beech and 40 spruce FolTrees reveal that individual leaf size is far more conservative in spruce than in beech (coefficient of variance 0.29 and 0.53 respectively, Fig. 1). Within the stem diameter distribution present in the stands at the time of measurement, beech leaf area increases by 83% from the 25th to the 75th d_0 percentile. In spruce, however, the comparable increase in individual needle area is only 38%. Similarly, the spread of leaf size between leaves collected at the top and bottom of the canopy represents 84% of mean leaf size at mean d_0 in beech, but only 28% in spruce.

Analogous to foliage area, we observed how SLA is affected by tree size and foliage position within the canopy (Fig. 2). The highest values for both species were recorded in overtopped trees growing underneath the main canopy. In contrast to leaf area, we did not observe such a strong effect of d_0 on the differentiation of SLA values between the two species. The spread of mean SLA at the top and bottom of the canopy represents 43% of mean SLA in beech and 33% in spruce. SLA of foliage growing in the middle of the canopy on the mean tree was 273 $\mathrm{cm}^2\,\mathrm{g}^{-1}$ in beech and 87 $\mathrm{cm}^2\,\mathrm{g}^{-1}$ in spruce.

Ten beech and ten spruce FolTrees were selected from each of the four crown classes considered in this study to evaluate the effect of tree size on SLA (Fig. 3). We observed no difference between the two species in the effect of crown class on SLA.

Table 1
Site-specific biomass equation parameters for European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*). Diameter at based is used as the single predictor in all models estimating compartment biomass.

Species	Compartment	b_0 (S.E.) P	b_1 (S.E.) P	R^2	MSE	Λ (S.D.)
Beech	Leaves	−6.576 (0.256) < 0.001	3.085 (0.081) < 0.001	0.960	0.102	1.047 (0.308)
	Woody mass	−3.357 (0.191) < 0.001	2.889 (0.060) < 0.001	0.974	0.056	1.027 (0.238)
	Whole tree	−3.318 (0.188) < 0.001	2.900 (0.060) < 0.001	0.975	0.055	1.026 (0.234)
Spruce	Needles	−3.079 (0.171) < 0.001	2.432 (0.054) < 0.001	0.964	0.106	1.053 (0.366)
	Woody mass	−1.719 (0.138) < 0.001	2.283 (0.043) < 0.001	0.974	0.069	1.035 (0.296)
	Whole tree	−1.489 (0.134) < 0.001	2.321 (0.042) < 0.001	0.976	0.065	1.034 (0.295)

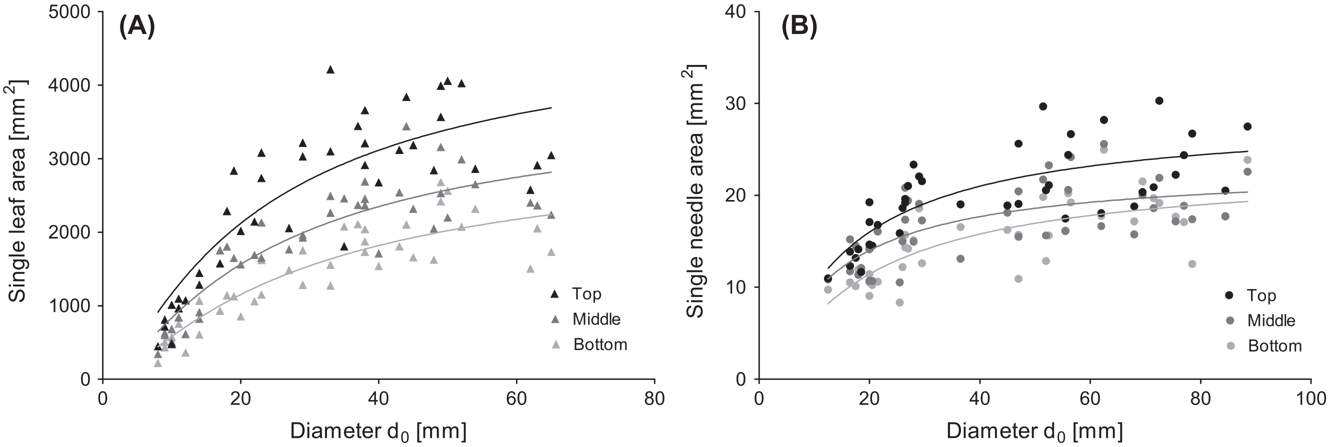

Fig. 1. Single leaf and needle area at three different canopy levels in European beech (A) and Norway spruce (B). Solid lines represent best fit models for top, middle and bottom of individual tree crown.

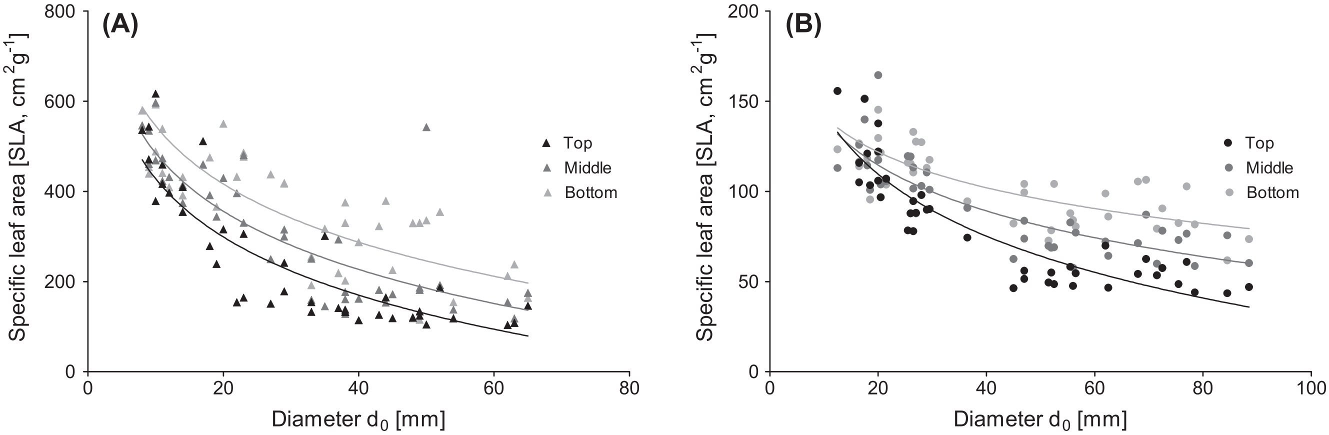

Fig. 2. Specific leaf area at three different canopy levels in European beech (A) and Norway spruce (B). Solid lines represent best fit models for top, middle and bottom of individual tree crown.

Dominant and co-dominant trees show the same SLA in beech ($P = 0.812$) and in spruce ($P = 0.986$). Intermediate and suppressed trees, however, have higher SLA than dominant trees in both species ($P < 0.001$). Foliage position within an individual tree crown does not affect SLA in overtopped trees in beech ($P = 0.856$) or spruce ($P > 0.999$), trees in other canopy classes however do show a significant effect of foliage position on SLA ($P < 0.026$).

Destructively sampled BiomTrees were used to construct biomass equations linking biomass compartments to diameter at base (Table 1). Fig. 4A shows total foliage mass of beech and spruce trees across the diameter distribution observed in this study. It is clear that spruce trees of the same size support more foliage mass than beech trees. At the same time, beech foliage has greater SLA in all tree sizes under investigation (Fig. 4B). Using data for whole tree foliage mass in combination with mean SLA, we observe that there is very little difference in whole tree leaf area between beech and spruce trees (Fig. 4C).

The observed similarity of whole tree leaf area of beech and spruce trees was reflected in calculated LAI. As already mentioned, basal area and tree density did not differ between the two stands. Coupled with very similar total leaf area of individual trees, it is not surprising that LAI did not differ between beech and spruce ($P = 0.865$, Fig. 5). From 2009 through 2011, modelled LAI increased from 11.4 to 14.9 $m^2\ m^{-2}$ in beech and 10.3 to 14.2 $m^2\ m^{-2}$ in spruce.

Finally, biomass equations and data describing foliage cover in both species were used to compare wood production efficiency expressed as wood mass produced per unit foliage mass or unit foliage area. Taller trees were always more efficient in using unit foliage to produce unit stem biomass (Fig. 6). The slope of linear regressions describing the relationship between foliage efficiency and tree height of all trees measured in permanent plots was always positive and significantly different from zero ($P < 0.0001$). Interestingly, as the stands grew older, the advantage of dominant and co-dominant trees in terms of wood production efficiency was slowly eroding – but only in beech. A tree 1 m taller than its competitors produced 0.63 more grams of stem wood per gram foliage in 2009, but this advantage in foliage productivity decreased to 0.33 $g\ g^{-1}$ in 2011 ($P = 0.0007$). This decrease was not evident in spruce, where the slope of the linear regression was 0.11 in 2009 and 0.09 in 2011 ($P = 0.304$). Similar to foliage mass, we observed the same dynamic when plotting the stem production efficiency expressed per unit of foliage area against tree height; a decrease of regression slope from 36.3 g of stem mass per metre square of foliage for every metre of height in 2009 to 22.7 in 2011 in beech ($P < 0.0001$). In spruce, the slope did not change over the period of observation; 19.2 $g\ m^{-2}\ m^{-1}$ in 2009 and 10.1 $g\ m^{-2}\ m^{-1}$ in 2011 ($P = 0.424$).

4. Discussion

Both stands considered in this study originate from natural regeneration following the removal of original tall forest. It is to

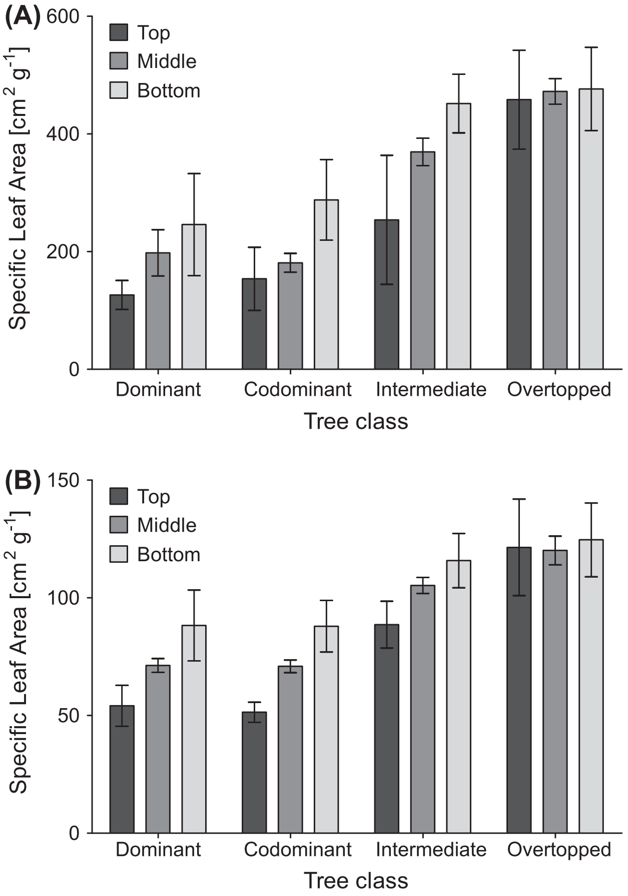

Fig. 3. Specific leaf area of European beech (A) and Norway spruce (B) foliage as affected by canopy position and socio-ecological status of individual trees (cm^2 g^{-1}, $N = 10$ in each class, mean ± S.D.).

be expected that not all trees are of the same age, however we established that the cohort of trees currently growing on the site is between 12 and 14 years old. The stands were dense, at the time of the study there was no difference in the number of trees per hectare. Beech trees were marginally taller, while spruce trees had thicker stems at the base. However, there was no difference in basal area, leading us to the assertion that any differences in foliage characteristics are due to differences in genetics and growth habit, rather than because of different tree size or stocking density and resulting competition.

4.1. Leaf level

Individual leaves with the largest area were always found at the top of the canopy, both in beech and in spruce. Leaves and needles were progressively smaller with increasing canopy depth, this differentiation of single leaf size appears to be stronger in beech than in spruce. Shorter trees had smaller leaves than taller trees, owing to the shading of their entire crowns by taller trees. Contrasting evidence exists on the effect of shading on individual leaf size. Our results in beech are in disagreement those of Barna (2004) and Tognetti et al. (1998) who found that the size of foliage increased with shading, but correspond with the study by Canham (1988) who found larger leaf size at high light levels in *Acer saccharum* Marsh. and *Fagus grandiflora* Ehrh. Similarly, Niinemets and Kull (1995) found no effect of irradiance on projected needle area in spruce and Gebauer et al. (2011) indicate that

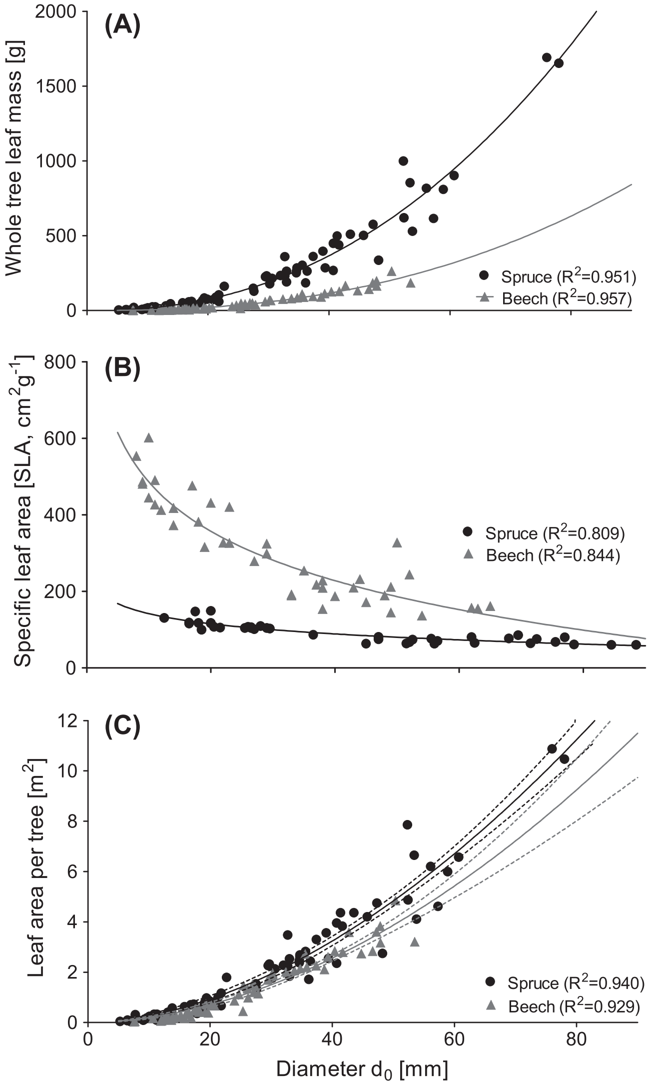

Fig. 4. Whole tree foliage mass (A), specific leaf area (B) and whole tree leaf area (C) of naturally regenerated European beech and Norway spruce trees. Dotted lines in pane C represent 95% confidence interval of fitted line.

Table 2
Stand characteristics for European beech and Norway spruce in November 2011, approximately 13 years after natural regeneration (means ± S.E., *P* values at $N = 5$, significant differences are highlighted in bold).

	European beech	Norway spruce	d.f./*F*	*P*
Number of trees (ths. ha^{-1})	124.3 ± 11.6	99.4 ± 6.6	1/3.45	0.100
Mean tree height (cm)	295.3 ± 22.2	213.0 ± 5.3	1/13.63	**0.006**
Mean diameter d_0[a] (cm)	2.42 ± 0.11	3.19 ± 0.11	1/25.57	**0.001**
H/D ratio (cm cm^{-1})	125.9 ± 8.5	76.3 ± 2.5	1/31.50	**0.001**
Mean stem volume (cm^3)	526.6 ± 56.7	645.9 ± 34.5	1/3.22	0.110
Basal area d_0[a] (m^2 ha^{-1})	356.2 ± 35.5	334.6 ± 28.5	1/0.22	0.648

[a] Stem diameter and basal area measured at ground level.

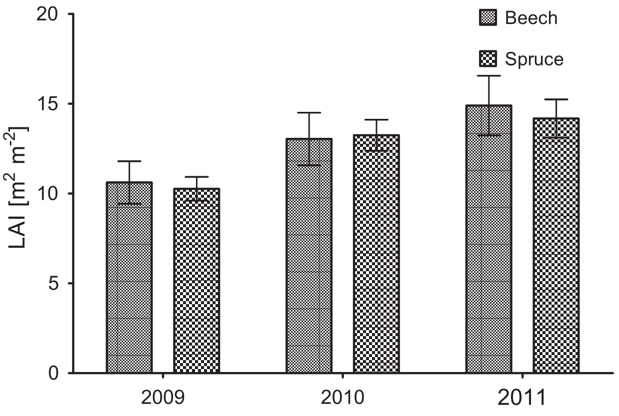

Fig. 5. Leaf Area Index (LAI) in naturally regenerated stands of European beech and Norway spruce trees measured in permanent plots (mean ± S.D., $N = 5$).

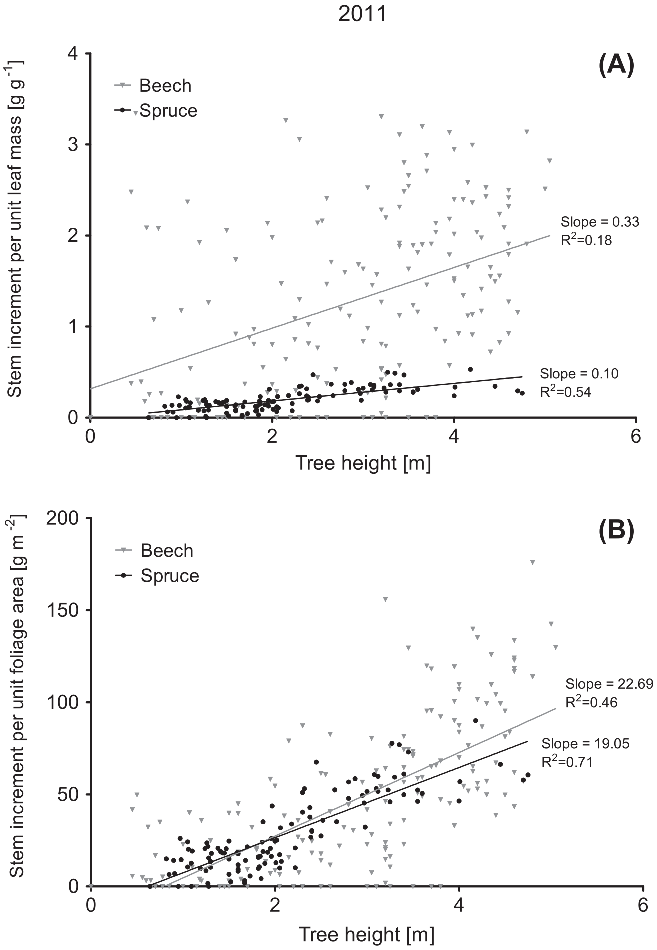

Fig. 6. Stem mass increment per unit foliage mass (A) and area (B) plotted against stem height of individual European beech and Norway spruce in 2011.

needle size increases with light intensity in most but not all of the 57 spruce provenances they compared. The wide variation in the relationship between leaf size and light intensity points to substantial plasticity in both species considered in this study. In general, Dombroskie and Aarssen (2012) propose that smaller leaves are favoured under low light exposure because they minimize overlap of closely spaced adjacent leaves and they are subject to a trade-off of selection favouring high number/low size strategy which in turn maximizes the size of the reserve bud bank.

SLA, calculated as leaf area per unit mass, was found to be the smallest at the top of the canopy in full light conditions and increases with shading both in beech and in spruce. Larger SLA with increasing shading is likely an adaptation for more efficient light interception in low light conditions (Niinemets et al., 2001). SLA was found to be greatest at the bottom compared to the top of the crown in 13- to 82-year-old Norway spruce (Merilo et al., 2009) and in spruce, beech and fir seedlings (Stancioiu and O'hara, 2006). In this study, both beech and spruce show the same decreasing trend, graphs in Fig. 2 indicate that leaf and needle SLA will decrease further as the stands mature before stabilising. Significant differences in SLA between socio-ecological classes of trees within the canopy were found. Dominant, co-dominant and intermediate crowns have shown strong effect of crown depth on SLA. Foliage SLA of overtopped trees, owing to growth in shade conditions, did not differ between the top and the bottom parts of tree crowns. The optimal partitioning theory suggests that a plant invests primarily to those compartments which are crucial for acquiring the most limiting resource (Niklas, 2004). Maximum available light must be captured by overtopped trees, leading to construction of large foliage area with minimum mass investment.

4.2. Tree level

As expected, beech trees had substantially smaller foliage mass than spruce trees of comparable size. However, we have established that the latest cohort of spruce needles constituted only 34% of the total needle mass. Comparing only the current year beech and spruce foliage mass shows that the two species invest exactly the same amount of resource to building their photosynthetic apparatus in a given year. Considering the effect of shading on SLA, mean SLA per tree is far larger in small (overtopped) trees, but approximates to that of spruce in lager (dominant) individuals. Higher SLA of shaded foliage in young beech stands was recorded by Closa et al. (2010). Barna (2004) showed lower values of SLA in dominant and co-dominant beech trees than in subdominant individuals. Our observations of beech SLA are in the same range as those of Barna (2004) who report 120–460 $\text{cm}^2\,\text{g}^{-1}$, Closa et al. (2010) with values between 180 and 480 $\text{cm}^2\,\text{g}^{-1}$, and those of Leuschner et al. (2006) who report a range between 190 and 240 $\text{cm}^2\,\text{g}^{-1}$. As for the SLA of spruce needles, our values are higher than those of Hager and Sterba (1985) who found SLA of 30–70 $\text{cm}^2\,\text{g}^{-1}$ in a 17-year-old stand, however the needles in the upper and middle part of the largest trees in our study were inside this range. Taken together, the observed contrasting trends of leaf area per tree and SLA mean that there is little difference in total leaf area per tree between beech and spruce trees of the same size. Despite one being conifer and the other broadleaf, beech and spruce trees of the same diameter class support nearly identical leaf area.

4.3. Stand level

Reflecting foliage area per tree and stand density, LAI indicates the potential of forest stands to utilise incident radiation to produce biomass. Stand LAI was steadily increasing during the period of observation, reaching approximately 15 $\text{m}^2\,\text{m}^{-2}$ in 2011. Most studies indicate LAI in a variety of forest tree species below 10 $\text{m}^2\,\text{m}^{-2}$ (e.g. Bréda, 2003; Leuschner et al., 2006), with higher values also reported but considered extreme (e.g. Ford, 1982; Albrektson, 1984; Bolstad and Gower, 1990). Waring et al. (1985) posit that very dense foliage can be found in some coniferous forests, exceptionally reaching LAI values as high as 20 $\text{m}^2\,\text{m}^{-2}$. Nock et al. (2008) found a relationship between tree size and LAI in *Acer saccharum* and *Betula alleghaniensis*, trees with DBH of 30 cm had LAI of 7.5 and 8.5 $\text{m}^2\,\text{m}^{-2}$, but trees with DBH of 70 cm showed

LAI of 4.0 and 6.0 m^2 m^{-2} in *Acer* and *Betula*, respectively. There are several reasons why we observed very high LAI values; methodological, ontogenetic and possibly climatic. The diameter-based allometric method of LAI estimation has been reported to show values higher than other methods (Marshall and Waring, 1986). The aggrading nature of our naturally regenerated stands may have caused the increasing LAI, which may reverse in the future as the stands age and self-thin. Finally, the exposition of the site is south-westerly, providing optimal insolation for these young stands.

Wood production efficiency, expressed as unit stem increase per unit foliage, did differ between beech and spruce. Stem increment per unit leaf mass was far higher in beech compared to spruce, the difference driven by retention of older needle cohorts in spruce which increases foliage mass. Dominant beech trees had significantly higher efficiency than overtopped trees, this advantage of taller trees was not as evident in spruce. A possible explanation for this difference can be that needle-shaped leaves can be arranged in a pattern that bounces the incoming radiation over a larger number of leaves deeper in the canopy (Sprugel, 1989). This effects increases photosynthesis of overtopped spruce trees by reducing the energy wastage that occurs when light falls on horizontally positioned beech leaves at the top of the canopy that are already light-saturated. However, when plotted against leaf area, wood production efficiency did not differ between the two species. This suggests that it is higher leaf thickness (Aranda et al., 2004) rather than leaf area at the top of the canopy that confers stem growth advantage in dominant beech trees.

5. Conclusion

Stands of beech and spruce around Central Europe occur as monospecific stands, but also as various mixtures of the two species. This study compared the development of foliage and canopy in the two species, with the view of contrasting their light utilisation strategies. Leaf area per tree, stand LAI and stem increment per unit leaf area were found not to differ between beech and spruce in our stands, suggesting that stands of both species are utilising close to maximum available light energy. We found that morphology of beech foliage is more plastic that than of spruce, possibly contributing to the competitive advantage of beech in locations where the two species co-occur.

Acknowledgements

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.12.005.

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Listy a jemné korene vo vzťahu k rastovej účinnosti – porovnanie buka a smreka v iniciálnych rastových štádiách

Abstrakt

Vykonali sme kvantifikáciu biomasy kmeňov (s kôrou a bez kôry), listov a jemných koreňov v 14-ročných porastoch buka a smreka rastúcich na rovnakom stanovišti. Vykopali sme po 60 stromov z každej dreviny, zistili sušinu kmeňov a listov a následne zostrojili alometrické rovnice kde nezávislou premennou bola hrúbka kmeňa a závislou premennou sušina kmeňa (resp. listov). Zistilo sa, že smrek obsahuje omnoho väčší podiel biomasy listov ako buk. Rovnice na úrovni stromu sme skonštruovali tiež pre špecifickú listovú plochu a jednostranne projektovanú listovú plochu. Pomocou pôdnych vývrtov sme skúmali množstvo a morfologické charakteristiky jemných koreňov na obidvoch stanovištiach. Zatiaľ čo zásoba jemných koreňov na obidvoch stanovištiach bola podobná, v morfologických vlastnostiach koreňov sa vyskytovali signifikantné medzidruhové rozdiely. Vypočítali sme rastovú účinnosť vyjadrenú ročnou produkciou kmeňa v závislosti od parametrov listov a jemných koreňov. Najväčšie rozdiely, konkrétne 5-násobne v prospech smreka sme zaznamenali v prípade rastovej účinnosti vyjadrenej na základe počtu koreňových zakončení.

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Foliage and fine roots in terms of growth efficiency – a comparison between European beech and Norway spruce at early growth stages

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ABSTRACT: The quantification of stems (under- and overbark), foliage and fine roots in 14-year-old stands of European beech and Norway spruce grown on the same site were evaluated. Therefore, 60 trees of each species were sampled, dry masses of stems and foliage were established and expressed by allometric equations with stem diameter as an independent variable. The spruce allocated a much larger portion of biomass into the foliage than beech. The equations on a tree level were constructed also for specific leaf area and one-sided projected leaf area. Moreover, the quantity and morphological characteristics of fine roots in both stands were surveyed through soil coring. While standing stocks of fine roots were similar in the stands of both tree species, significant interspecies differences occurred in morphological properties of roots. Growth efficiency, expressing annual stem production on a variety of foliage and fine root parameters was calculated. The largest differences, specifically fivefold in favour of spruce, were found in growth efficiency based on a number of root tips.

Keywords: allometric equations; fine root morphology; leaf area; stem diameter; stem mass production; interspecies differences

Plants including forest trees are composed of a structural complex of organs which are characterized not only by their forms but also by their specific functions. Compartments of forest trees in elementary structuring are: foliage, branches, stem and root system. Kozlowski and Pallardy (1997) explained that the physiologically most active parts of trees are foliage and fine roots (the latter are usually characterized by the upper diameter of 1 or 2 mm; see for instance Smit et al. 2000).

It is well known that while foliage is involved in photosynthesis, roots – especially their tiny fragments and tips – serve for the absorption of nutrients and water from the soil medium. These two cardinal processes make up conditions for development and production of woody compartments, specifically branches, stem and coarse roots.

In many scientific works, the structuring of produced biomass into separate plant organs is called as "biomass allocation" (e.g. Poorter et al. 2012). The proportion of the specific parts in total plant biomass is determined by species, genetic properties, and is controlled by external conditions to a large extent (Kozlowski, Pallardy 1997). Recently, issues related to tree biomass allocation have prevailingly been studied with regard to carbon cycling and sequestration in forest ecosystems (Litton et al. 2007). At the same time, since foliage and fine roots are compartments with the shortest lifespan of all tree parts, they are the most dynamic elements of carbon rotation in forests (Helmisaari et al. 2002).

Internal and external factors modify not only quantitative but also qualitative properties of the

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particular tree compartments. It is evident especially in the case of foliage and fine roots which react to growth conditions sensitively through morphological adaptations. Foliage for instance changes size, weight and consequently also specific leaf area (SLA; i.e. foliage area expressed per weight unit) according to light intensity (e.g. Barna 2004; Closa et al. 2012). In scientific literature SLA is the most frequent indicator of foliage structure (Reich et al. 1998). Besides the indication of morphological features it may serve also as a conversion factor for expressing the area of assimilatory organs from their mass either on a tree or stand level. In fact, measurements of foliage properties are much more complex for some species of evergreen trees (prevailingly coniferous) than for deciduous ones (usually broadleaved). In the case of some evergreen tree species, differences between needles of specific age must be considered (see e.g. Zha et al. 2002).

As for morphological properties of fine roots a variety of indicators have been used, they are often composed of two root parameters – in the form of a ratio. The ratio between length and mass of fine roots (specific root length; SRL) or between the number of root tips and root mass (specific density of root tips; SDT) is used most frequently. These indicators were implemented for instance as characteristics of soil properties (Ostonen et al. 2007), changes in soil conditions (Konôpka, Takáčová 2010), or specific stand conditions (Kucbel et al. 2011).

As it was mentioned above, tree development and growth may be in process thanks to the input of external energy and matters absorbed by foliage and root system (especially fine roots and tips). From ecological, physiological and productive points of view a plenty of authors (e.g. Gersonde, O'Hara 2005; Konôpka et al. 2010) focused on a relationship between the quantity of assimilatory organs and production of tree biomass. Commonly ratios of stem mass production to unit area or mass of foliage were used, which is called growth efficiency (GE). We suggest that GE will be studied not only in the context of foliage but also in terms of fine roots. In general, research activities focused on tree fine roots were much less frequent in comparison with all other compartments (Brunner, Godbold 2007). At the same time, information on the relationship between quantitative and/or qualitative properties of foliage and fine roots is still missing for forest trees. This kind of knowledge would help to explain development and growth strategies in the individual tree species with regard to environmental conditions, potentially it would serve also for process modelling of these phenomena.

The principal aim of this paper is to quantify the biomass of foliage and fine roots, and to estimate some qualitative parameters of these compartments in young European beech and Norway spruce stands. Another goal is to estimate the production of stem mass and GE, i.e. stem production expressed per unit area and weight of foliage and fine roots. Based on these findings we will make interspecies comparisons between beech and spruce at young growth stages.

MATERIAL AND METHODS

Site description

The studies were performed in the Vrchslatina research site (48°38'50''N and 19°36'12''E) located at an altitude of 960 m a.s.l. belonging to the southernmost part of the Veporské vrchy massif, Central Slovakia. The site is located ca 10 km northeast of the town of Hriňová, the area belongs to the Kriváň Forest Enterprise, the Poľana Forest Unit. Long-term average of the annual amount of precipitation is about 900 mm, average temperature 6°C.

The bedrock is built of granodiorite covered with the soil classified as Cambisol (Humic, Eutric). The textural class of the fine earth fraction is qualified as sandy loam. Though the rock fragment content is relatively high (about 30–35 volume percent in the entire assessed soil profile), almost all rock fragments are in the fraction of fine gravel (0.2–0.6 cm) and so it does not influence the soil properties negatively. Values of pH measured in hydro suspension were between 5.1 and 5.4 and values measured in $CaCl_2$ extract were between 4.3 and 4.6 (gently decreasing towards the soil surface). The C/N ratio values (about 17 in the upper 10 cm of soil) indicate good quality of soil organic matter.

The site was covered prevailingly by groups of young forest stands which were exclusively composed of either beeches or spruces. The area of the young stand complex comprised about 0.7 hectare. Treeless patches among the groups of beeches or spruces were occupied by the grass community with bushgrass (*Calamagrostis epigejos*) as a dominant species. The young forest stands originated from natural regeneration and their age was around 14 years. More detailed descriptions of the site and forest stands are given in Konôpka et al. (2013a).

Tree measurements

At the beginning of the experiment, five circular plots were established in beech stands and another five plots in spruce stands. The radius of the plots varied between 70 and 100 cm, its size depended on stand density intending to include 30–50 trees. The trees on the plots were measured twice in 2011 – in March and November. Specifically, stem diameters on the ground level (diameter d_0 hereinafter) and tree heights were recorded. These measurements served to calculate some basic stand characteristics, i.e. number of trees per hectare, mean diameter and mean height, basal area (based on d_0).

During September 2011 we harvested 60 individuals of beech and 60 of spruce for determination of aboveground tree compartments. The sample trees were selected outside of circular plots and in such a way that they would represent the full range of tree sizes recorded in the stands. The sampled trees were cut according to specific compartments, i.e. stem and branches with foliage. The samples were transported to a laboratory. Here we measured stem diameter d_0, bark was separated from stems as well as foliage from branches. Then, stem, stem bark and foliage were oven dried (below 95°C for 48 h) and weighed to the nearest 0.1 g. These values were used for the construction of stand-specific allometric equations expressing stem mass (under- and overbark) and foliage mass using diameter d_0 as independent variable. The allometric equation (after logarithmic transformation) was as follows:

$$y = e^{(b_0 + b_1 \times \ln d_0)} \times \lambda \qquad (1)$$

where:

b_0, b_1 – regression coefficients,
d_0 – diameter,
λ – logarithmic bias.

A more detailed description of the procedure for the construction of this type of allometric relations was given for instance in Pajtík et al. (2008). Further, allometric relations expressing stem mass and data on diameter d_0 measured on the plots in March and November (i.e. diameter increments in the stands were considered) were combined to calculate stem mass production at the level of stands.

Foliage sampling

To conduct more detailed analyses of foliage, 40 trees of beech and spruce were selected so that 10 individuals always represented a specific biosociological position (i.e. dominant, subdominant, codominant, and suppressed). On each selected beech, 9 samples of foliage were taken, always 3 samples from the upper, middle and lower part of the tree crown. Sampling in spruce differed from that in beech. Since the spruces had five needle age classes, starting from 2007, each of them had to be included in the sampling. Thus, 3 samples (comprised of 10 needles) were taken not only with regard to the vertical profile but also by the age class. Therefore, 15 samples were taken from each selected spruce. Besides that, the selected spruces were used to determine a contribution of each age class to the total needle mass. Thus, we cut separately specific needle classes, dried and weighed them to establish dry masses.

Individual samples of foliage were scanned and consequently their one-sided projected areas (leaf areas hereinafter) were measured by the Leaf Area Measurement software to the nearest 0.1 mm². Then, the foliage was oven dried (85°C for 24 h) and weighed to the nearest 0.0001 g. Data on the area and weight of assimilatory organs were used to calculate SLA on a foliage level. Then, the values from 9 foliage samples were used to calculate average foliage area, mass and SLA. By means of a logarithmically transformed allometric equation SLA on a tree level was determined based on diameter d_0. Using the allometric relations for foliage mass and SLA, the total leaf area of the crown was expressed as follows:

$$\mathrm{LA} = m \times \mathrm{SLA} \qquad (2)$$

where:

LA – leaf area in beech,
m – mass of leaves,
SLA – specific leaf area.

While only one model was necessary for beech, five models (specific for each needle age class) had to be constructed for spruce needles. The final model of total leaf area in the crown was calculated by means of an allometric relation for SLA of each needle age class and mass proportion of each needle set in the total needle biomass using the equation:

$$\mathrm{LA} = \sum_{1}^{p} \mathrm{LA}_k = \sum_{1}^{p} (m \times P_k \times \mathrm{SLA}_k) \qquad (3)$$

where:

LA – leaf area in beech,
k – 1st, 2nd, ..., 5th – needle age class,
m – mass of leaves,
P_k – contribution of specific needle age class to the total needle biomass,
SLA – specific leaf area.

Fine root sampling

Besides studies on aboveground tree parts in beech and spruce, we focused on the quantity and morphological properties of fine roots (up to 1 mm in diameter). Therefore in April 2011 we collected 15 soil cores of both beech and spruce stands.

The soil cores were collected randomly all over the stands avoiding the areas of circular plots. We used a metal auger with the inner diameter of 7 cm, penetrating the soil environment to the depth of 50 cm. In fact, we did not include any deeper soil layers because our previous studies showed that there were only few fine roots at the depth of 40–50 cm (Konôpka et al. 2013b).

The soil cores were put into plastic bags and transported to a laboratory. The samples were deep-freezer stored until further processing. Later defrosted samples were spread on a plastic pad and live fine roots of beech and spruce were separated from the soil. The fine roots were carefully washed and ca 1/5 of them was scanned.

The images were analysed by the WinRHIZO program (Regent Instruments, Quebec, Canada). The output of the analysis showed these fine root parameters: average root diameter, total length, number of branchings, surface area, number of root tips. Then, these morphological parameters were expressed as fine root mass or unit length.

Thus, we obtained: SRL, SDT, specific root weight (SRW; root mass per unit root volume), specific root surface (SRS; root surface per unit root mass), and specific branching density (SBD; number of branchings per unit root mass).

All fine roots were oven dried (85°C for 24 h) and weighed to the nearest 0.0001 g. The quantity and morphological features determined for the known space (i.e. the volume of sampled soil column – that was ca 550 cm^3) were also calculated per unit stand area.

Growth efficiency estimates and statistical analysis

Data on stem production and properties of foliage and/or fine roots (all results were expressed on the same area unit basis, specifically 1 m^2) were used for the calculation of GE in beech and spruce. Thus, GE was expressed as stem production per units of area or mass in foliage, further, per units of fine root mass, fine root surface, and per million root tips.

Since all allometric relations expressing tree compartments were linearized by means of logarithmic transformation, parameters of regression equations were calculated by the least-squares method. Logarithmic bias (λ) was estimated according to the method suggested by Marklund (1987). The Kruskal-Wallis test was used (on a 95% probability level) to test interspecies differences in tree and stand parameters, and the GEs. Statistical analyses were performed by the Statistica 10 (Statsoft, Tulsa, USA) program package.

RESULTS AND DISCUSSION

Stand development indices

The per-hectare number of trees in the beech stand in March 2011 was about 135,000 then in November 2011 it dropped to 125,000 (Table 1). An evident decrease in the number of trees was in spruce, from 134 to 98 thousand trees per hectare. This phenomenon relates most probably to a harsh competitive pressure for light in the spruce stand because the crowns caused more intensive shading than in the beech stand. After further comparisons of the stands we realized that the spruce stand had larger mean stem diameter d_0 but a reverse situation was for mean tree height. Similar values in both stands were in mean stem volume and stem base.

Table 1. The characteristics of beech and spruce stands as measured in March and November 2011 (means and standard deviations)

Stand characteristic	Beech		Spruce	
	March	November	March	November
Number of trees ($10^3 \cdot ha^{-1}$)	135 ± 10	125 ± 12	134 ± 10	98 ± 7
Mean tree height (cm)	253 ± 16	287 ± 22	164 ± 7	211 ± 5
Mean diameter d_0 (cm)	2.43 ± 0.09	2.66 ± 0.12	2.71 ± 0.12	3.23 ± 0.11
Mean stem volume (cm^3)	391 ± 36	501 ± 57	355 ± 34	647 ± 35
Basal area* ($m^2 \cdot ha^{-1}$)	62.9 ± 6.4	69.5 ± 7.0	75.7 ± 2.5	80.2 ± 4.6

*basal area calculated for diameter d_0, i.e. on the ground level

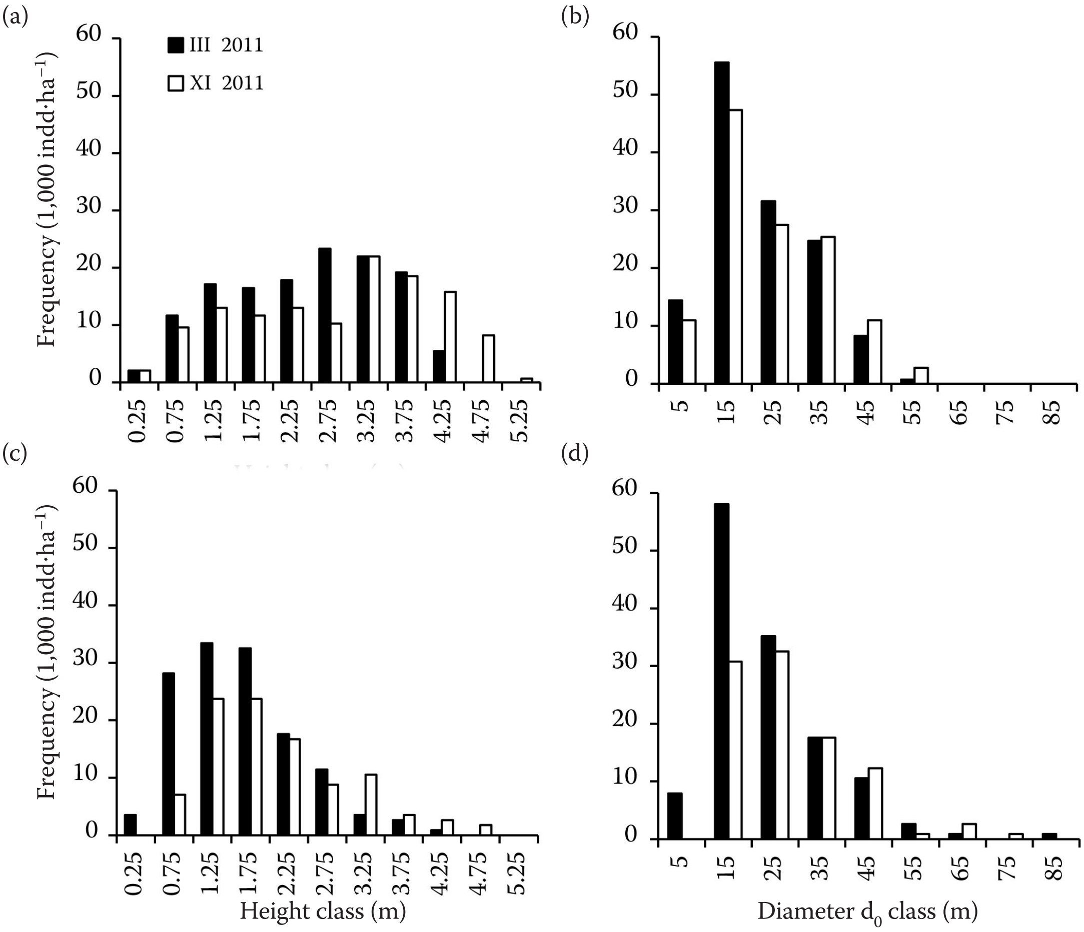

Fig. 1. Frequency diagram for tree heights (left plates) and stem diameter d_0 (right plates) in beech (upper plates) and spruce (lower plates)

As for the frequency distribution of tree heights, beech showed symmetric but spruce showed left-skewed distribution (Fig. 1a, b). In the case of diameter d_0, frequency distribution was left-skewed in both stands (Fig. 1c, d). In fact, the high density of trees (over 100 thousand per hectare) is common for this growth stage not only in spruce and beech but also it was previously recorded in full-canopy stands of sessile oak (see for instance Pajtík et al. 2008, 2011).

Allometry and growth efficiency on a tree level

Allometric relations for masses of stem (both over- and underbark) using diameter d_0 as an independent variable indicated large differences between the species (Fig. 2 and Table 2). The stems of beeches with specific diameter d_0 represented much larger mass in beech than in spruce. This difference relates to contrasting specific weights (see Pajtík et al. 2011), and also to a different ratio between height and diameter in these species; actually, this ratio was by 72% higher in beech than in spruce. Allometric equations expressing the mass of foliage brought opposite findings than in stem mass. It means that spruces with specific diameter d_0 had much larger foliage mass than beeches of the same diameter (Fig. 3 and Table 2). These allometric relations showed that the ratio of foliage mass to stem mass is dramatically higher in spruce than in beech. In general, allometric relations are missing for young growth stages of tree stands

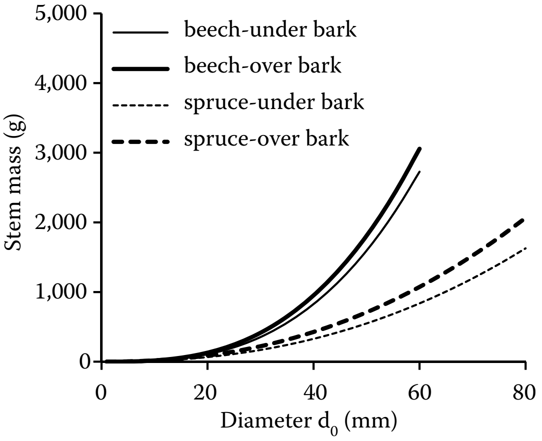

Fig. 2. Stem mass (under- and over-bark) in beech and spruce against stem diameter d_0

Table 2. Basic statistical characteristics for regression models expressing stem mass (under- and overbark) and foliage mass in beech and spruce with regard to stem diameter d_0

Species	Compartment	b_0 (S.E.) *P*	b_1 (S.E.) *P*	R^2	MSE	λ	S.D.
Beech	stem overbark	−3.800 (0.222) < 0.001	2.879 (0.070) < 0.001	0.965	0.076	1.038	0.297
	stem underbark	−4.184 (0.222) < 0.001	2.945 (0.070) < 0.001	0.967	0.076	1.038	0.296
	foliage	−6.576 (0.256) < 0.001	3.085 (0.081) < 0.001	0.960	0.102	1.047	0.308
Spruce	stem overbark	−2.369 (0.142) < 0.001	2.273 (0.045) < 0.001	0.970	0.077	1.042	0.348
	stem underbark	−2.775 (0.152) < 0.001	2.310 (0.048) < 0.001	0.967	0.089	1.048	0.369
	needles	−3.079 (0.171) < 0.001	2.432 (0.054) < 0.001	0.964	0.106	1.053	0.366

b_0, b_1 – regression coefficients with their standard errors (S.E.), R^2 – coefficient of determination, MSE – mean squared error, λ – logarithmic bias with its standard deviation (S.D.)

(Wirth et al. 2004). At the same time Pajtík et al. (2011) found that biomass allocation in European beech, sessile oak, Scots pine and Norway spruce changed most dramatically with stand development at the initial growth stages.

As it was mentioned in the Introduction section, while SLA is quite easily measurable in beech (just one – current year foliage set), a more complex situation is in spruce where each needle age class represents different properties. Thus, each needle age class had to be analysed individually, in fact, our spruce stand retained five needle sets. We found that proportions of the separate needle sets in total needle biomass did not change significantly with the tree size, i.e. in relation to diameter d_0. Hence, we could use for further calculations just average values of the needle set proportions for all trees. The proportions of needle sets were as follows: born in 2007 – 1.5%, 2008 – 10.3%, 2009 – 22.0%, 2010 – 31.6%, and 2011 (current year) – 34.6%. Statistical characteristics for regression relations expressing SLA in beech and spruce in relation to diameter d_0 are shown in Table 3. Here, SLA for spruce on a tree level was calculated as weighted average (weight was proportions of the individual needle sets in the total needle mass) of SLA in the specific needle sets. The results showed that SLA on a tree level decreased with the increasing tree size in both species, but more clearly in beech (Fig. 4). These findings indicated that morphological features of foliage depended on the tree size (and/or on the bio-sociological position in the stand) that in general would relate to light conditions. Our knowledge is in accordance with results of Closa et al. (2012), who studied a young beech stand whose shaded foliage had much higher values of SLA (between ca 250 to 470 cm^2 per gram of mass) than the foliage exposed to sunlight (150–180 cm^2·g^{-1}). For instance Milla et al. (2008) stated that large leaves tend to require higher biomass investment per unit leaf area than the small ones. Therefore SLA which is a cardinal trait for a plenty of physiological and ecological issues is dependent on the leaf size variation.

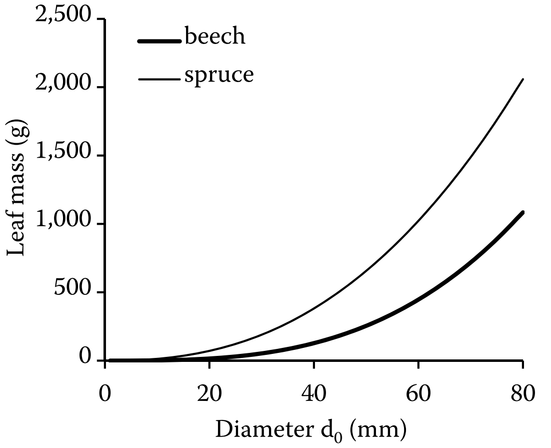

Fig. 3. Leaf mass in beech and spruce against stem diameter d_0

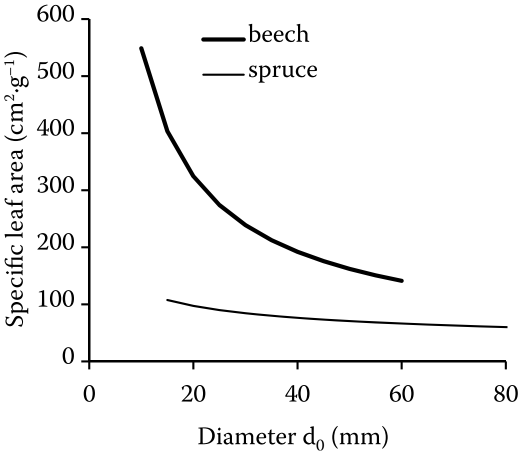

Fig 4. Specific leaf area in beech and spruce against stem diameter d_0

Table 3. Basic statistical characteristics for regression models expressing SLA in beech and spruce with regard to diameter d_0

Species and age class of foliage	b_0 (S.E.) P	b_1 (S.E.) P	R^2	MSE	λ	S.D.
Beech 2011	8.026 (0.110) < 0.001	−0.757 (0.033) < 0.001	0.816	0.051	1.026	0.239
Spruce 2007	4.890 (0.129) < 0.001	−0.242 (0.034) < 0.001	0.657	0.011	1.005	0.102
Spruce 2008	4.955 (0.119) < 0.001	−0.234 (0.031) < 0.001	0.672	0.009	1.004	0.097
Spruce 2009	5.179 (0.135) < 0.001	−0.263 (0.035) < 0.001	0.667	0.012	1.006	0.109
Spruce 2010	5.542 (0.187) < 0.001	−0.329 (0.049) < 0.001	0.629	0.022	1.011	0.150
Spruce 2011	6.036 (0.091) < 0.001	−0.427 (0.025) < 0.001	0.713	0.024	1.012	0.160

b_0, b_1 – regression coefficients with their standard errors (S.E.), R^2 – coefficient of determination, MSE – mean squared error, λ – logarithmic bias with its standard deviation (S.D.)

By combination of allometric models for foliage mass (Fig. 3) and for SLA (Fig. 4) a relationship between diameter d_0 and leaf area on a tree level was determined (Fig. 5). Interspecies comparisons showed that while the mass of foliage was much larger in spruce than in beech, the leaf area was nearly the same in both species. In the Czech Republic, allometric models for leaf mass and area of young beech and spruce trees were constructed by Kantor et al. (2009). However, the results are not compatible with ours, because they used diameter at breast height as an independent variable.

Further on a tree level, allometric relations for leaf area (Fig. 5) and for annual stem production (Fig. 6) were used to calculate GE according to diameter d_0 (Fig. 7). We found that GE was much higher in beech than in spruce. Thus, for instance GE in trees with diameter d_0 of 40 mm was 110 g of stem mass per 1 m^2 of foliage area in beech, but only 40 $g \cdot m^{-2}$ in spruce. At the same time, GE grew with the increasing tree size in both species. This situation is very probably related to contrasting levels of light availability in trees of different sizes (large trees receive more solar energy than the small ones). Therefore the unit area of foliage in suppressed (small) trees is able to produce less assimilates, consequently less woody mass, than that of dominant (large) trees. Similar findings were reported by Gspaltl et al. (2013) in a spruce pole-stage stand where GE increased with the stem volume. The authors showed the same phenomenon as our works that the sharpest change in GE rate with the tree size occurred among the smallest individuals (probably suppressed and co-dominant tree classes).

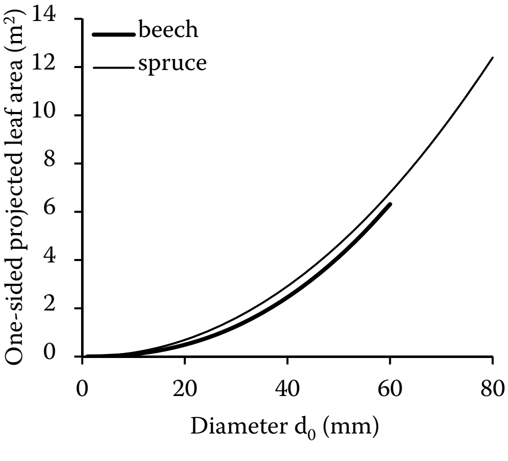

Fig. 5. One-sided projected leaf area in beech and spruce against stem diameter d_0

Growth efficiency on a stand level

Interspecies comparisons of morphological properties in fine roots indicated that beech roots are composed of a higher proportion of very thin fragments (average diameter was twice smaller in beech than in spruce; Table 4). Besides that, fine roots of beech were more frequently branched with denser occupancy of

Table 4. Morphological features in beech and spruce fine roots (means and standard deviations)

Species	Mean diameter (mm)	SRW (10^3 $g \cdot m^{-3}$)	SRL ($m \cdot g^{-1}$)	SRS (10^3 $m^2 \cdot g^{-1}$)	SDT (10^3 $tips \cdot g^{-1}$)	SBD (10^3 $branches \cdot g^{-1}$)
Beech	0.21 ± 0.01	388 ± 19	75.25 ± 2.38	47.32 ± 0.87	47.22 ±1.83	66.58 ± 2.08
Spruce	0.46 ± 0.02*	335 ± 15	19.60 ± 1.59*	30.71 ± 3.73*	8.69 ± 0.49*	9.77 ± 0.61*

*significant interspecies differences (Kruskal-Wallis test; α = 0.95), SRW – specific root weight, SRL – specific root length, SRS – specific root surface, SDT – specific density of root tips, SBD – specific branching density

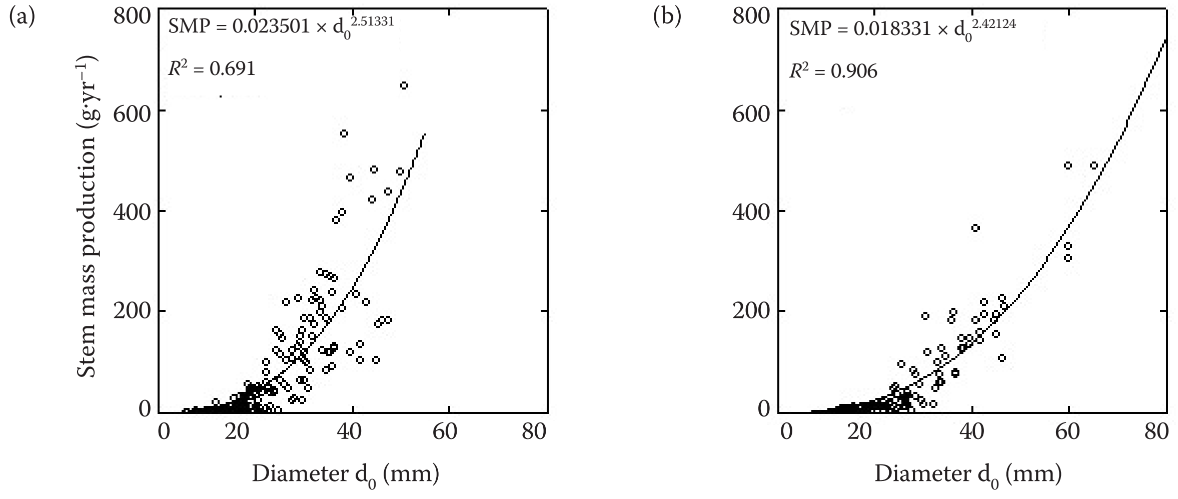

Fig. 6. Annual production of stem mass underbark in beech (a) and spruce (b) against stem diameter d_0

tips. Hence, fine roots of beech represented a four times larger surface area (that relates to the absorption potential) on a mass base in comparison with spruce. Similar results were presented by Ostonen et al. (2012), who compared SRL of fine roots in beech and spruce originating from a variety of countries using the latitude as an independent variable. They found that SRL was between two- and threefold larger in beech than in spruce. These results might suggest that beech needs a less quantity of fine roots for the production of a certain amount of stem mass than spruce. This would be applicable in case that we omit the role of hyphae of ectomycorrhizal fungi for the absorption of water and nutrients from the soil. Our results from the same stands proved that the standing stock of hyphae was much larger in spruce than in beech. It means that the "handicap" of morphological properties of fine roots in spruce might be compensated by the hyphae.

Further, we expressed standing stocks of stem biomass, foliage and fine roots as well as leaf area, surface area of fine roots and number of root tips per unit area (m^2) of stand. Moreover, the production of stem mass per 1 m^2 of stand was calculated (Table 5). While the standing stock of stem biomass was higher in beech, an opposite situation was in foliage. Standing stocks of fine roots were very similar in both stands. On the other hand, while beech stands had a larger surface area of fine roots than spruce stands, an opposite situation was in foliage area. Higher stem mass production was estimated in beech than in spruce stand.

Data on stem production in combination with characteristics of foliage and fine roots (Table 5) were used for determination of GE. At the same time, stem production was expressed per both unit mass and area of foliage and fine roots. Further, stem production was linked to the number of root tips. GE calculated on a variety of bases is given in Table 6. GE based on the mass and also area of foliage was higher in the beech stand than in the spruce stand. This phenomenon might relate to

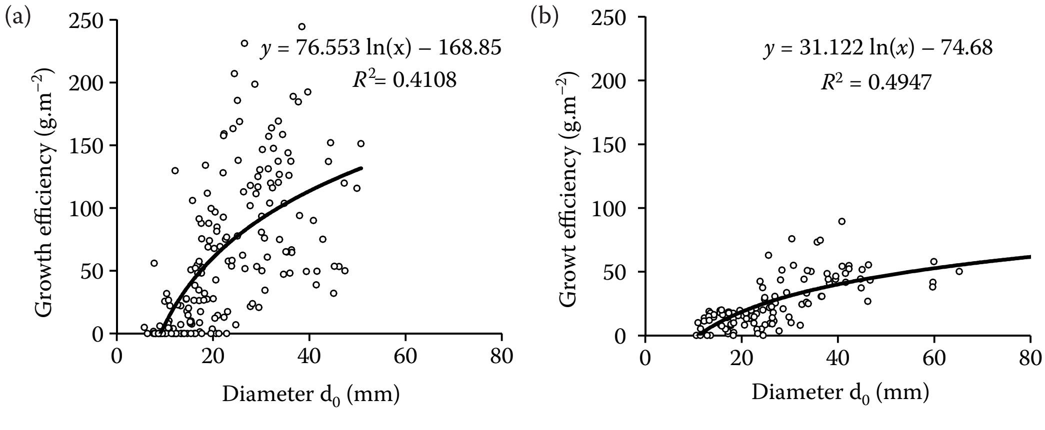

Fig. 7. Growth efficiency expressed as annual production of stems underbark per foliage unit area in beech (a) and spruce (b) against stem diameter d_0

Table 5. Quantitative characteristics of stems and foliage in beech and spruce expressed per square meter of stand area (means ± standard deviations)

Characteristics	Beech	Spruce
Standing stock of stems overbark ($g \cdot m^{-2}$)	4 476 ± 496	3142 ± 178*
Standing stock of stems underbark ($g \cdot m^{-2}$)	3 856 ± 437	2431 ± 139*
Standing stock of foliage ($g \cdot m^{-2}$)	603 ± 77	2626 ± 151*
Standing stock of fine roots ($g \cdot m^{-2}$)	494 ± 95	402 ± 82
Area of foliage ($m \cdot m^{-2}$)	12.77 ± 1.40	18.64 ± 1.08*
Surface area of fine roots ($m^2 \cdot m^{-2}$)	23.42 ± 5.31	12.30 ± 3.29*
Number of root tips (10^6 indd$\cdot m^{-2}$)	33.12 ± 10.02	4.18 ± 1.19*
Production of stems overbark ($g \cdot m^{-2} \cdot yr^{-1}$)	1 011 ± 131	714 ± 53*
Production of stems underbark ($g \cdot m^{-2} \cdot yr^{-1}$)	887 ± 116	572 ± 42*

*significant interspecies differences (Kruskal-Wallis test; $\alpha = 0.95$)

Table 6. Growth efficiency in beech and spruce stands as production of stems underbark expressed as a variety of foliage and fine root parameters (means ± standard deviations)

Growth efficiency based on	Beech	Spruce
Foliage mass ($g \cdot g^{-1}$)	1.47 ± 0.10	0.22 ± 0.01*
Foliage area ($g \cdot m^{-2}$)	69.46 ± 4.20	30.69 ± 1.11*
Fine root mass ($g \cdot g^{-1}$)	1.80 ± 0.73	1.42 ± 0.40
Surface of fine roots ($g \cdot m^{-2}$)	37.90 ± 8.94	46.51 ± 12.70
Number of root tips ($g \cdot 10^{-6}$ tips)	26.88 ± 3.85	143.00 ± 15.42*

*significant interspecies differences (Kruskal-Wallis test; $\alpha = 0.95$)

contrasting ages in leaves and needles. While beech bears only current-year leaves, needles retained in spruce crowns were between 1- and 5-years old. According to results of Kayama et al. (2007) photosynthetic rates decreased continuously with needle senescence. Moreover, the assimilatory system of spruce in comparison with that of beech might endure more intensive shading (both among the whorls and among tree individuals), it means less light energy reaching the foliage surface in spruce than in beech if expressed per unit area.

As for GE expressed as the fine root mass, a higher value was found out in beech than in spruce, however, a reverse situation occurred for GE calculated as the fine root surface. The largest interspecies differences in GE, namely in favour of spruce, were revealed if the number of root tips was used as a base. However, as it was mentioned above, we found the much larger mass of hyphae in the spruce stand than in the beech stand. We assume that the hyphae of ectomycorrhizal fungi would enhance GE as calculated per fine root unit surface and/or per number of root tips (it is related to the enlarged surface area of the root system by means of hyphae; e.g. Bolan 1991). Hence, we can anticipate that while beech is characterized by better morphological properties of fine roots for the acquisition of resources, spruce fine roots might enhance their absorptive capability thanks to the intensive association with ectomycorrhizal fungi.

Jack et al. (2002) pointed out that so far interspecies comparisons of GE of forest trees were missing; that kind of information would help to elucidate ecological demands and growth strategies of trees. Therefore, we assume that our results will help to understand these phenomena in terms of stem, foliage and fine root development in young full-canopy stands of beech and spruce.

CONCLUSIONS

Comparative studies in young stands proved that beech in comparison with spruce allocated much more biomass to the stem than to foliage. On the other hand, both tree species had similar values of foliage area that was related to higher SLA in beech than in spruce. Standing stocks of fine roots were similar in both stands, however, we found significant interspecies differences in fine root morphology. Beech fine roots were thinner and more intensively branched with higher density of root tips than spruce fine roots. GE expressed as annual stem production per unit area of foliage was much higher in beech than in spruce. GE in both species increased with the tree size. The phenomenon probably relates to light availability to the crown of trees which is determined by a biosociological position in the stand. If GE was expressed as fine root mass, the values were higher in beech; an opposite situation occurred if GE was calculated as the fine root surface area. The largest interspecies differences (more than fivefold in favour of spruce) were revealed for GE expressed as the number of roots tips. We assume that in the case of GE based on fine root parameters (especially on surface area and number of root tips) interspecies differences might relate, besides other factors, also to the status of mycorrhizal fungi associated with the tree species. The results of this work might contribute to the knowledge useful for instance in process modelling in beech and spruce of young growth stages.

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5.3 Ohryz jeleňou zverou a potravinový potenciál

Modelovanie potravinového potenciálu pre jeleniu zver. Prípadová štúdia z mladých postkalamitných porastov jarabiny vtáčej

Abstrakt

Vŕba rakytová *(Salix caprea L.)* a jarabina vtáčia *(Sorbus aucuparia L.)* sú dreviny, ktoré sú obľúbenou potravou mnohých bylinožravcov vrátane jeleňa lesného. Obidve dreviny by mohli byť považované za vhodného biologického regulátora pri zmierňovaní škôd na hospodársky cenných druhoch drevín. Naše výskumné aktivity sa zamerali na postkalamitné územie, ktoré vzniklo po víchrici v TANAP-e. Skúmali sme zožrateľnú biomasu, konkrétne terminálne výhonky, konáre, listy a kôru kmeňa v mladých porastoch rakyty a jarabiny. Zostrojili sme regresné modely na výpočet zožrateľnej biomasy na úrovni stromu. Tie zahŕňajú jednotlivé stromové komponenty ako aj skupiny komponentov zlúčených podľa ročného obdobia, kedy sú dostupné pre jeleniu zver (tzv. zimný a letný ohryz). Pri rakyte je maximálny potravinový potenciál 251 g a 361 g pre zimný, resp. letný ohryz pre jednotlivé stromy s hrúbkou na báze kmeňa d_0 do 40 mm. V prípade jarabiny je maximálny potravinový potenciál 315 g, resp. 322 g pre zimný a letný ohryz vypočítaný pre jedince s d_0 do 80 mm. Potravinový potenciál bol nižší pre jarabinu ako pre rakytu pri stromoch s hrúbkou d_0 do 50 mm. Opačná situácia platí pre hrubšie stromy. V budúcnosti by mohol byť modelovaný potravinový potenciál zahrnutý do odvodenia potravinovej kapacity biotopu pre jeleniu zver.

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Modelling forage potential for red deer: A case study in post-disturbance young stands of rowan

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Abstract. Recently, the red deer (*Cervus elaphus*) population has increased considerably and caused serious damage in forest stands in Slovakia as well as in other Central-European countries. Rowan (*Sorbus aucuparia* L.) is the tree species that is most intensively browsed and stripped by deer, especially during young stages of tree development. Our research focuses on estimating rowan mass consumption by red deer in young stands which developed after large-scale wind disturbance that occurred in the Tatra National Park in 2004. New models were developed for estimating the mass of tree components that are potentially edible by red deer using tree-base diameter as an independent variable. The results showed that the mass contribution of particular tree components to accessible deer forage depended on tree size (tree-base diameter). At stand level, total forage potential increased with an increase in tree size. However, whereas the quantity of bark available for stripping increased with tree size, the total mass accessible for browsing (leader shoot and branches with foliage) decreased. For instance, the contribution of stem bark to total forage potential in stands with a mean tree-base diameter of 20 mm and 50 mm was 15% and 50%, respectively. Theoretically, if all tree mass potential is consumed by red deer, young rowan stands (considering tree coverage of 50%) growing within an area of 100 m^2 might provide sufficient forage for one adult deer for ca. 10 days. It is suggested that rowan species should not be removed from forest stands in territories with a high deer population in order to decrease the potential damage of other, commercially important, tree species.

Keywords *Cervus elaphus, Sorbus aucuparia,* browsing, bark stripping, feed potential.

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Introduction

In general, the presence of red deer (*Cervus elaphus*) as one of the most common, large-intermediate feeding herbivores in forested areas cause conflicts between forestry interests and wildlife management because the species produce intensive damage to forest stands due to browsing and bark stripping (Gill 1992). For instance in Slovakia, the degree of forests damaged by game is significant and can be attributed to red deer over-population. Estimates of the red deer population in 2000 was approximately 33,000, whereas the estimated population in 2010 was as high as 51,000 (Bučko et al. 2011). Repeated selective browsing by red dear not only delays forest regeneration, but also dramatically alters tree species composition (e.g. Motta 2003). Bark stripping causes a reduction in stem increment (Vasiliasukas 2001) and often results in biological damage, since de-barked stems are highly susceptible to pathogenic fungi (Kiffner et al. 2008).

In addition to browsing woody vegetation - i.e. foliage, small twigs and bark, red deer graze grasslands. The proportion of these two forage resources, browsing and grazing, depend, on the properties of the habitat (Trdan & Vidrih 2008). Renaud et al. (2003) suggested that the red deer is a selective herbivore for which food selection is determined not only by preferences associated with quality and taste, but also by the cost or effort of obtaining forage. For red deer grasses and low lying branches are the most easily accessible forage components. Therefore, it is assumed that young forest stands distributed over large-scale post-disturbance areas would be considered very attractive sites for obtaining forage, the young trees with branches situated close to the ground, easily accessible to red deer with patches of grass for resting and comfort behaviour (e.g. lying, ruminating and self-grooming). Such conditions exist in the marginal foothills of the High Tatra Mountains within the protective zone of the Tatra National Park, Slovakia. On the 19th of November 2004 a storm destroyed large areas of spruce-dominated forest in this region. In the subsequent two or three consecutive years, broken and uprooted trees were harvested and both natural regeneration and artificial reforestation occurred simultaneously. In addition to Norway spruce (*Picea abies*), prevailingly pioneer tree species such as rowan (*Sorbus aucuparia)*, white birch (*Betula pendula*), and sallow (*Salix caprea*) regenerated naturally within the affected area. In fact, Šebeň (2010) showed that nearly 21% of natural regeneration (expressed as the number of tree bases) in the post-disturbance area was comprised of rowan. Recently, serious game derived forest damage caused by red deer in young rowan stands in the Tatra National Park was reported (Kaštier & Bučko 2011).

Rowan is a native species distributed throughout Europe with the exception of southern Europe. According to the Atlas of Woody Plants (Pagan & Randuška 1987), rowan is a relatively rare tree species within Slovakia but however, it is present almost throughout the entire country (ranging from an altitude of 300 m to the tree line located ca 1,600 m and in a few isolated cases, up to 2,010 m a.s.l.). Rowan is a pioneer species and does not usually form typical even-aged and homogeneous stands. For example, the species is a stable component of mountain spruce complexes of *Sorbeto-Piceetum*, a forest type determined by Zlatník (1976), which is predominantly located at altitudes of between 1,250 and 1,550 m a.s.l. The commercial importance of rowan wood is low because of its growth characteristics (i.e. stem shape, stem forking, multi-stem growth and other wood properties). An ecological advantage of this species are the modest demands for nutrients and water, which make it able to colonise unfavourable sites, where the foliage litter of rowan subsequently improves soil properties (Myking et al. 2013). Even though the species is somewhat rare, a high abundance can be found in young stands of mixed coniferous-broadleaves species. Usually, multiple rowan trees develop post-disturbance events due to its rapid regeneration and growth; in such cases, the species can spread over large areas with rowan fruits widely distributed by birds (Paulsen & Högstedt 2002).

In terms of the intensity of game derived forest damage, rowan is one of the most frequently affected tree species. This is supported by data from the Slovak National Forest Inventory (NFI 2005-2006, unpubl. data), which indicates that more than 15% of rowan trees, expressed per unit area, were damaged due to game browsing (the mean intensity of game damage for all tree species was 2.8%). The most intensively damaged rowan trees were recorded at young growth stages, where nearly half of the trees were browsed or stripped. Similarly, Myking et al. (2013) showed that rowan and sallow were the preferred winter forage of red deer and moose in the Scandinavian Peninsula. In Germany, Eiberle & Bucher (1989) identified that rowan is an attractive food species for game and its local presence reduced browsing damage to commercial trees such as *Fagus sylvatica, Picea abies* and *Abies alba*. Thus, rowan is a suitable species to control game derived forest damage in young forest stands (see also Čermák et al. 2009). On the other hand, breakage of rowan by red deer can severely decrease the regeneration capacity of forest stands in *Sorbeto-Piceetum* stands (Heroldová et al. 2003).

The general aim of the paper is to analyse the red deer feeding and forage potential in rowan trees. Research was conducted im post-disturbance areas from the protected zone of the Tatra National Park. The specific objectives of this study were: (i) to quantify consumed tree biomass (leader shoot, branch, foliage browsing and bark) and (ii) to estimate the amount of forage potential for game, mainly red deer, in young rowan stands, at the branch, tree and stand level. To fulfil the aims, a procedure was developed to estimate consumed and potentially edible rowan biomass by red deer. The procedure is novel without having any analogy in the existing scientific papers. Also we consider that the procedure can be used in other forest tree species, in any region, with red deer presence.

Material and methods

Overview of site conditions

The total area of the Tatra National Park is nearly 74,000 ha, of which almost 21,000 ha is protected. The mountains show unique glacier features and the largest number of endemic species in the Carpathians. Moreover, the Tatra Mountains contain the highest summits of the Carpathian range, with 17 peaks over 2,500 m a.s.l. The prevailing forest soils are cambisols and podzols and the bedrock is predominantly formed of granodiorit. The climate is characterised by low mean annual temperatures (around 4.0°C), high precipitation (nearly 1,000 mm) and 140 days of snow cover (Vološčuk et al. 1994). The fauna in the National Park is abundant, particularly the diversity of birds and mammals. The red deer is the most frequent ungulate species and inhabits almost the entire area of the National Park, ranging from the low altitudes, adjacent to agricultural land, to the tree line, dominated by dwarf pine (*Pinus mugo*) (Vološčuk et al. 1994).

This study focuses on post-disturbance sites that were created during a significant, intense storm in 19 November 2004, wich destroyed a total of 12,000 ha of Norway spruce dominated forest within the Tatra National Park (Koreň 2005). The storm mostly affected intermediate and lower altitudes forests of the National Park, including the foothills and basin of the High Tatra Mountains. Approximately 10,000 ha of the destroyed area represented a relatively uninterrupted forest belt that extended 35 km long and 5 km wide, situated at an altitudinal range between approximately 700 and 1,400 m a.s.l. (Šebeň 2010). This storm event created some of the most significant forest damage in the history of Slovakia and was certainly the most destructive storm disaster documented within the Tatra National Park.

To quantify game consumption (almost exclusively by red deer) and forage-potential in rowan stands, field data was collected during the growing season in 2012. During that year, the post-disturbance areas were covered by young forest stands that originated mostly from natural regeneration with some areas artificially reforested between 2006 and 2008. Open areas among the young forest stands were dominated by grasses, herbs and shrubs, with a predominance of *Epilobium angustifolium, Calamagrostis* sp., *Avenella flexuosa*, *Luzula luzoloides, Senecio nemorensis, Rubus idaeus, Vaccinium myrtillus* mixed with other species (Máliš et al. 2013).

Data collection

Rowan stands were randomly selected from forest management plans (FMP) database in post-disturbance areas in the High Tatra region and young stands with minimum rowan tree species composition of 30% were identified. Field survey in the Tatra National Park within the target area (around 3.000 ha) with high proportions of rowan indicated more or less four different sub-areas typical with certain prevailing mean heights of stands. To cover entire range of tree heights of young rowan stands, 5 tree clusters in each sub-area were randomly selected (subareas A, B, C, D hereinafter). Further, 20 circle plots were established for detailed rowan measurements. The radius of the plots varied between 1.0–3.0 m depending on the stand density and included a minimum of 30 individual rowan trees. The plots were established among groups of trees where rowans dominated (90% of the tree species composition). Each tree in the plot was measured for height (*h*), stem diameter at 130 cm from the ground (*dbh*) and stem base diameter at ground level (diameter d_0 hereafter). In addition, game browsing, defined as leader shoot, branch with foliage browsing or bark stripping, was recorded. For leader shoot and branch browsing, the diameter at the browsing point and its distance from the ground were recorded. For bark stripping, the size (area) and upper and lower distance from the ground was recorded. In total, we measured over 800 rowan trees in all the plots. On each plot, canopy coverage (based on rowan tree crown projection) was estimated visually.

In addition to the circular plots, 90 sample trees with a diameter d_0 between 5 and 80 mm were selected to proportionally represent the entire range of stem diameters observed in the study area. The entire above-ground biomass was harvested and transported to the laboratory, where tree height and diameter (*dbh* and diameter d_0) were measured. Particular tree components (foliage, branches, bark and under-bark stem) were separated and packed into paper bags. Simultaneously, foliage and branches were divided into two groups: those that could potentially be consumed by red deer (within 0–200 cm from ground level and with a diameter of branches up to 1.0 cm) (Konôpka et al. 2012) and the rest, which was not accessible to red deer. For bark-stripping potential, the same 90 sample trees were used. All bark on the stems was considered from ground level to a height of 180 cm (e.g. Konôpka et al. 2012).

The samples were dried to constant weight in an oven at 95°C and were weighed to the nearest 0.05 g. The data was used to construct allometric equations for tree component masses using tree height and diameter d_0 as independent variables. A detailed description of the construction of models for tree components using allometric equations has previously been documented (Pajtík et al. 2008, Konôpka et al. 2010).

To obtain empiric material for constructing regression relationships between consumed dry mass (branch without foliage and branch with foliage) and diameter of the branch base, approximately 100 samples of excised branches with a base diameter up to 10 mm were randomly selected and used for modelling constraints.

Data analysis

Estimates of tree biomass were performed at three levels: branch level (BL), tree level (TL) and stand level (SL).

Edible mass (B_e) at the BL was estimated separately for two categories: branch without foliage (B_{eb}) and branches with foliage (B_{eb+ef}), using the diameter of branch at the broken point using the equations:

$$B_{eb}(BL) = b_1 d_b^{b_2} \tag{1a}$$

$$B_{eb+ef}(BL) = b_1 d_b^{b_2} \tag{1b}$$

where: d_b - the branch diameter at the point of breakage (independent variable); b_1, b_2 - regression coefficients to be estimated.

A regression equation of the same type was also used to estimate the specific surface mass of bark (w_s) based on the diameter d_0:

$$w_s = b_1 d_0^{b_2} \tag{2}$$

Allometric equations for the calculation of the dry mass of specific tree components were constructed for two independent variables: diameter d_0 and/or tree height (h). Since the tree diameter d_0 is not a conventional characteristic in growth modelling studies, curves were constructed to convert diameter d_0 to *dbh* and tree height.

Then, equations including diameter d_0 in the following form were used for the construction of models for all tree components, specifically stem (B_s), branches (B_b), and foliage (B_f):

$$B(TL) = e^{\left(b_1 + b_2 \ln d_0\right)} \cdot \lambda \tag{3}$$

where: b_1, b_2 - regression coefficients; λ - correction coefficient.

Edible dry mass (B_e) at the TL was quantified separately for the particular components; branches, foliage, leader shoot and stem bark. The potential edible branch mass (B_{eb}) and foliage mass (B_{ef}) was calculated following the allometric equation related to branch mass (B_b) and foliage mass (B_f), the following equation was used:

$$B_e(TL) = B \cdot r \tag{4}$$

where: r (r_b and r_f) is the proportion of edible branch and foliage mass related to the total branch and foliage mass.

This proportion was calculated from the dry mass weight of both edible and non-edible branch fractions for each sampled tree.

Beta regression (Ferrari & Cribari-Neto 2004) was used to model the proportion of the tree mass consumed by red deer, with the diameter d_0 used as an independent variable. This type of regression is used for modelling continuous variables and assumes that values are in standard unit intervals e.g. rates, proportions or concentration indices. The beta regression model is defined as:

$$g(\mu_i) = x_i^{\mathrm{T}}\beta = \eta_i$$

where $\beta = (\beta_1, ..., \beta_k)^{\mathrm{T}}$ is a $k \times 1$ vector of unknown regression parameters; $x_i = (x_{i1}, ..., x_{ik})^{\mathrm{T}}$ are independent variables or covariates and η_i is a linear predictor (i.e. $\eta_i = \beta_1 x_{i1} + ... + \beta_k x_{ik}$), and finally $g(.): (0,1)$ is a link function. In this study, the following link functions were tested: logit $\exp(X \cdot \beta)/[1 + \exp(X \cdot \beta)]$, complementary loglog: $1 - \exp[-\exp(X \cdot \beta)]$, log: $\exp(X \cdot \beta)$ and Cauchy: $1/2 + \operatorname{atan}(X \cdot \beta)/\mathrm{pi}$.

To identify the link function that best explains the variability and shape of data distribution, the AIC criterion (Akaike 1974) was used. From this comparison, complementary loglog was identified as the best for these data and was subsequently selected for modelling:

$$r = 1 - exp(-exp(b_1 + b_2 \cdot d_0)) \tag{5}$$

where r is the proportion of edible mass previously defined in equation (4). To model the edible part of the stem (i.e. leader shoot), it was assumed that the maximum distance from ground level for browsing is 200 cm and the maximum diameter d_0 is 1.0 cm after measurements for European ash (*Fraxinus excelsior)* and rowan plots (Konôpka et al. 2012). This means that for trees with a diameter d_0 lower than 1.0 cm, the entire dry stem mass can be consumed by red deer. Thus, in such trees, edible stem potential equates to the dry stem mass calculated using the allometric equation. Alternatively, if the diameter d_0 is greater than 1.0 cm, the amount of edible dry stem mass does not increase with stem diameter d_0. It is assumed that stem volume for trees with d_0 equal to 1.0 cm is approximately the same as the volume of leader shoot with the same diameter at the point of breakage by a red deer i.e.:

$$B_{es}(TL) = B_s(TL) \tag{6}$$

for $d_0 \leq 10$ mm

$$\text{or } B_{es}(TL) = B_{s(10)}(TL) = 21.17 \text{ g}, \tag{7}$$

where $B_{s(10)}$ is the dry stem mass from a thickness of 10 mm to the top for $10 < d_0 < 16.4$ mm (this diameter is approximately equivalent to a tree height of around 2 m).

To model the edible dry mass of tree bark, it is assumed that red deer do not strip trees with a diameter d_0 under 2.0 cm and that the maximum height of bark stripping is 180 cm from the ground as in the previous measurements in *F. excelsior* and rowan plots (Konôpka et al. 2012). First, the specific surface mass of bark (w_s) was estimated based on the diameter d_0 using equation (2).

The dry mass of edible stem bark (B_{ebark}) was then calculated for the individual sampled trees as:

$$B_{ebark}(TL) = S \cdot w_s \tag{8}$$

where: S - the area of edible bark; w_s - specific surface area of bark.

To calculate S, the equation for expressing the surface area of a blunted cone (frustum) with a radius of base $r_{0.0}$, radius of upper side $r_{1.8}$ and height of 180 cm was implemented. Edible dry mass of bark for each sample was calculated using equation (8). A point cloud, created by pairing the diameter d_0 with the dry mass of each sample, was fitted by the regression function (1), where the only independent variable is diameter d_0:

$$B_{ebark}(TL) = b_1 d_0^{b_2} \text{, for } d_0 \geq 20 \text{ mm} \tag{9}$$

where b_1, b_2 are regression coefficients.

Equation (9) was used to estimate potential edible dry mass of bark only. In the case of estimating the currently consumed dry mass of bark equation (8) is used, in which S denotes the surface of the browsed area of bark.

The models were implemented for the 20 research plots to calculate the dry mass for leader shoot, branches, foliage, bark and all combined components actually consumed by red deer. Moreover, the models were used to estimate the forage potential or edible biomass of leader shoot, branches, foliage, bark and all combined components on the SL. Both actual forage consumed and forage potential per 100 m^2 were calculated, considering consistent rowan coverage (canopy projection) of 50%. For this model, a regression function (using method of least squares) that accurately approximate the empiric values measured for the plots was identified and from amongst the functions that were tested, the following functions were best suited:

For dry mass of edible foliage:

$$B_{ef}(SL) = b_1 d_{m0}^2 + b_2 d_{m0} \tag{10}$$

For dry mass of edible branches:

$$B_{eb}(SL) = \frac{d_{m0}^2}{b_1 d_{m0}^2 + b_2 d_{m0} + b_3} \tag{11}$$

For dry mass of edible leader shoot (modified from Warren 1980, Warren & MacWilliam 1981):

$$B_{es}(SL) = d_{m0}^{b_1} e^{b_2 d_{m0}} \tag{12}$$

For dry mass of edible bark:

$$B_{ebark}(SL) = b_1 d_{m0} + b_2 \tag{13}$$

For dry mass of all edible parts:

$$B_{etot}(SL) = b_1 d_{m0}^{b_2} \tag{14}$$

Schematic explanations of procedures for the estimation of consumed biomass and the construction of models to estimate edible biomass in rowan trees and stands are available in Supp. Info. I, II.

Regression models were constructed and all statistical analyses were performed in the Statistica 10.0 program and R program (R Development Core Team, 2012). The regression functions with parameter estimates and goodness-of-fit are expressed by the coefficient of determination (R^2) and are presented for each model.

Results

The mean tree diameter d_{m0} of the measured rowan stands varied between 5.1 and 45.5 mm and the mean tree height varied between 31 and 467 cm (Table 1). A high variability amongst the plots was also recorded for number of trees per hectare, approximately 11,000 to 66,000 individuals. Most plots with a high mean diameter (especially plot numbers 11–20) were composed not only of trees close to the mean size (i.e. height over 300 cm) but also by much smaller individuals. This means that there is the potential for trees within plots to be suitable for both branch browsing (small trees)

Table 1 Characteristics of the research plots in the rowan stands (average values ± standard deviation)

Subarea (A-D)	Plot number	Radius (m)	Coverage (%)	Tree density (10^3 pcs.ha^{-1})	Mean diameter d_{m0} (mm)	Mean height (cm)	Top height (cm)
A	1	3.0	10	20.5	5.1 ± 2.1	31.1 ± 12.6	40.4
	2	3.0	10	19.6	8.9 ± 3.7	72.9 ± 30.0	91.6
	3	2.0	35	66.0	10.6 ± 4.2	132.7 ± 58.4	168.8
	4	2.0	35	50.1	14.2 ± 4.8	152.3 ± 46.7	183.6
	5	2.0	20	29.4	15.4 ± 4.4	123.0 ± 39.4	154.7
B	6	1.4	75	60.1	21.8 ± 8.3	297.4 ± 76.1	340.7
	7	2.0	30	33.4	22.4 ± 11.8	274.3 ± 129.9	315.6
	8	1.5	35	43.9	22.5 ± 11.8	290.2 ± 111.4	313.3
	9	1.5	50	60.8	23.9 ± 15.1	306.6 ± 192.6	334.2
	10	2.0	75	45.4	23.6 ± 8.9	318.4 ± 90.7	375.5
C	11	1.2	85	75.2	23.1 ± 11.0	362.2 ± 153.5	406.4
	12	1.5	80	59.4	27.2 ± 12.3	369.9 ± 115.0	411.3
	13	1.5	50	35.4	27.6 ± 16.8	373.2 ± 176.7	402.0
	14	2.0	65	34.2	27.7 ± 10.1	365.3 ± 101.3	424.4
	15	3.0	20	11.3	36.7 ± 13.8	410.1 ± 103.4	456.7
D	16	1.3	85	52.7	36.0 ± 18.2	439.6 ± 199.7	506.7
	17	2.0	80	32.6	37.7 ± 14.8	464.3 ± 112.8	523.1
	18	2.0	60	23.1	40.6 ± 14.3	466.6 ± 108.9	525.8
	19	1.5	50	21.2	44.6 ± 14.8	430.7 ± 78.3	480.0
	20	1.0	75	25.5	45.5 ± 11.9	441.7 ± 59.7	475.0

Note. Top height represents the mean value from the 20% of the tallest trees in the stands.

and bark stripping (large trees).

Regression modelling on BL showed a high correlation between diameter at branch base and dry branch mass (Fig. 1a and Table 2), and eventually branches including foliage mass (Fig. 1b, Table 2). This indicates that the models are suitable for estimating missing or browsed branches via measurements of diameter at the browsing point. The sum of browsed branches provides a reasonable estimate for consumed dry mass of branches (winter season) or branches with foliage (growing season). At the same time, the models indicated that dry mass of branches prevailed slightly over that of foliage in young rowan trees. A close relation ship was also found between specific surface mass and diameter d_0 (Fig. 2). Here, the specific surface mass of bark of the

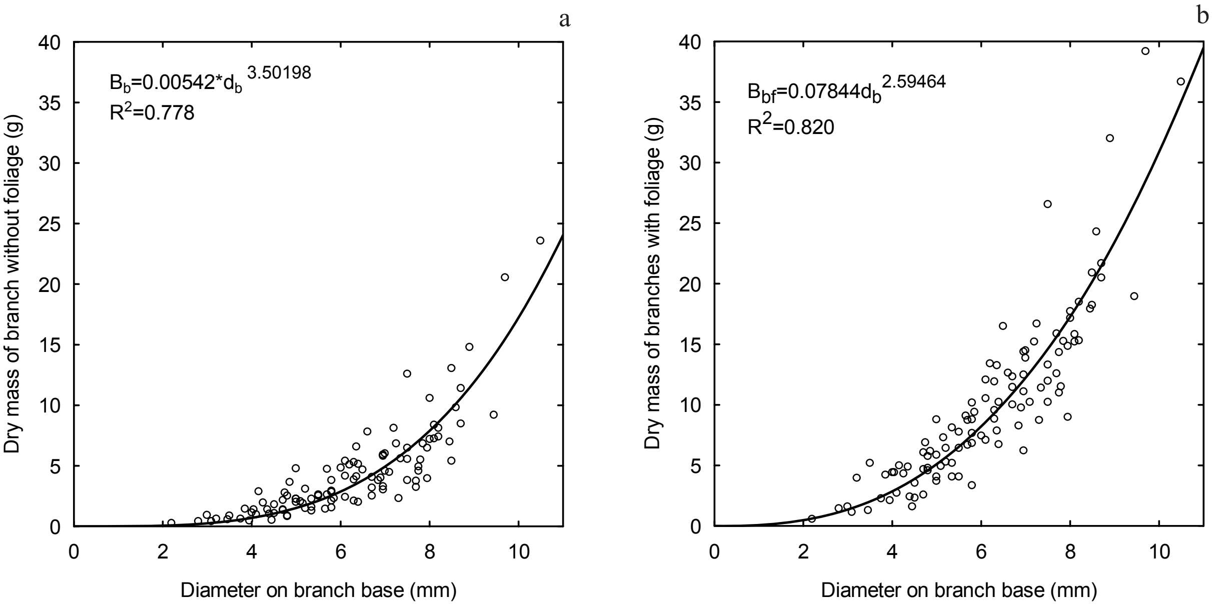

Figure 1 Dry mass of branches (a) without foliage and (b) with foliage compared to diameter at branch base

Table 2 Regression models for edible dry mass of branches (B_{eb}) and edible dry mass of branches with foliages (B_{eb+ef}) expressed on the branch level (*BL*), further, surface mass of bark (w_s), stem mass (B_s), branch mass (B_f), conversion coefficient for edible branch (r_b), conversion coefficient for edible foliage (r_f) and edible bark dry mass (B_{ebark}) expressed on the tree level (*TL*)

Eq.	Dependent variable	b_1 (SE) P	b_2 (SE) P	R^2	*MSE*	λ	*SD*
(1a)	B_{eb} (BL)	0.005 (0.002) <0.017	3.502 (0.195) <0.001	0.778	3.284		
(1b)	B_{eb+ef} (BL)	0.078 (0.021) <0.001	2.595 (0.132) <0.001	0.820	9.027		
(2)	w_s (TL)	1.253 (0.110) <0.001	0.398 (0.023) <0.001	0.789	0.439		
(3)	B_s (TL)	-2.515 (0.088) <0.001	2.412 (0.025) <0.001	0.990	0.028	1.014	0.171
	B_b (TL)	-7.336 (0.312) <0.001	3.334 (0.090) <0.001	0.943	0.280	1.138	0.596
	B_f (TL)	-3.383 (0.161) <0.001	2.237 (0.046) <0.001	0.962	0.096	1.047	0.322
(5)	r_b (TL)	2.411 (0.181) <0.001	-0.068 (0.005) <0.001	0.772	0.141		
	r_f (TL)	2.288 (0.226) <0.001	-0.073 (0.006) <0.001	0.635	0.163		
(9)	B_{ebark} (TL)	0.249 (0.066) <0.001	1.585 (0.064) <0.001	0.938	286.6		

Note. Abbreviations in the table captions means; b_1, b_2 - coefficients, *SE* - their standard errors, *P* - p-value, R^2 - coefficient of determination, *MSE* - mean square error, λ - logarithmic transformation bias, and *SD* - its standard deviation.

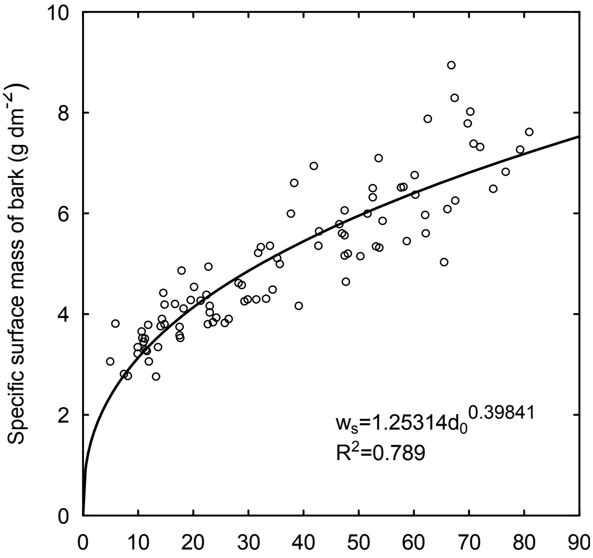

Figure 2 Specific surface mass of bark compared to tree diameter at stem base

largest observed trees was more than two times larger than that of the smallest trees. Since tree diameter d_0 is not a conventional tree characteristic used in growth studies, regression functions are included to convert the diameter d_0 to dbh and tree height (Fig. 3a, b).

The inventory of deer browsing on the 20 plots showed that whereas branch browsing was considered very frequent, bark stripping occurred sporadically (Table 3). In fact, all cases of bark stripping only occurred on plots with large trees, i.e. at plots located on the sub-areas C and D. The mean percentage of trees subjected to browsing when considering all plots was 80% (±18%). Here, both branches and leader shoot browsing were included in the analysis and this was typical for trees up to

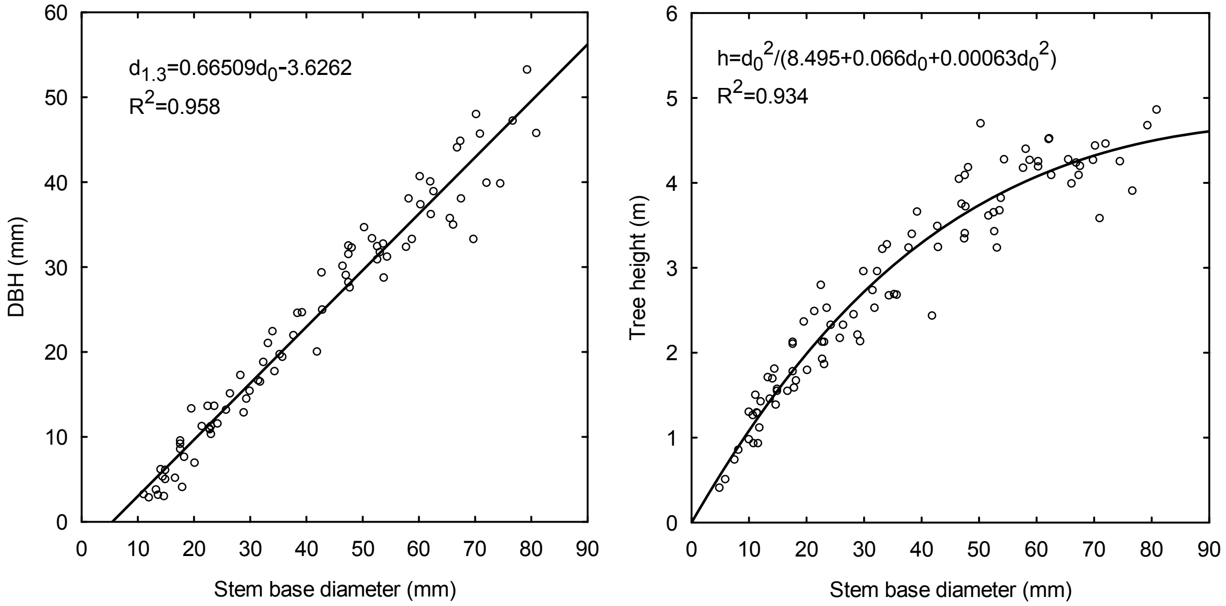

Figure 3 Estimations of tree diameter at breast height (a) and tree height (b) using tree base diameter as independent variable

Table 3 Characteristics of red deer browsing on rowan trees in the research plots. Data for branch browsing (including leader shoot) are in the white cells and for bark stripping in the grey cells.

Characteristics of tree damage by red deer	Mean	Standard deviation
Number of browsed branches per 100 m^2	1,323.0	1,219.0
Mean diameter of bases on browsed branches (mm)	3.3	0.5
Percentage of trees with browsing	80.0	18.0
Number of stripped areas per 100 m^2	19.0	31.0
Mean size of stripped areas (cm^2)	96.0	92.0
Percentage of trees with bark stripping	7.0	16.0

200 cm in height. As for bark stripping the percentage was 7% (±16%). These results might indicate that if the forest stand is composed of both small and large trees, red deer prefer easily accessible branches for browsing, instead of bark stripping.

For branch and leader shoot browsing, all cases identified were recorded from between 0 cm to nearly 270 cm from the ground (Fig. 4a). However, the maximum occurrence of the browsing was between 121 and 130 cm from the ground and browsing was considered frequent up to 200 cm from the ground but rarely at higher positions. Bark stripping occurred from the ground level to a height of ca 180 cm (Fig. 4b). Since bark stripping is characterized by one or more areas on the stem surface, the frequency of the lower and higher points are shown. The lowest point of stem de-barking was most frequent at a height between 41 and 60 cm from ground level, with the highest positions occurred between 101 and 120 cm.

A combination of models for branch with foliage (Fig. 1b) and bark dry mass and measurements on the plots relating to game browsing (Table 3) allowed an estimation of the dry mass of rowan trees consumed by red deer by browsing and bark stripping (Table 4). The results show that the average amount of branch dry mass consumed by deer was 2,931 g (±2,658 g) per 100 m^2. The average amount of bark stripped by deer was 101 g (±214 g) per

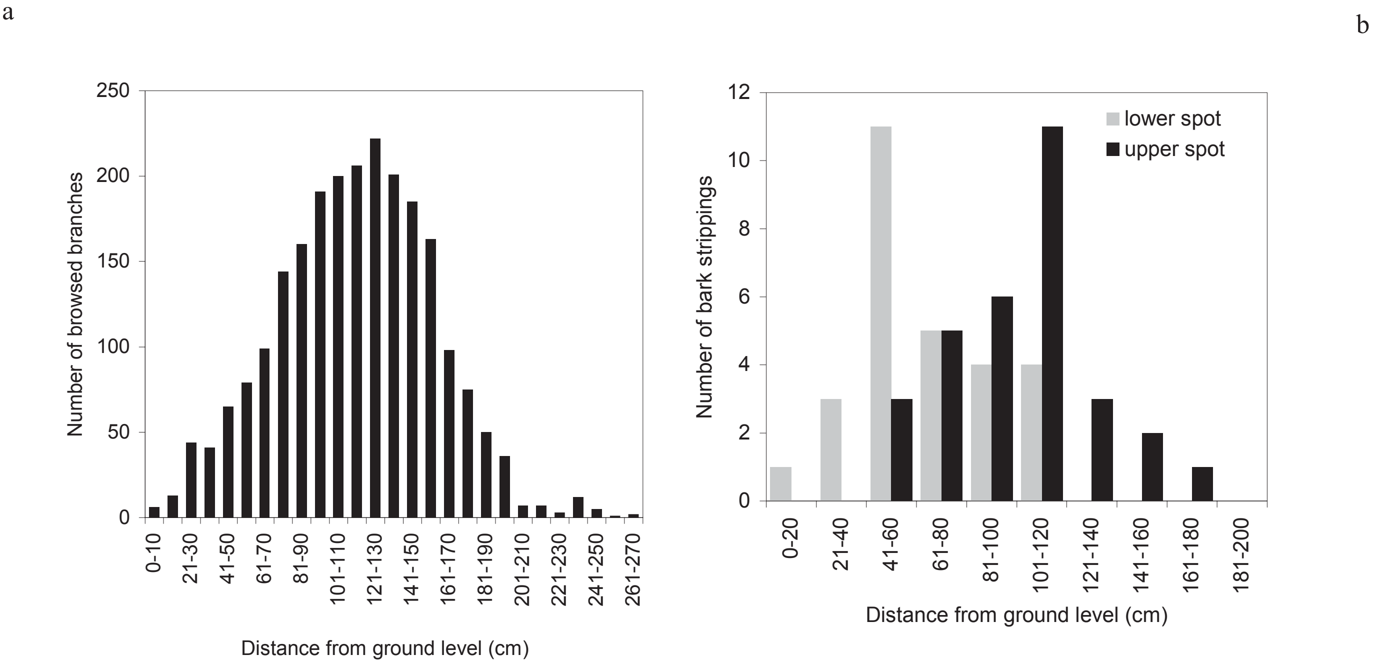

Figure 4 The number of browsed branches (a) and bark strippings (b) with regards to distance from the ground

Table 4 Summary of rowan tree dry mass consumed by red deer

Characteristics of dry mass consumed by red deer	Mean ± standard deviation	Minimum and maximum among plots
Total dry mass of branch browsing (g per 100 m^2) [A]	2,931 ± 2,658	93-10,617
Total dry mass of bark stripping (g per 100 m^2) [B]	101 ± 214	0-750
Sum of consumed dry mass (g per 100 m^2) [C = A + B]	3,033 ± 2,668	93-10,621
Percentage ratio of browsed branch dry mass to consumed dry mass [A/C]	96 ± 9	61-100

100 m^2. Thus, much more dry mass was consumed in form of branch browsing than bark stripping.

Models concerning rowan dry mass potentially edible by deer constructed on the TL showed specific tendencies for each tree component regarding tree size (Fig. 5 and Table 5. The edible dry mass of leader shoot increased concomitantly with tree size up to a diameter d_0 of ca. 10 mm and subsequently stabilised at a constant level (about 20 g) once a diameter of 20 mm (equal to a tree height of about 180 cm) was reached. Larger trees were not obviously damaged by red deer by browsing of the leader shoot. A significantly different result was found for bark, where no browsing was expected for trees with a diameter d_0 less than 20 mm. The result for potentially edible branches and foliage was similar; first increasing but later declining with increasing tree diameter. The maximum edible forage resource for red deer was trees with a diameter between about 35 mm and 50 mm for foliage and branches, respectively.

Modelling potential forage resources by tree components (at TL) on the 20 plots served as the basis for the construction of models on the SL, based on a rowan tree coverage (canopy projection) of 50% (Fig. 6 a–d) and the mean stand diameter d_0. The amount of edible dry mass varied between the particular components; while the modelled dry mass of branches and bark accessible to red deer increased together with mean stand diameter d_{m0}, it first increased then decreased for foliage and stem. The maximum estimates of dry mass of branch and bark was found for the largest rowan stand and reached about 17 and 23 kg per 100 m^2, respectively. In turn, the maximum estimated foliage dry mass of 11 kg per 100 m^2 and maximum leader shoot dry mass of 13 kg per 100 m^2 was observed for stands with a mean diameter d_{m0} of 27 mm and 10 mm, respectively.

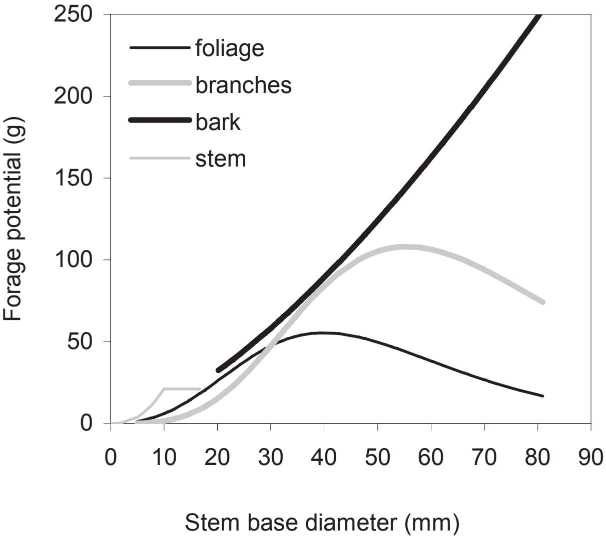

Figure 5 Dry mass of potential browsed items for red deer by tree components with respect to the diameter at stem base

The largest forage potential was estimated for bark and the smallest for foliage. However, in reality, bark is clearly not completely

Table 5 Regression models for edible dry mass of: foliages (B_{ef}), branches (B_{eb}), leader shoot (B_{es}), bark (B_{ebark}) and all parts together (B_{etot}) expressed on the stand level (SL)

Eq.	Dependent variable	b_1 (SE) P	b_2 (*SE*) P	b_3 (*SE*) *P*	R^2	*MSE*
(10)	B_{ef}(SL)	-0.014 (0.001) <0.001	0.790 (0.048) <0.001	-	0.607	2.500
(11)	B_{eb}(SL)	0.065 (0.033) 0.063	-1.261 (2.023) 0.541	48.952 (29.419) 0.114	0.902	2.934
(12)	B_{es} (SL)	2.075 (0.077) <0.001	-0.220 (0.014) <0.001	-	0.917	1.734
(13)	B_{ebark} (SL)	0.637 (0.055) <0.001	-8.925 (1.750) <0.001	-	0.912	3.097
(14)	B_{etot}(SL)	6.182 (1.574) <0.001	0.515 (0.075) <0.001	-	0.773	20.850

Note. Abbreviations in the table captions means; b_1, b_2 - coefficients, *SE* - their standard errors, *P* - p-value, R^2 - coefficient of determination, and *MSE* - mean square error.

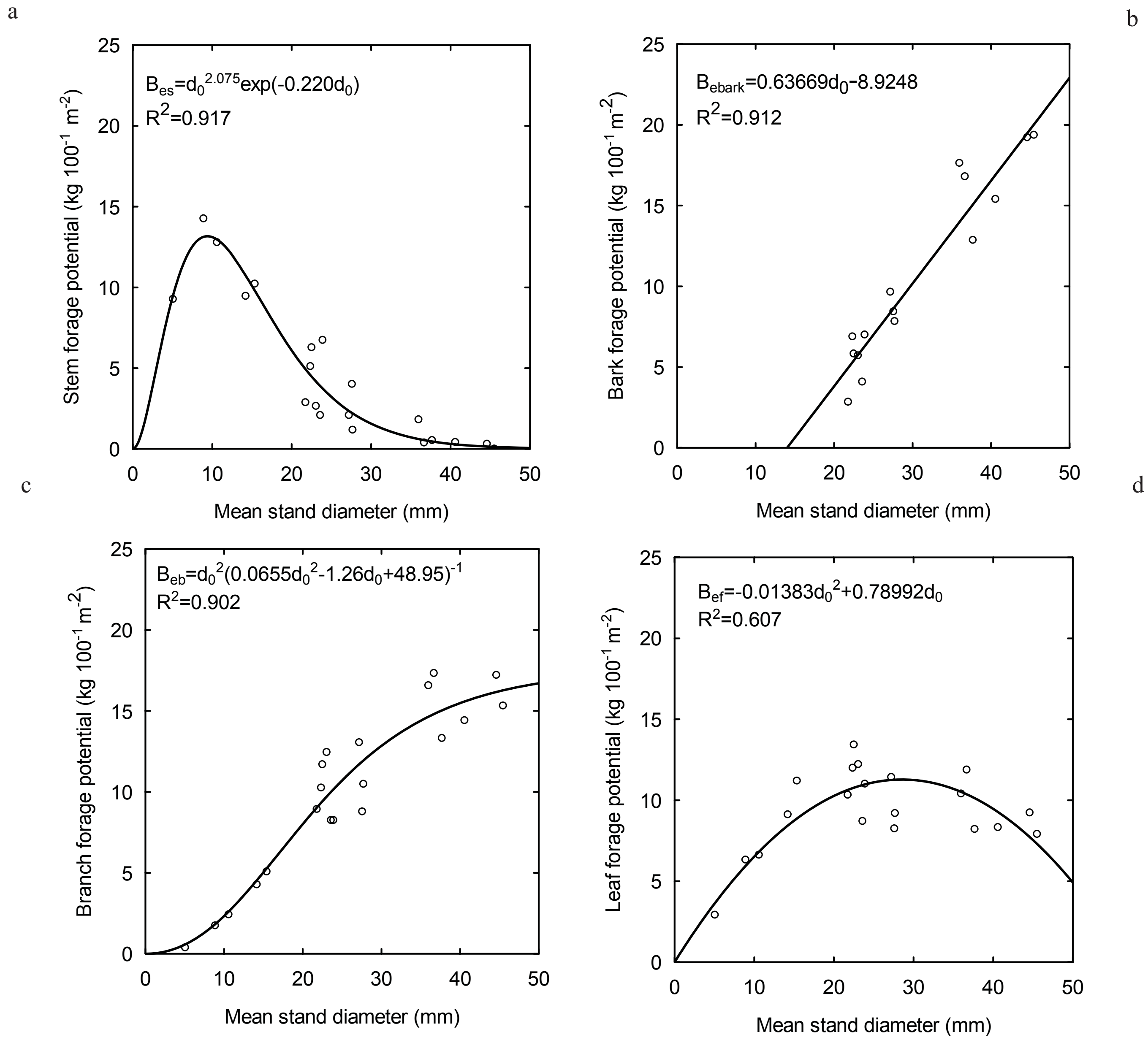

Figure 6 (a) Stem, (b) bark, (c) branch and (d) leaf forage potential for red deer with respect to mean stand diameter (measured on stem base). The model is constructed for rowan stands with a tree cover of 50%

surface-stripped by deer; therefore, the model probably overestimates the natural situation. Summing the models of all components resulted in a total forage potential on a rowan SL based on tree coverage of 50% (Fig. 7a). The model estimates ca. 45 kg of edible dry mass by red deer per 100 m^2 for a mean stand diameter d_{m0} of 50 mm. This figure is the maximum number which might be reached in exceptional conditions, for example, in a small isolated system such as a fenced area, without any other forage resources for the red deer. Our model shows that the contribution of the specific tree components to the total forage potential in a rowan stand depends on the mean stand diameter (Fig. 7b). The contribution of browsing potential decreased and the contribution of bark-stripping potential increased, with increasing stand size.

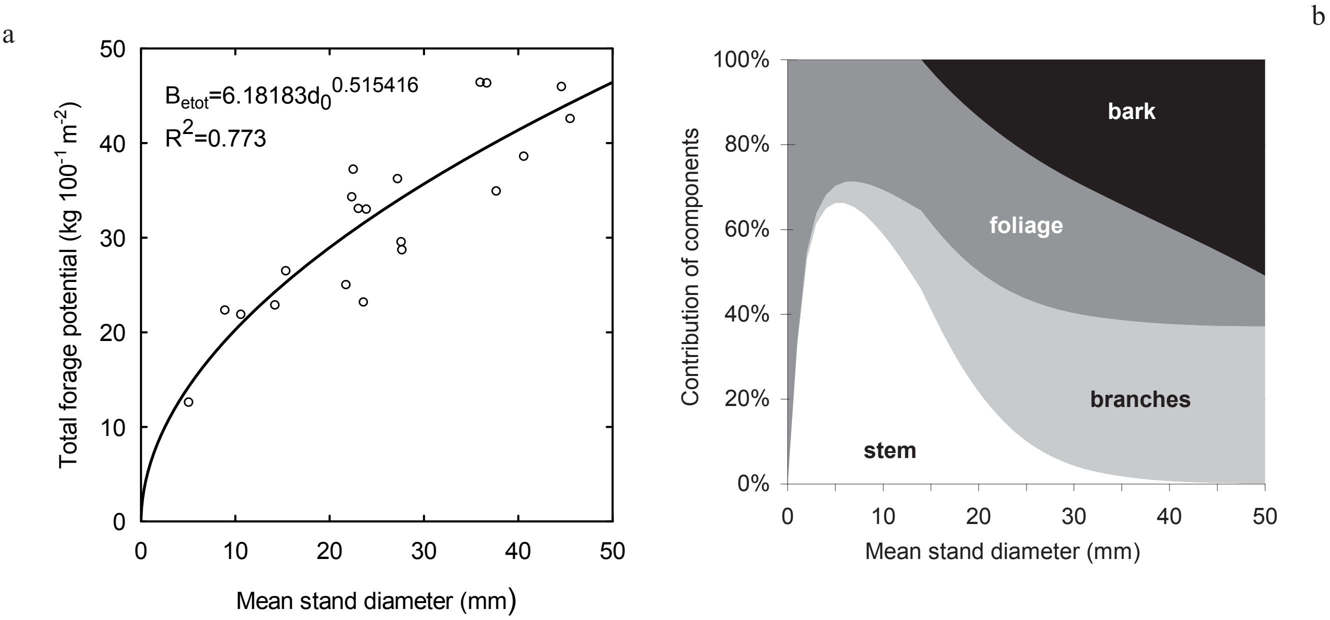

Figure 7 (a) Forage potential for red deer and (b) contribution of the particular tree components in rowan stands with respect to mean stand diameter (measured at the stem base). The model (a) is constructed for rowan stands with a tree cover of 50%

Discussion and conclusion

This survey of research plots indicates that a high proportion of rowan trees browsed by red deer in the form of leader shoot and branch browsing, so that in total, over three-quarters of individuals were affected. Conversely, bark stripping was found rare. It appears that red deer prefer rowan trees for forage, but for stands with a heterogeneous height structure, browsing small trees is preferred to bark stripping on larger trees. A study by Konôpka et al. (2012) performed on ash trees (*F. excelsior*), concluded that a higher proportion of stripped bark contributed to total tree biomass consumption compared to the results found for rowan in this study. However, the ash stands were more even-sized. Therefore, only a few branches in stands with a mean height over 4 m were accessible to the red deer. Konôpka et al. (2012) showed that whereas the dry mass of browsed branches predominated over that of stripped bark in ash trees with a diameter d_0 up to ca 50 mm, the opposite situation was observed for thicker trees.

However, browsing and stripping intensity highly depends on game density (Hörnberg 2001, Kiffner et al. 2008), the abundance of tree species and their nutrient content (e.g. Duncan et al. 1994, Čermák 1998), the site productivity of the biotope (Langbein 1997, Bergqvist 2014) as well as forest management (Bergqvist 2014, Edenius et al. 2014, Schulze et al. 2014). As for most areas of Slovakia, the High Tatra National Park has as a typically high population of red deer, due to its gradual increase in population size in the last decade; from approximatly 400 individuals in 2003 to nearly 700 in 2012 (Dr. Fleischer – personal communication). Regarding the abundance of rowan trees in the observed area, the species is one of the three most common species (together with *B. pendula* and *S. caprea*) in the naturally regenerated complexes (Šebeň 2010). For nutrient content in general, browsers prefers plants with a high nitrogen level and low fibre content (Danell et al. 1991). Unfortunately, no study that focused on the nutritional status in different components of rowan trees could be found although this type of analysis has previously been performed for foliage and branches of *F. excelsior* (Konôpka et al. 2012).

Previous studies (e.g. Padajga 1984) have shown that a high content of tree shoots in total red deer forage indicate that this tree component is sufficiently rich in nutrition and is often preferred to grasses. In habitats with frequently browsed tree species, woody plants form between about 40% (in the growing season) to ca. 90% (in the winter) of the red deer diet (Jamrozy 1980, Homolka 1990). In biotopes where woody plants were absent or rare, grasses predominated and composed of between 50% to 90% of the diet volume of red deer (Latham et al. 1999, Homolka & Heroldová 2001). In general, woody plants represent a significantly larger proportion of the red deer diet compared to other ungulate diets including that of roe deer (e.g. Prokešová 2004). If research had focused on nutritional conditions at the experimental sites, it might be assumed that red deer consume tree biomass more frequently than grazing. This is supported by the evidence observed over a relatively long period, nearly 5 months, of snow cover (Vološčuk et al. 1994). Moreover, in terms of light-tolerant herbs (especially *E. angustifolium* and *Calamagrostis* sp.), rapid growth occurs within post-disturbance areas, which are most probably not attractive for red deer grazing.

These results demonstrate that red deer browse branches of rowan from the ground level to a height of 200 cm and very rarely higher, with most frequent browsing occurring at heights of between 121 and 130 cm. Similar results were recorded for bark stripping, however, the maximum height was limited to 180 cm. Both browsing and bark stripping preferences of red deer probably relate to their body size. Red deer clearly browse shoots at the height of their shoulder (Renaud et al. 2001). For example, Hodge & Pepper (1998) observed that the most frequent browsing by red deer is up to a height of 180 cm. Konôpka et al. (2012) recorded frequent browsing on ash trees at heights of between 40 and 160 cm with an extreme upper limit of 260 cm. The same upper limit for bark stripping (ca 180 cm) as for rowan was also recorded for ash trees.

The results show that mean edible potential among all observed plots was 32 kg (composed of 10 kg of leader shoot, 12 kg of branches and 10 kg of foliage) per 100 m^2. The mean potential of strippable bark was about 3.0 kg per 100 m^2. Altogether, 35 kg of rowan dry mass per 100 m^2, potentially edible by red deer, was found in the studied area. Hell et al. (2000) showed that red deer require between 1.2 kg (calf) and 3.0 kg (adult) plant dry mass per day. Thus, 100 m^2 of young rowan stand can theoretically serve as a food resource for 10 days for one adult red deer, in case of the total browsing and stripping of all forage-potential. Thus, a single red deer requires seasonally minimum of 0.4 hectares of this type of forest stand (considering the standard tree crown coverage of 50%) for its diet. However, in our plot conditions, only 11.8% of edible dry mass (leader shoot, branches with foliage) and 1.2% of strippable dry mass (bark) was actually consumed by red deer.

Red deer can be considered as a selective consumer of tree biomass preferring rowan to other species which was supported by previous studies conducted in the territory of the Tatra National Park (Table 1 - Supp. Info III, modified data from Kaštier & Bučko 2011). Altogether nearly 4 000 young trees were inspected and categorised into five classes of game browsing: 0 – undamaged (no browsing), 1 – browsed branches, 2 – browsed stem, 3 – browsed branches and stem, 4 – whole tree intensively damaged by browsing. Rowan trees were the most frequently and also most intensively browsed species (Table 1 - Supp. Info. III). While only 5.0 % (± 1.0) of all spruce trees were damaged by game (all species together 29.2 %) as much as 72.9 % (± 2.6) of rowan trees were affected by browsing. Moreover, if we considered all damaged trees as a base, only 17.9 % (± 8.3) of spruce belonged to classes 3 and 4 (average for all species was 71.5 %). However, the proportion in rowan trees was as much as 83.1% (± 2.6) hence, the results clearly prove that rowan might represent a suitable biological control for mitigating forest damage by reducing browsing or economic damage to neighbouring commercial trees e.g. Norway spruce and Scots pine.

This study presents the initial step in achieving optimisation of different demands between interests of foresters and hunters (or wildlife management). We have shown that the novel procedure based on the regression models is applicable for quantification of consumed tree biomass as well as estimation of forage potential for game, mainly red deer, in young forest stands. In principle, this kind of modelling of forage potential would further serve for evaluation of carrying capacity of biotops for red deer and consequently for decision-making on regulation on population to avoid serious damage to commercial tree species in forest stands. However, to reach the final goal more specific, scientific knowledge is required. Specifically, forage potential has to be quantified, not only for main forest tree species (as we have done for rowan) but also for other plants, i.e. shrubs, grasses and herbs co-existing in the area. Moreover, exact information related to ’bearable’ branch browsing and bark stripping on commercial forest trees does not yet exist. Therefore, currently a threshold of branch and bark reduction that does not endanger interests (sufficient number of undamaged trees in each stand growth stages without implementing inadequately high costs for protection measures against game) of forest owners is unknown.

On the other hand, these results indicated that rowan, especially in young growth stages, can play a considerable role in enhancing carrying capacity of forest biotops for red deer. Therefore, traditional attitudes of foresters to the presence of rowan in forest stands should be re-evaluated. Rowan trees should be maintained preferably as young stands together with commercial trees species, which are attractive for red deer barking and stripping, for instance, silver fir, maple and ash. This might represent a suitable biological control for mitigating commercial forest damage. Moreover, foresters or hunters could establish and maintain specific browsing plots to entice deer from threatened stands with commercially valuable trees to stands with a high proportion of rowan trees. Here, rowan trees would preferably consist of different size trees for both browsing (height under ca 3 m), bark stripping and perhaps also for fruit consumption (those over 3 m in height).

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Supporting Information

The online version of the article includes the Supp. Info.

Supp. Info. I: Schematic for the procedure of estimating

Supp. Info. II: Schematic for the construction of a model

Supp. Info. III: Proportion of damaged trees by game (browsing)

Kvantifikácia zožrateľnej biomasy mladých stromov vŕby rakytovej a jarabiny vtáčej pre jeleniu zver. Odhady pomocou regresných modelov

Abstrakt

V poslednej dobe značne vzrástla populácia jelenej zveri a zapríčiňuje vážne škody na lesných porastoch na Slovensku, rovnako ako aj v iných krajinách strednej Európy. Jarabina vtáčia *(Sorbus aucuparia L.)* je jedným z druhov, ktoré sú najintenzívnejšie ohrýzané a lúpané jeleňou zverou, obzvlášť v ranných štádiách vývoja. Náš výskum sa zameral na vyhodnotenie biomasy jarabiny skonzumovanej jeleňou zverou v mladých porastoch, ktoré vznikli po veľkoplošnej disturbancii na území Tatranského národného parku v roku 2004. Vytvorili sme nové modely na výpočet biomasy jednotlivých komponentov stromu, ktoré sú potenciálne zožrateľné jeleňou zverou na základe hrúbky na báze kmeňa ako nezávislej premennej. Výsledky ukazujú, že podiel jednotlivých stromových komponentov, ktoré sú dostupné ako potrava pre jeleniu zver závisí od veľkosti stromu. Na úrovni porastu sa celkový potravinový potenciál zvyšuje s rastom strednej hrúbky porastu. Avšak, zatiaľ čo množstvo kôry dostupnej pri lúpaní narastá s veľkosťou stromu, celková biomasa prístupná pre odhryz (terminálne výhonky a konáre s listami) sa zmenšuje. Napríklad podiel kôry kmeňa na celkovom potravinovom potenciáli porastu s priemernou hrúbkou na báze kmeňa 20 mm bol 15 %, pri hrúbke 50 mm už dosahoval hodnotu 50 %. Teoreticky, ak by bol jeleňou zverou skonzumovaný celý potenciál zožrateľnej biomasy v mladých porastoch jarabiny (ak uvažujeme so zápojom porastu 50 %) rastúci na ploche 100 m^2, mohol by poskytnúť dostatok potravy pre jedného dospelého jeleňa na cca 10 dní. To naznačuje, že by sa jarabina nemala odstraňovať z lesných porastov na územiach s vysokou populáciou jelenej zveri, pretože svojou prítomnosťou znižuje riziko poškodenia iných, hospodársky dôležitých druhov drevín.

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Quantifying edible biomass on young Salix caprea and Sorbus aucuparia trees for Cervus elaphus: estimates by regression models

Quantifizierung der Biomasse von jungen Salweiden (Salix caprea) und Ebereschen (Sorbus aucuparia) die für Cervus elaphus genießbar ist: eine Bestimmung durch Regressionsmodelle

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Keywords: Red deer, Browsing, Forage potential, Goat willow, Rowan, Tree components

Schlagworte: Rothirsch, Verbiss, Äsungspotential, Salweide, Eberesche, Baumbestandteile

Abstract

Goat willow (*Salix caprea*) and rowan (*Sorbus aucuparia*) species are the preferred forage for large herbivores including red deer (*Cervus elaphus*). Both species could be considered as suitable biological control for mitigating damage to commercial tree species. Research activities focused on a post-disturbance area that originated after an intensive windstorm in the Tatra National Park (Slovakia). We estimated edible biomass specifically; leader shoot, branches, foliage and stem bark in young trees of willow and rowan. Regression models of edible biomass on a tree level were

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constructed. They covered forage by particular tree components as well as forage by groups of components associated with forage availability for deer in the winter and growing season. In willow, the maximum feed potential (251 g and 361 g for winter and growing season, respectively) were found for individuals with diameter at stem base d_0 of 41 mm. In rowan, the maximum feed potential (315 g and 322 g for winter and growing season, respectively) occurred for individuals with d_0 of 80 mm. The feed potential was lower in rowan than in willow for trees with d_0 up to 50 mm, and the opposite situation occurred in larger trees. In future, feed potential modelling could be implemented in evaluating the carrying capacity of biotopes for red deer.

Zusammenfassung

Sal-Weiden (*Salix caprea*) und Eberschen (*Sorbus aucuparia*) sind bevorzugte Äsungspflanzen für Großherbivoren einschließlich des Rothirsches (*Cervus elaphus*). Beide Baumarten können als geeignete biologische Kontrolle für die Verminderung von Wildschäden an kommerziellen Baumarten berücksichtigt werden. Die Forschungsaktivitäten fokussierten sich auf eine Schadfläche die durch einem intensiven Sturm im Nationalpark Tatra (Slowakei) entstanden ist. Wir bestimmten die vom Rothirsch verwertbare Biomasse, speziell Haupttriebe, Zweige, Belaubung und Stammrinde von jungen Salweiden und Ebereschen. Die Regressionmodelle für die vom Rothirsch verwertbare Biomasse wurden aufbauend auf ein Einzelbaumlevel erstellt. Sie berücksichtigten Äsungspflanzen durch einzelne Baumbestandteile ebenso wie Äsungspflanzen von Gruppen der Komponenten verbunden mit der Verfügbarkeit von Äsungspflanzen für Rothirsche im Winter und in der Wachstumsperiode. Für die Salweide betrug das maximale Äsungspotenzial 251 g im Winter und 361 g in der Wachstumsperiode für Individuen mit einem Durchmesser an der Stammbasis d_0 von 41 mm. Für die Eberesche war das maximale Äsungspotential 315 g im Winter und 322 g in der Wachstumsperiode für Individuen mit einem d_0 von 80 mm. Das Äsungspotential war geringer für Eberesche als für Salweide für Bäume mit einem d_0 kleiner als 50 mm, und das Gegenteil trat für größere Bäume ein. Zukünftig kann die Modellierung des Äsungspotenzials in die Auswertung der Tragfähigkeit von Biotopen für Rothirsche einfließen.

1. Introduction

Both goat willow (*Salix caprea*) and rowan (*Sorbus aucuparia*) are not considered important for commercial purposes due to their stem characteristics, especially their irregular shape, frequent forking, multi-stem formation and wood properties. However, they are common species types with modest ecological demands that allow them to occupy less desirable sites such as post-disturbance areas. Their presence improves soil conditions and micro-climate properties creating favorable conditions that promote the establishment of other tree species (Myking et al., 2013).

In Slovakia, the distribution of goat willow ranges from the lowlands to the mountainous regions, up to altitudes of between 1300 and 1400 m a.s.l. In contrast, rowan is also distributed from lowlands, up to very high altitudes of nearly 2,000 m a.s.l. (Pagan and Randuška, 1987). It is well documented (e.g. Shipley et al., 1998; Månson et al., 2007; Jager and Pastor, 2010; Finďo and Petráš, 2011; Myking et al., 2013) that goat willow and rowan together with aspen (*Populus tremula*) are tree species identified as the preferred forage for large herbivores including red deer (*Cervus elaphus*). Thus, as species identified as attractive for large herbivores (i.e. ungulate ruminating game), with good regeneration capacity and are fast growing; they can increase the carrying capacity of biotopes (hunting grounds). Therefore, their presence might reduce damage by ungulate ruminating game (biological control) to commercial trees (e.g. Čermák et al., 2009).

In European temperate forests, red deer is a largest herbivore with high forage (tree biomass) requirements for food, including leader shoot, branches, foliage and bark. Hell et al. (2000) showed that red deer consumed daily between 1.2 kg (calf) and 3.0 kg (adult) of biomass expressed as dry matter. Contribution of tree biomass depends on landscape characteristics. For example, Finďo et al. (1993) showed that for mountainous areas in Central Slovakia (specifically the Poľana Mts. and Sitno Mts.), biomass of forest trees represented as much as 79% of total forage. Similarly, Prokešová (2004) calculated that tree biomass contributed to 71% of total red deer feed in wetland forests in the southern part of Moravia (Czech Republic). For other region of the Czech Republic, Fišer and Lochman (1969) estimated a much lower share (between 6% and 29%) of red deer forage was allocated to tree biomass. However, this data came from landscapes with low proportions of forest covers. Composition of red deer feed also changes relative to seasonally and availability of particular forage, e.g. wood plants from 40% of total forage during the growing season to nearly 90% of total forage during the winter season (Jamrozy, 1980; Homolka, 1990).

Red deer can cause extensive damage to forest stands including damage to leader shoots (terminal part of stem), branch and foliage browsing and bark stripping (e.g. Heroldová et al., 2003; Kiffner et al., 2008; Čermák et al., 2009; Iszkulo et al., 2014 and others). However, there are not any studies detailing potential edible tree biomass by red deer using tree biomass models constructed by components for young (small) trees (such biomass models can be found in Wirth et al., 2004; Pajtík et al., 2008 and few others). So far, perhaps only one study by Konôpka et al. (2012) estimates forage resources in young trees, specifically in European ash (*Fraxinus excelsior*). This is a problem because there is an increase in red deer population in most of the countries in Central Europe (Milner et al., 2007). Red deer browsing in the forest creates not only economic loss but also, in some regions, ecological loss by threatening the biodiversity of biotopes (Schulze et al., 2014).

The aim of this paper is to construct models for the estimation of edible tree biomass (leader shoot, branches, foliage and bark) by red deer in young goat willow and rowan using regression models. Also, to analyze inert-specific differences in forage resources between goat willow and rowan and to compare these results to other broadleaved species in young growth stages.

2. Material and Methods

2.1. Site description

Research activities focused on a post-disturbance area that originated after an intensive windstorm on 19th November 2004 in the Tatra National Park (TNP, hereinafter). The disturbance affected approximately 12,000 ha of Norway spruce (*Picea abies*) dominated forest in the TNP (Koreň, 2005). The storm mostly damaged forests between low and intermediate altitudes (between 700 and 1,400 m a.s.l.) in the TNP with over 80% of all damaged trees located in a continual belt, approximately 35 km long and 5 km wide, oriented in a west-east direction (Šebeň, 2010). The forest soils consist mainly of cambisols and podzols and the bedrock is predominantly formed of granodiorit. The climate is characterized by low mean annual temperatures (around 4.0°C), high precipitation (nearly 1,000 mm) and 140 days of snow cover (Vološčuk et al. 1994). The fauna in the TNP is abundant, particularly the diversity of birds and mammals. The red deer is the most frequent ungulate species and inhabits almost the entire area of the TNP, ranging from the low altitudes, adjacent to agricultural land, to the tree line (Vološčuk et al. 1994). In 2014, density of red deer in the TNP was 16 per 1000 hectares. This means the population density has doubled during the last fifteen years (Dr. Peter Kaštier – pers. comm.).

During 2012 and 2013 (the eighth and ninth growing seasons post-disturbance), the areas were prevailingly covered by young forest that originated from both natural regeneration and planting. Pioneer broadleaved tree species such as goat willow, rowan and aspen natural regeneration prevailed over few coniferous species e.g. Norway spruce, Scots pine (*Pinus sylvestris*), European larch (*Larix decidua*) and silver fir (*Abies alba*; Šebeň, 2010). However, plantations of conifer species, including sycamore maple (*Acer pseudoplatanus*) were common. Open areas among the young forest stands were covered by grasses (e.g. *Calamagrostis* sp., *Avenella flexuosa*, *Luzula* *luzuloides*), herbs (e.g. *Epilobium angustifolium, Senecio nemoralis*) and shrubs (mostly *Rubus idaeus, Vaccinium myrtillus*).

2.2. Field and laboratory work

Filed work was performed in the territories of Smokovce, Tatranské Matliare and Vyšné Hagy which are all Protective Units and belong to the State Forests of the TNP. Preliminary, young forest stands were identified for potential sampling and were chosen in collaboration with employees at the State Forests of the TNP. Individual trees (100 trees of each species) of different dimensions covering height interval from cca 0.5 m to approx. 4.5 m were selected. The trees were selected from 14 forest stands with both willow and rowan trees present. The forest stands were located within the post-disturbance area between an altitudinal range of approx. 820 and 1040 m a.s.l. Another criterion for the selection of sampled trees was none (or negligible) damage caused by red deer browsing. However, this was challenging as most of the willow and rowan trees (approx. two thirds of all trees) in the stands were affected by browsing.

Each tree was cut by handsaw at the ground level and a code number was marked on the stem base using permanent marker. Tree height and diameter d_0 (at stem base) were measured. Foliage and branches were divided into two groups: potentially edible biomass and inedible (or unreachable) biomass for red deer. These two groups were defined in accordance to previous results (see also Konôpka et al., 2012). Specifically, branches situated above 2.0 m from the ground level and/or with a diameter exceeding 10 mm were inedible (unreachable). Branches and foliage were identified, cut by garden shears and packed separately into paper bags. Similarly, stems were also packed into bags. The stems were defined as a main axis of trees, including range from the ground level to the terminal point. Trees with a clear main stem were included in the analysis and we avoided multiple-stem individuals. All bags were labeled by code number and component specification, i.e. edible foliage and branches, inedible foliage and branches, stem with bark.

The bags containing the samples were transported to the laboratory. The stems were divided into approximately 50 cm-long sections and if trees were under 150 cm in height they were divided into three equal sections. Three diameters were measured on each section; the middle and the diameter at both ends. These measurements were used to calculate the surface of stem sequences. Stems were debarked and both bark and stem were packed separately. After few days, when foliage dropped from the branches, for each tree we separated and identified the following sub-compartments: edible foliage, edible branches, inedible foliage, inedible branches, bark (from stem) and debarked stem. The samples were oven-dried at temperatures below 95°C for five days and weighed at a precision of 0.1 g.

2.3. Calculations and constructions of models

The data measured on sample trees were used to construct allometric equations for tree compartments using stem diameter d_0 as an independent variable. Constructions of models for quantification of biomass in tree components were based on allometric relationships which are described in e.g. Pajtík et al. (2008) and Konôpka et al. (2010). More details on the procedure followed for the calculations and the construction of the models, including formulas 1-14, are given in Appendix 1.

Regression models were constructed and statistical analyses were performed in Statistica 10.0 and R (R Development Core Team 2012). The regression functions with parameter estimates and goodness of fit are expressed by the coefficient of determination and are presented for each model.

3. Results and discussion

Diameter d_0 of sampled goat willows is between 3.7 and 68.7 mm with a height ranges from 0.49 to 4.50 m (Table 1). As for rowan trees, diameters d_0 are between 5.0 and 81.0 mm and the height ranges from 0.41 up to 4.86 m (Table 2). Consumable biomass in willow ranges between 0.4 and 249 g for branches and from 0.8 to 186 g for foliage. Consumable biomass in rowan is between 0 and 325 g for branches and between 1.6 and 244 g for foliage. Since all allometric models are based on diameter d_0 (considered the best predictor for biomass estimates but not a common characteristic in forestry), the relationship between the diameter and tree height was expressed (Fig. 1a and 1b). The inter-specific comparison shows that rowan trees were slightly taller than willow trees with the same stem thickness (diameter d_0).

Table 1: Descriptive statistics for characteristics measured on the sample trees for goat willow

Characteristics	Mean	Median	Min.	Max.	Lower quartile	Upper quartile	Standard deviation	Standard error	Skewness
Diameter d_0 (mm)	25.0	22.6	3.7	68.7	14.6	33.3	13.2	1.3	1.023
Tree height (m)	2.04	2.03	0.49	4.50	1.38	2.37	0.85	0.08	0.806
Branch biomass (g)	106	43	0.4	1186	13	120	173	17	3.526
Biomass of edible branches (g)	55	38	0.4	249	13	74	54	5	1.367
Foliage biomass (g)	78	47	0.8	467	20	110	87	9	2.175
Biomass of edible foliage (g)	47	39	0.8	186	17	63	40	4	1.492
Biomass of stem underbark (g)	153	75	0.7	1258	20	160	240	24	3.100
Bark biomass on stem (g)	45	27	0.5	265	9	54	54	5	2.365

Table 2: Descriptive statistics for characteristics measured on the sample trees for rowan

Characteristics	Mean	Median	Min.	Max.	Lower quartile	Upper quartile	Standard deviation	Standard error	Skewness
Diameter d_0 (mm)	36.7	33.2	5.0	81.0	17.6	53.7	21.4	2.2	0.337
Tree height (m)	2.82	2.74	0.41	4.86	1.78	3.99	1.21	0.12	-0.116
Branch biomass (g)	293	103	0.5	2715	10	374	478	52	2.812
Biomass of edible branches (g)	51	30	0.0	325	7	82	62	6	2.299
Foliage biomass (g)	170	70	1.6	916	19	283	202	21	1.622
Biomass of edible foliage (g)	27	18	1.6	244	9	32	33	3	3.805
Biomass of stem underbark (g)	626	319	1.9	2749	59	1003	690	72	1.132
Bark biomass on stem (g)	117	74	1.3	419	23	190	111	11	0.908

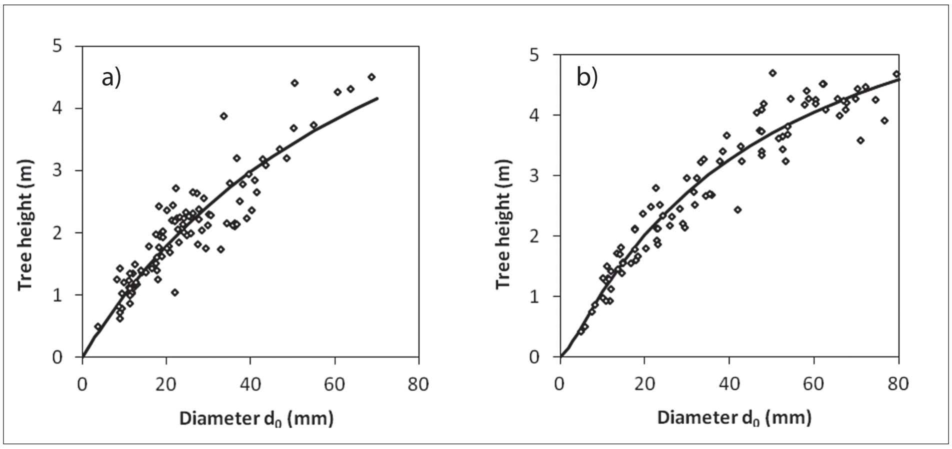

Fig. 1: Relationship between diameter d_0 and tree height in (a) goat willow and (b) rowan

The inter-specific differences between biomass of the specific tree components were relatively small (Fig. 2a and 2b, Table 3 and 4). The largest differences occurred for stems (without bark) e.g. trees with diameter d_0 of 60 mm recorded biomass values of 913 g in willow and 1369 g in rowan. For bark, trees with diameter d_0 of 60 mm, bark biomass of 222 g was recorded in willow and 239 g in rowan. At the same time, 60-mm-thick trees recorded branch biomass of 699 g and 629 g in willow and rowan, respectively, and further, retained 365 g of foliage on willow and 338 g of foliage on rowan. The willow and rowan trees show very similar bark biomass relative to similar stem surface and/or similar bark thickness. Our analyses suggest that bark thickness, or biomass quantity per stem surface unit did not differ considerably between the species (Fig. 3a versus Fig. 3b). For instance, specific surface masses of bark in trees with diameter d_0 of 60 mm were 6.7 $g.dm^{-2}$ and 6.4 $g.dm^{-2}$ in willow and rowan, respectively.

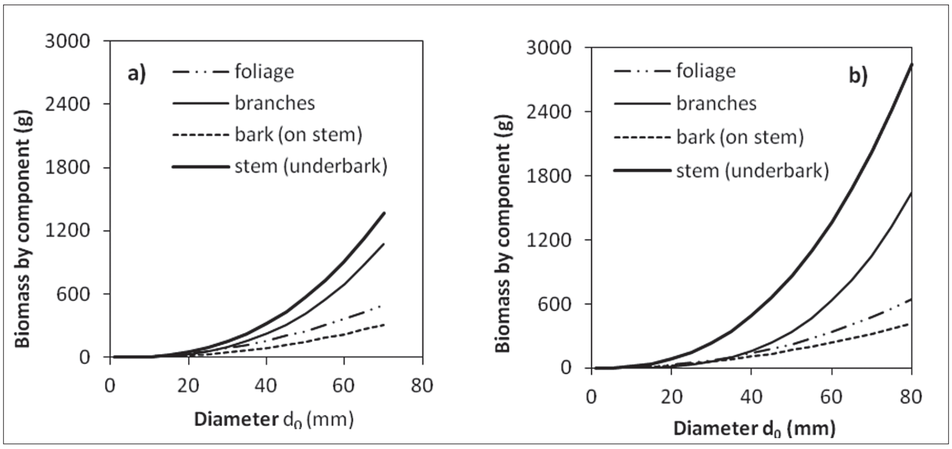

Fig. 2: Biomass by tree components against diameter d_0 in (a) goat willow and (b) rowan

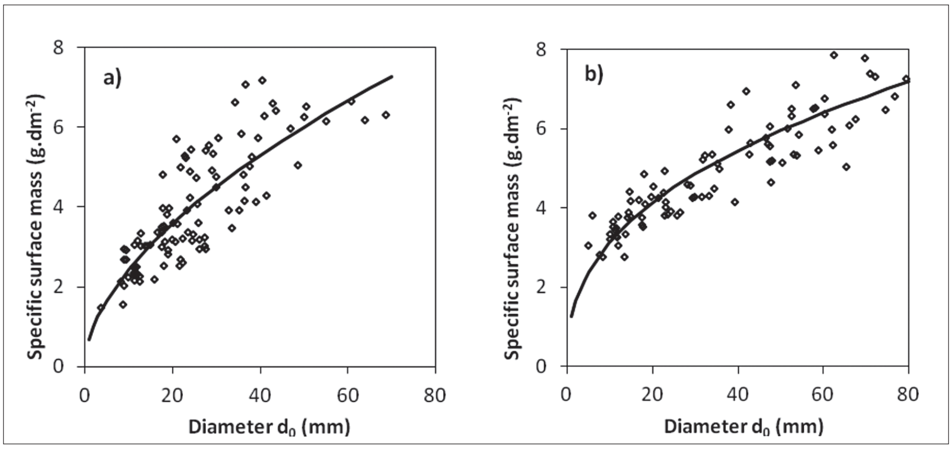

Fig. 3: Specific surface mass of bark against diameter d_0 in (a) goat willow and (b) rowan

Not all tree biomass is available as forage for red deer. Some parts of the trees can not be consumed by red deer because of branch thickness (branches and stem terminal thicker than 10 mm) or inaccessibility (usually for branch browsing over 2.0 m and for bark stripping over 1.8 m from the ground level; see for instance Konôpka et al., 2012). Fig. 4a and Fig. 4b demonstrate models describing the share of edible branches (foliage) to total tree biomass of branches (foliage) in both willow and rowan. While trees with diameter d_0 up to cca 30 mm provide nearly 100% of branches and foliage for red deer forage, consumable branch and foliage biomass sharply decreases with increasing diameter. Thus, in trees with diameter d_0 of 60 mm, the theoretically edible proportions of branches were 17.2% and 9.7% in willow and rowan, respectively. Similarly, theoretically edible proportions of foliage in trees with diameter d_0 of 60 mm were 11.0% and 9.9% in willow and rowan, respectively. These models show that in trees with diameter d_0 of 80 mm, the share of edible branches and foliage is only approximately 3 - 4% of total component biomass.

Table 3: Regression models for B_s – stem biomass; B_b – branch biomass; B_f – foliage biomass; r_b – proportion of edible branch biomass to total branch biomass; r_f - proportion of edible foliage biomass to total foliage biomass; $d_{1.8}$ – stem diameter located 1.8 m from ground level; h_{10} – distance from ground level to spot where stem diameter equals 10 mm; w_s – specific surface area of bark; B_{ebark}- biomass of edible bark in goat willow. All variables are expressed on diameter d_0 as an independent variable.

Eq.	Dependent variable	b_1 (S. E.) P	b_2 (S. E.) P	R^2	MSE	λ	S. D.
(1)	B_s	-3.178 (0.189) <0.001	2.479 (0.061) <0.001	0.945	0.107	1.048	0.306
	B_b	-5.018 (0.236) <0.001	2.807 (0.075) <0.001	0.935	0.166	1.078	0.403
	B_f	-2.409 (0.206) <0.001	2.015 (0.066) <0.001	0.906	0.127	1.061	0.360
(3)	r_b	8.848 (1.207) <0.001	-0.200 (0.029) <0.001	0.524	0.017	–-	–-
	r_f	8.461 (1.259) <0.001	-0.193 (0.030) <0.001	0.452	0.023	–-	–-
(10)	$d_{1.8}$	-8.103 (1.273) <0.001	0.542 (0.037) <0.001	0.791	11.287	–-	–-
(12)	h_{10}	-0.421 (0.078) <0.001	0.063 (0.003) <0.001	0.863	0.103	–-	–-
(13)	w_s	0.675 (0.093) <0.001	0.559 (0.041) <0.001	0.679	0.663	–-	–-
(14)	B_{ebark}	-66.085 (1.164) <0.001	3.706 (0.034) <0.001	0.995	8.700	–-	–-

Note: abbreviations in the table captions means; b_1, b_2 - coefficients, R^2 - coefficient of determination, MSE - mean square error, λ - logarithmic transformation bias, and SD - its standard deviation.

In fact, while inter-specific comparisons between willow and rowan indicate little difference in biomass of specific tree components, differences occurred in their availability for red deer. Smaller inter-specific differences were found for branches (Fig. 4a) compared to foliage (Fig. 4b). Thus, there is a difference in biomass between theoretically edible branches and foliage in willows and rowans (Fig. 5a versus Fig. 5b). Biomass of edible branches in willow shows a steep increase with diameter d_0 compared to rowan. On the other hand, after reaching a peak, edible branch biomass decreases quicker in willow than in rowan. While maximum edible branch biomass (163 g) was found for willows with diameter d_0 of 41 mm, in rowan the maximum value (108 g) occurred at d_0 55 mm. Similarly, biomass of edible foliage in willow manifests a steeper increase in diameter d_0 compared to rowan. Then, after reaching a peak, the decrease of edible foliage biomass is steeper in willow than it is in rowan. Maximum edible foliage biomass (113 g) was found with diameter d_0 of 40 mm for willow while in rowan the maximum value (55 g) occurred for diameter d_0 of 39 mm.

While the amount and course of edible branches and foliage differs between species, edible leader shoot were similar in both species (Fig. 5a versus Fig. 5b). The figures clearly show that tree dimensions influence the proportions of biomass available for browsing (leader shoot, branches and foliage) and bark stripping. In both species, contribution of bark (possibly consumable for red deer stripping) ranges from negligible values in small trees to 60 – 70% in the largest trees.

Table 4: Regression models for B_s – stem biomass; B_b – branch biomass; B_f – foliage biomass; r_b – proportion of edible branch biomass to total branch biomass; r_f - proportion of edible foliage biomass to total foliage biomass; $d_{1.8}$ – stem diameter located 1.8 m from ground level; h_{10} – distance from ground level to spot where stem diameter equals 10 mm; w_s – specific surface area of bark; B_{ebark}- biomass of edible bark in rowan. All variables are expressed on diameter d_0 as an independent variable.

Eq.	Dependent variable	b_1 (S. E.) P	b_2 (S. E.) P	b_3 (S. E.) P	R^2	MSE	λ	S. D.
(1)	B_s	-2.515 (0.088) <0.001	2.412 (0.025) <0.001	–-	0.990	0.028	1.014	0.171
	B_b	-7.336 (0.312) <0.001	3.334 (0.090) <0.001	–-	0.943	0.280	1.138	0.596
	B_f	-3.383 (0.161) <0.001	2.237 (0.046) <0.001	–-	0.962	0.096	1.047	0.322
(4)	r_b	2.411 (0.181) <0.001	-0.068 (0.005) <0.001	–-	0.772	0.026	–-	–-
	r_f	2.288 (0.226) <0.001	-0.073 (0.006) <0.001	–-	0.635	0.020	–-	–-
(10)	$d_{1.8}$	-5.660 (0.968) <0.001	0.592 (0.020) <0.001	–-	0.931	8.490	–-	–-
(11)	h_{10}	-0.0009 (0.0001) <0.001	0.130 (0.007) <0.001	-1.153 (0.129) <0.001	0.951	0.082	–-	–-
(13)	w_s	1.253 (0.110) <0.001	0.398 (0.023) <0.001	–-	0.789	0.439	–-	–-
(14)	B_{ebark}	-53.687 (1.445) <0.001	3.643 (0.029) <0.001	–-	0.996	15.900	–-	–-

Note: abbreviations in the table captions means; b_1, b_2, b_3 - coefficients, R^2 - coefficient of determination, MSE - mean square error, λ - logarithmic transformation bias, and SD - its standard deviation.

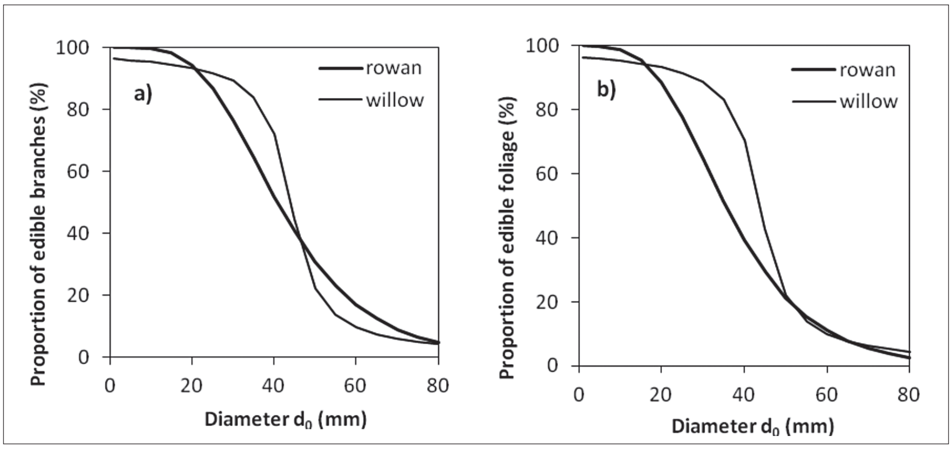

Fig. 4: Proportion of (a) edible branches to total branch biomass and (b) edible foliage to total foliage biomass in both goat willow and rowan

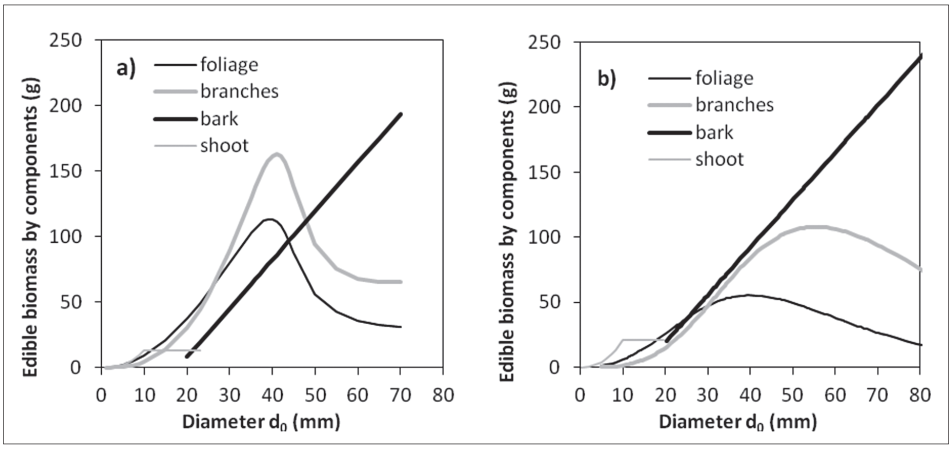

Fig. 5: Edible biomass for foliage, branches, bark (on stem) and leader shoot in (a) willow and (b) rowan

Forage potential on willow and rowan biomass was expressed for winter (includes edible leader shoot, branches and bark; Fig. 6a) and growing season (edible leader shoot, branches, foliage and bark; Fig. 6b). Inter-specific comparisons between willow and rowan show contrasting results for edible potential in both the winter and growing season. While in willow the maximum values (251 g and 361 g for winter and growing season, respectively) were found for individuals with diameter d_0 of 41 mm, in rowan the maximum (315 g and 322 g for winter and growing season, respectively) occurred for trees with a diameter d_0 of 80 mm. The results on total feed potential for the winter and growing seasons suggest that differences are small between willow and rowan. However, it is worth explaining that red deer usually exploit branch and foliage browsing more intensively than bark stripping. For instance, Konôpka et al. (2012) showed that in young stands of European ash, red deer consumed between 25% and 86% of branch and foliage edible potential, while bark striping only occurred on up to 4.2% of total available biomass. Hence, foliage and especially branches in young forest stands are more important for the carrying capacity of hunting ground than stem bark. As for seasonal changes in tree biomass (presence or absence of foliage in crown), branches are the most important feed resource, especially in winter time during periods of snow cover. For instance, Homolka (1990) showed that composition of red deer diet in forest environment fluctuated during the year. While woody plants contributed to 40% of total forage during the growing season, in winter this proportion was nearly 90%. If an average daily edible biomass of 3 kg per adult red deer is considered (see Hell et al., 2000), our model suggest that approx. 30 individuals of willow or rowan trees (in the case of 100%-exploitation of edible branches) with diameter d_0 around 50 mm might provide sufficient diet during the winter season. In reality, this "daily damage" to trees is very probably much higher (only some part of consumable potential on individual trees is eaten) especially if deer game does not have any other forage resources (e.g. during periods of snow cover without supplementary feeding). If we consider current red deer population density in the TNP, 16 individuals per 1000 hectares, "mean annual feed demand" of red deer might equal 17 kg of dry mass per hectare. Thus, this amount of dry mass represented as edible biomass (winter aspect) is approx. 170 trees of willow or rowan with diameter d_0 around 50 mm.

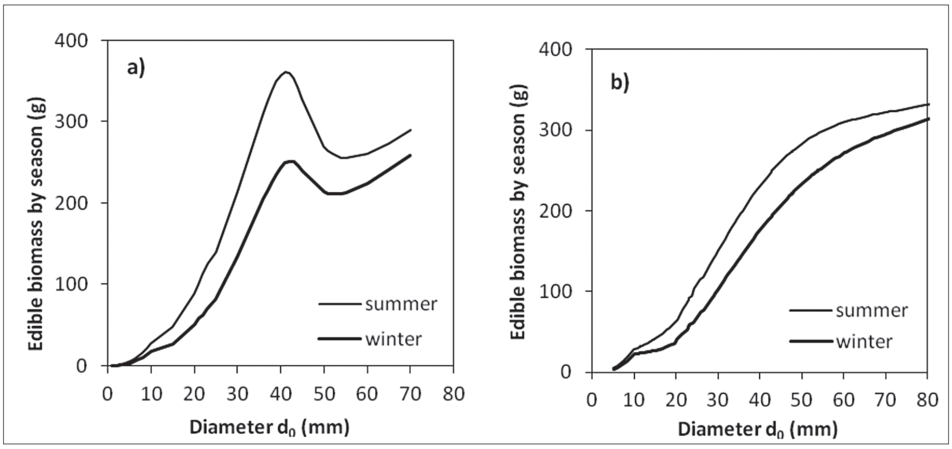

Fig. 6: Edible biomass by season, i.e. summer (growing season) and winter for (a) goat willow and for (b) rowan

The preference of willow and rowan biomass for red deer diet was identified by Kaštier and Bučko (2011) who surveyed damage by red deer browsing (specifically leader shoot and branches) to young post-disturbance stands in TNP. They showed a higher percentage of browsed trees in rowan (72.9%) compared to goat willow (50.7%) and silver fir (Abies alba; 50.6%). All other species (Norway spruce, European larch, Scots pine and silver birch) were less frequently damaged by browsing. To understand interactions between red deer and forest ecosystems, knowledge on attractiveness (quality) of different tree species for deer forage, as well as information about edible biomass (quantity) on specific tree species are necessary. Our previous studies (see Pajtík et al., 2011; Konôpka et al., 2015) focused on models for tree components in young trees of broadleaved species. These models for trees of certain dimensions can be implemented for inter-specific comparisons of edible biomass between goat willow, rowan, sycamore maple, European beech (*Fagus slyvatica*), European ash, and sessile oak (*Quercus petraea*). In summary, branch (Fig. 7a) and foliage (Fig. 7b) models were constructed for trees with height up to 2.0 m as nearly 100% of their biomass would be theoretically available for red deer diet. The results indicate that goat willow recorded the largest biomass of both branches and foliage in tree height between 1.5 and 2.0 m, while the lowest biomass was for braches in maple and for foliage in oak. Rowan ranked among the species with mean branch and foliage biomass.

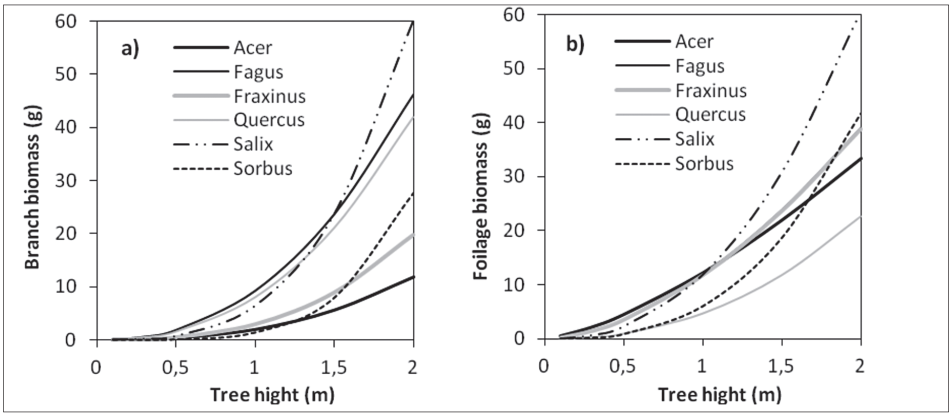

Fig. 7: Inter-specific comparison of (a) branch biomass, (b) foliage biomass for *Acer pseudoplatanus* (Konôpka et al., 2015), *Fagus sylvatica* (Pajtík et al., 2011), *Fraxinus excelsior* (Konôpka et al., 2015), *Quercus petraea* (Pajtík et al., 2011), *Salix caprea*, and *Sorbus aucuparia* against tree height

Feed potential modelling could be implemented to evaluate the carrying capacity of biotopes for red deer. However, to reach this aim, additional scientific knowledge is required. For instance, feed potential has to be quantified, not only for the main forest tree species (as we have done for willow and rowan in this paper) but also for other plants, i.e. shrubs, herbs and grasses co-existing in the areas that are edible for red deer. Further, more exact information relating to maximum branch browsing and bark stripping on commercial forest trees is required. Consequently, the knowledge would be utilized for decision-making on population density regulations of red deer game to avoid serious damage to forest stands (e.g. Augustine and McNaughton, 1998; Shipley et al., 1999).

4. Conclusions

Our results suggest that goat willow and rowan could enhance carrying capacity of forest biotopes for red deer. Both species are palatable for red deer, especially young goat willow provides above-average (compared to other broadleaved species) edible branch and foliage potential. Our estimates show that "winter" (leader shoot, branches and bark) and "summer" (leader shoot, branches, foliage and bark) feed potential was lower in rowan than for willow for small trees (up to diameter d_0 around 50 mm) with the opposite situation for larger trees. It is suggested that the traditional approach of foresters: the inclusion of willow and rowan in young stands, should be re-considered. In principal, both willow and rowan could be maintained within young stands in "reasonable" proportions alongside commercially important trees species. This is extremely important in the case of commercial species which are attractive for red deer browsing and stripping, e.g. silver fir, maple and ash in territories with a high population density of game. The presence of willow and rowan might present a suitable biological control for mitigating damage by red deer to commercial tree species.

Moreover, we suggest establishing and maintaining specific browsing plots to entice red deer away from threatened stands with commercially valuable trees, towards stands with a high proportion of willow and rowan trees. Combining these species ("two species are better than one") to establish browsing plots would create interspecific differences in development of edible potential with tree size and would also provide a diverse food resources. The browsing plots would preferably consist of individuals with variable dimensions to provide biomass for both browsing and bark stripping and fruit consumption from rowan.

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Appendix 1. Procedure for constructions of models

A particular model was constructed to estimate the specific surface mass of bark (i.e. weight of bark from 1 dm² of stem surface). Specific surface mass of bark originated from data based on total bark biomass of the entire surface of stem. Allometric equations for biomass of tree components were based on the form:

$$B = e^{(b_1 + b_2 \ln d_0)} \lambda \tag{1}$$

where b_1, b_2 are coefficients and λ is logarithmic transformation bias.

Edible biomass on a tree level was quantified specifically for each tree components, i.e. leader shoot, branches, foliage, and stem bark. As for potentially edible branch biomass (B_{eb}) a relationship based on total biomass of branches (B_b) was implemented:

$$B_{eb} = B_b * r_b \tag{2}$$

where rb is the proportion of edible biomass of branches to the total biomass of branches. The proportion was calculated using data that originated from sample trees referring to branch biomass (both edible and total). Beta regression, proposed by Ferrari and Cribari-Neto (2004) was used to model the proportion of the part of a tree biomass eaten by a deer species. This type of regression is used for modelling continuous variables that assume values are in the standard unit interval, e.g. rates, proportions, or concentration indices. The model is based on the assumption that a response variable is beta-distributed. Moreover, the motivation to use beta regression lies in the flexibility delivered by the assumed beta law. The beta density can assume a number of different shapes depending on the combination of parameter values, including left- and right-skewed or the flat shape of the uniform density (Cribari-Neto and Zeileis, 2010).

The beta regression model is defined as:

$g(\mu_i) = x_i^T \beta = \eta_i$

where $\beta = (\beta_1, ..., \beta_k)^T$ is a $k\ x\ 1$ vector of unknown regression parameters, $x_i = (x_{i1}, ..., x_{ik})^T$

are independent variables or co-variates and η$_i$ is a linear predictor (i.e. $\eta_i = \beta_0 x_{i1} + ... + \beta_k x_{ik}$), and finally, *g(.): (0,1)* is a link function. In this study we tested the following link functions:

logit : exp(X * *β*)/[1 + exp(X * *β*)]; complementary loglog: 1 - exp[-exp(X * *β*)]; log: exp(X * *β*); and Cauchy: 1/2 + ATAN(X * *β*)/pi

To select the link function that best explain the variability and the shape of data distribution we employed the AIC method (Akaike, 1974).

A similar procedure was used for the edible biomass of foliage. However, the most suitable method for calculating proportion of edible branch (rb) and foliage biomass to total biomass of the components in goat willow is Cauchy function therefore this was implemented:

$$r_b(r_f) = \frac{\frac{1}{2} + arctg(b_1 + b_2 d_0)}{\pi} \tag{3}$$

and for rowan loglog function:

$$r_b(r_f) = 1 - \exp(-\exp(b_1 + b_2 d_0)) \tag{4}$$

To model edible biomass of leader shoot, it was assumed that browsing is limited by maximum distance 2.0 m from the ground level and stem diameter of 10 mm. This means that if a tree has diameter d_0 of up to 10 mm, theoretically the whole stem can be consumed by red deer. Therefore, the edible biomass of the leader shoot is equal to the total biomass of the stem (expressed by allometric equation). On the other hand, if diameter d_0 is large than 10 mm quantity of edible biomass of leader shoot does not increase but remains constant under the condition that volume of stem with diameter d_0 is conform with volume of leader shoot at the point of browsing equaling 10 mm:

$$B_{es} = B_s \tag{5}$$

for $d_0 \leq 10$ mm ,

eventually $B_{es} = B_{s(10)}$ (6)

for d_0 >10 mm and $d_0 \leq d_{h=2}$, where $d_{h=2}$ is diameter conforming with spot on stem situated 2.0 m from the ground level.

As for modeling edible bark on stem, it is anticipated that red deer brows trees with minimum diameter d_0 of 20 mm and at the same time, bark browsing can reach a height up to the point where stem diameter (d_k) equals 10 mm and is a maximum distance up to 1.8 m from the ground level (see Konôpka et al., 2012). Biomass of edible stem bark (B_{ebark}) was calculated for individual sample trees using the formula:

$$B_{ebark} = S * w_s \tag{7}$$

where S is area of edible bark and w_s is specific surface mass of bark.

The area (S) was calculated using the formula for surface of truncated cone with radius of lower base $r_{0.0}$, radius of upper base r_k and height h_k:

$$S = \pi(r_{0.0} + r_k).s\text{, where } s = \sqrt{h_k^2 + (r_{0.0} - r_k)^2} \tag{8}$$

If stem diameter at 1.8 m is more than 10 mm, then h_k=1.8 m and the related diameter is expressed as:

$$r_k = \frac{d_{1.8}}{2} \tag{9}$$

On the other hand, if stem diameter at 1.8 m is less than 10 mm, then r_k in the formula (8) is equal to 5 mm and $h_k = h_{10}$. The relationship between diameter $d_{1.8}$ and diameter d_0 in both trees species was established from data measured on the sample trees and expressed by means of linear function:

$$d_{1.8} = b_1 + b_2 d_0 \tag{10}$$

Height h_{10} where rowan stem reaches a thickness of 10 mm was for rowan calculated by quadratic relationship:

$$h_{10} = b_1 d_0^2 + b_2 d_0 + b_3 \tag{11}$$

and for willow by linear function:

$$h_{10} = b_1 + b_2 d_0 \tag{12}$$

To express the relationship between specific surface mass of bark w_s and diameter d_0 the following allometric equation was used:

$$w_s = b_1 d_0^{b_2} \tag{13}$$

Then, calculated values B_{ebark} in both tree species were fitted by linear function:

$$B_{ebark} = b_1 + b_2 d_0 \text{, for } d_0 \geq 20 \text{ mm} \qquad (14).$$

5.4 Stručný súhrn najvýznamnejších výsledkov

Skonštruovali sme alometrické rovnice na výpočet sušiny biomasy jednotlivých komponentov stromu pre dreviny buk lesný, dub zimný, javor horský, jaseň štíhly, jarabinu vtáčiu a vŕbu rakytovú. Parametre týchto rovníc a štatistické charakteristiky pre nezávislé premenné hrúbka na báze kmeňa, výška stromu a ich vzájomná kombinácia uvádzame v prílohách 1-6.

Pre vyššie uvedené dreviny sme odvodili BCEFy a opísali výhody a nevýhody výpočtu biomasy pomocou alometrických rovníc a BCEFov. Urobili sme medzidruhové porovnanie hodnôt BCEFov pre jednotlivé frakcie stromu pre dreviny javor horský, jaseň štíhly a buk lesný. Tiež sme ukázali štruktúru biomasy týchto drevín a medzidruhové rozdiely v jej alokácii do jednotlivých komponentov.

Sledovali sme prispôsobenie asimilačných orgánov buka na zatienenie a pomocou odmeranej špecifickej listovej plochy SLA a vytvorených alometrických rovníc na výpočet sušiny listov sme odvodili index listovej plochy LAI pre dané stanovište. Priemerné hodnoty LAI sa pohybovali okolo 15 $m^2.m^{-2}$, čo sú hodnoty podstatne vyššie ako v dospelých porastoch buka (pod 10 $m^2.m^{-2}$). Urobili sme medzidruhové porovnanie SLA a LAI medzi bukom a smrekom. Celkovo sme zistili širšiu plasticitu listov vo vzťahu ku svetelným podmienkam pri buku než pri smreku

Rast buka a jeho čistú ročnú primárnu produkciu sme porovnávali s rastom smreka a jeho NPP. Porasty buka a smreka rástli v rovnakých podmienkach vo výskumnom objekte Vrchslatina. Zaznamenali sme iba malé rozdiely v zásobe kmeňov buka a smreka ak bola zásoba vyjadrená v tonách na hektár. Zároveň sme pre tieto porasty vypočítali aj rastovú účinnosť v závislosti od parametrov listov a jemných koreňov. Zaznamenali sme približne rovnakú rastovú účinnosť vyjadrenú v ročnej produkcii kmeňa s kôrou na jednotku listovej plochy, ale takmer 5-násobne vyššiu rastovú účinnosť v prospech buka, ak je vyjadrená v ročnej produkcii kmeňa na hmotnostnú jednotku sušiny listov.

Zostrojili sme regresné modely na výpočet zožrateľnej biomasy na úrovni stromu a porastu pre jarabinu vtáčiu a vŕbu rakytovú na základe hrúbky na báze kmeňa ako nezávislej premennej, ktorá predstavuje teoretický potravinový potenciál pre jeleniu zver.

6 DISKUSIA

Pri tvorbe alometrických rovníc na výpočet biomasy jednotlivých komponentov stromu a následnej tvorbe expanzno-konverzných faktorov biomasy BCEF, ktoré boli vytvorené za rovnakým účelom, sa preukázali výhody a nevýhody obidvoch metód. Čo sa týka presnosti stanovenia biomasy sú obidve metódy rovnocenné, avšak najväčšou nevýhodou pri používaní BCEF je fakt, že sú založené na objeme kmeňa. Táto nevýhoda pramení zo stavu, keď existuje celý rad matematických funkcií na vypočítanie objemu kmeňa dospelých stromov, avšak rovnice na výpočet objemu kmeňa stromov v iniciálnych štádiách rastu sú zriedkavé. Preto nevyhnutnou súčasťou tejto práce bolo aj alometrické odvodenie objemu mladých stromov javora a jaseňa. Pri konštrukcii BCEF sa preukázal jeho prudký pokles pri frakciách celkovej biomasy, nadzemnej biomasy, koreňov a listov pri najmenších stromoch javora, jaseňa a buka. Výsledky korešpondujú s rovnakými zisteniami pre dreviny dub a borovica (Pajtík et al., 2011) a smrek (Pajtík et al., 2008). Hodnoty BCEF pre konáre sú vyrovnané (dub, borovica), alebo mierne rastú (buk, javor, jaseň). Môžeme konštatovať, že hodnoty BCEF pre všetky frakcie stromu sa viacmenej stabilizujú pri všetkých drevinách akonáhle strom dosiahne hrúbku na báze 60-70 mm, čo naznačuje prípustnosť používania jednej „defaultnej“ hodnoty pre dospelé stromy konkrétneho druhu a môžeme to hodnotiť ako výhodu tejto metódy. Na skutočnosť, že hodnoty BCEF sú vo vyššom veku takmer konštantné poukázal vo svojej práci Lehtonen et al. (2004).

Počas rastu všetky dreviny zväčšujú distribúciu biomasy do kmeňa a do konárov, zatiaľ čo znižujú relatívny prírastok koreňov a asimilačných orgánov. V alokácii biomasy sú však jasné rozdiely medzi drevinami a tiež ak porovnávame prezentované výsledky pre listnaté dreviny javor, jaseň a buk s predošlými prácami (Pajtík et al., 2008; Pajtík et al., 2011), kde sa zisťovala alokácia biomasy aj pre ihličnaté dreviny (smrek, borovica) uvidíme výrazné rozdiely medzi skupinou listnatých a ihličnatých drevín. Značné rozdiely medzi listnatými a ihličnatými drevinami boli v pomere podzemnej a nadzemnej biomasy (R/S ratio), kde listnaté dreviny vykazujú vyššie hodnoty R/S ratio než dreviny ihličnaté (Konôpka et al., 2010). Naopak, malé medzidruhové rozdiely sa zistili medzi mladými javormi, jaseňmi a bukmi v zásobe biomasy celého stromu vyjadrenej na základe hrúbky na báze kmeňa, ako aj v pomere R/S ratio. Tieto poznatky poukazujú na to, že ak chceme redukovať neistotu v oceňovaní zmien v zásobe uhlíka, musíme vo väčšine prípadov použiť druhovo špecifické koeficienty.

Naše výsledky ukazujú, že štruktúra biomasy a podiely jednotlivých frakcií sa výrazne menia hlavne do veku, kým strom dosiahne 30 mm hrúbku na báze kmeňa. Tieto zmeny súvisia s rastovou stratégiou v najmladšom veku (primárna snaha obsadiť dostatočný pôdny priestor), ktorá sa neskôr mení na prioritu boja o svetlo.

Alokácia biomasy, listová plocha, index listovej plochy a rastové javy dvoch najvýznamnejších drevín na Slovenku – buka a smreka sa sledovali vo výskumnom objekte Vrchslatina v priebehu rokov 2009-2015. Zistilo sa, že buk mal väčší podiel kmeňa a menší podiel konárov ako smrek, zatiaľ čo podiel asimilačných orgánov bol približne rovnaký. S veľkosťou podielov jednotlivých komponentov úzko súvisia príspevky týchto častí do čistej primárnej produkcie (NPP). Buk má vyššiu NPP kmeňa ako smrek (o 2-4 $Mg.ha^{-1}.rok^{-1}$ v čistých 12-14 ročných porastoch s plným zakmenením), ale nižšiu NPP konárov (o 0,8-1,5 $Mg.ha^{-1}.rok^{-1}$). NPP asimilačných orgánov nevykazuje významné rozdiely. Naopak, čo sa týka zásoby asimilačných orgánov, existovali veľké medzidruhové rozdiely, pretože ich zásoba je pri smreku oproti buku približne trojnásobná.

Pri meraní plochy listov a ihlíc sme zistili, že ich veľkosť sa zväčšuje od dolných častí koruny k jej vrcholu, pričom diferencie vo veľkosti plochy listov sú väčšie u buka ako u smreka. Tieto výsledky sú v protiklade s prácami Barnu (2004) a Tognettiho et al. (1998), ktorí zistili, že veľkosť listov sa zväčšuje so zatienením, ale korešpondujú s prácou Canhama (1988), ktorý zistil väčšiu listovú plochu v horných osvetlených častiach koruny u druhov *Acer saccharinum* Marsch. a *Fagus grandiflora* Ehrh. Listová plocha zároveň rastie aj s veľkosťou stromu až do určitej hodnoty, kedy dochádza k jej stabilizácii. Špecifická listová plocha (SLA) rastie so zatienením, takže najvyššie hodnoty sú v spodnej časti koruny. To znamená, že listy v zatienenej časti sú najmenšie a zároveň aj najtenšie. Zväčšovanie SLA s rastom zatienenia je pravdepodobne prispôsobením sa na lepšie zachytenie svetla v zlých svetelných podmienkach (Niinemets et al., 2001). Taktiež sme zistili štatisticky významné rozdiely v SLA pri stromoch rozdielneho sociologického postavenia. Nadúrovňové, úrovňové a vrastavé stromy ukazujú silnú závislosť SLA od umiestnenia listov v korune. Naproti tomu, podúrovňové stromy rastúce v trvalom zatienení nevykazujú rozdiely v SLA v jednotlivých častiach koruny.

Hodnoty LAI v pozorovaných porastoch počas sledovaného obdobia pravidelne rástli až na hodnotu 15 $m^2.m^{-2}$. Tieto hodnoty sú pomerne vysoké a je predpoklad, že postupne budú kulminovať a v dospelosti klesnú pod hodnotu 10 $m^2.m^{-2}$. Hodnoty LAI pod touto hranicou sa vyskytujú vo väčšine prác (napr. Bréda, 20023; Leuschner et al., 2006), s vyššími hodnotami sa stretávame výnimočne (Ford, 1982; Albrektson, 1984; Bolstad a Gower, 1990). Waring et al. (1985) predpokladá, že pri vysokej miere olistenia môže táto hodnota výnimočne dosiahnuť aj 20 $m^2.m^{-2}$.

Keď sa rastová účinnosť (GE) vyjadrila ako prírastok na sušine kmeňa na jednotku listovej plochy ($g.m^{-2}$) v závislosti na výške stromu, nezaznamenali sa signifikantné rozdiely medzi bukom a smrekom. Avšak pri vyjadrení GE ako prírastku sušiny kmeňa na jednotku sušiny listov ($g.g^{-1}$) je GE buka v porovnaní so smrekom ďaleko vyššia, čo je zapríčinené tým, že pri zhruba rovnakej listovej ploche porastov buka a smreka je SLA buka približne štyrikrát vyššia ako SLA smreka.

Stanovištné zásoby jemných koreňov boli podobné v oboch porastoch, avšak našli sme signifikantné medzidruhové rozdiely v ich morfológii. Jemné korene buka sú tenšie a intenzívnejšie rozvetvené s väčšou hustotou koreňových zakončení ako jemné korene smreka. GE pri oboch drevinách rastie s veľkosťou stromu. Keď sa GE vyjadrila pomocou biomasy jemných koreňov, boli jej hodnoty vyššie pri buku, opačná situácia nastala ak GE bola vypočítaná na základe plochy jemných koreňov. Najväčšie medzidruhové rozdiely (viac ako päťnásobne v prospech smreka) boli zistené pre GE vyjadrenú na počet koreňových zakončení.

Poslednou oblasťou, ktorou sa táto práca zaoberá, bola kvantifikácia ohryzu drevín jeleňou zverou a výpočet potravinového potenciálu pre jarabinu vtáčiu a vŕbu rakytovú. Výsledky výskumu pre jarabinu vtáčiu ukázali, že odhryz konárov a terminálov bol najčastejší vo výške 121 – 130 cm od úrovne pôdy. Vyskytoval sa od bázy kmeňa až do maximálnej výšky 240 cm, avšak nad 200 cm bol veľmi zriedkavý. Podobná frekvencia vo vzťahu na vzdialenosť od úrovne terénu bol aj pri obhryze kôry, ale iba do maximálnej výšky 180 cm. Tieto výsledky sú takmer úplne zhodné s údajmi získanými pre jaseň štíhly v oblasti Javoria a Poľany (Konôpka *et al.*, 2012). Renaud *et al.* (2003) uvádza, že ohryz jeleňmi súvisí s ich veľkosťou, pritom najčastejšie sa vyskytuje vo výške pleca zveri.

Pri príprave modelu na úrovni konára sa zistilo, že sušina drevných častí a listov sa dala tesne vyjadriť v závislosti od hrúbky d_b. Špecifická plošná hmotnosť kôry, vyjadrujúca hmotnosť 1 dm^2 sušiny kôry kmeňa bola odvodená na základe hrúbky d_0.

Na úrovni stromu sa pomocou odobratých vzorníkov odvodili štyri funkcie vyjadrujúce potravinový potenciál v delení: listy, konáre, terminál a kôra. Aj tu sa ako nezávislá premenná použila hrúbka d_0. V prípade konárov a listov potenciál rastie až do určitej hodnoty (maximum pre listy bolo pri cca 35 mm, pri konároch 55 mm) a následne klesá. V prípade kôry sa obhryz očakával od hrúbky d_0 približne 20 mm, potom rastie s veľkosťou stromu (s hrúbkou kmeňa sa zväčšuje aj jeho povrch a zároveň rastie aj hrúbka kôry). V prípade terminálu potenciál rastie od najmenších stromov, pri hrúbke cca 10 mm sa stabilizuje a pri asi 20 mm (zodpovedá výške okolo 2 m) je už terminál pre jeleniu zver spravidla neprístupný, resp. sa takéto poškodenie vyskytuje iba ojedinele. Tieto modely sú v oblasti potravinovej ekológie prežúvavej raticovej zveri priekopnícke. Žiadne podobné výsledky sme v odbornej literatúre nenašli, preto nebola možnosť ich konfrontovať s poznatkami z iných prác.

Kombináciou údajov nameraných na pokusných plochách a modelov (úroveň konár a strom) sa odvodili finálne modely potravinového potenciálu na úrovni porastu. A to samostatne pre konáre, listy, terminál a kôru. Tu sa zistilo, že dendromasa zožrateľných konárov a kôry rastie so strednou hrúbkou porastu, v prípade listov a terminálu najprv kvantita rastie, potom klesá. Po zosumovaní hodnôt odvodených týmito modelmi (ide teda o „zožrateľné" množstvá sušiny všetkých štyroch zložiek) sme zistili, že celkový potravinový potenciál rastie so zväčšovaním strednej hrúbky porastu. Po spriemerovaní údajov zo všetkých pokusných plôch sme zistili, že potravinový potenciál pre odhryz jeleňom bol 32 kg sušiny na 100 m^2 (10 kg terminály, 12 kg konáre a 10 kg listy). Priemerný potenciál pre obhryz bol 3 kg sušiny kôry na 100 m^2. To spolu predstavuje 35 kg zožrateľnej dendromasy na 100 m^2. Hell *et al.* (2000) zdokumentoval, že denná spotreba jelenej zveri je medzi 1,2 kg (jelienča) a 3,0 kg (dospelý jedinec) v prepočte na sušinu. Pri veľkom zjednodušení tejto problematiky by teoreticky jednému dospelému jeleňovi malo ako potravinový zdroj postačovať ročne iba 0,4 ha takýchto porastov (ale pri ich totálnom poškodení). V skutočnosti však na sledovaných plochách jelenia zver zožrala iba 11,8 % potenciálu pre odhryz a 0,9 % pre obhryz. Uvedený odhad úživnosti treba brať len ako modelový, pretože jeleň neexistuje na izolovanom území, kde sú homogénne porastové podmienky. Aj tieto poznatky sú novátorské a nenašli sme žiadne iné podobné výsledky týkajúce sa potravinového potenciálu v biomase lesných drevín pre prežúvavú raticovú, najmä jeleniu zver.

7 ZÁVER A DOPORUČENIA PRE PRAX

Hlavný prínos tejto práce spočíva v tom, že sa zaoberá mladými porastmi do veku približne 10 rokov (definuje sa maximálnou hrúbkou kmeňa stromu rovnou 7 cm), ktorým sa doposiaľ venovala minimálna pozornosť. Originalitu zvýrazňuje predovšetkým fakt, že sa jedná o iniciálne štádiá buka lesného, duba zimného, javora horského, jaseňa štíhleho, jarabiny vtáčej a vŕby rakytovej, ktorých zásoby biomasy pomocou špecifických rovníc zostrojených pre tieto dreviny dodnes nikto nezisťoval. Na Slovensku boli vytvorené objemové rovnice pre dospelé stromy jaseňa (Petráš, Pajtík, 1991), ktoré vyjadrujú objem kmeňa a speňažiteľný objem stromu (hrubiny do 7 cm). Údaje o ostatných komponentoch biomasy stromu absentujú aj na úrovni dospelého stromu. V rámci Európy zozbierali a generalizovali rovnice biomasy Zianis (2005), Muukkonen, Mäkipää (2006) a Muukkonen (2007). Z týchto prehľadov zistíme, že rovnice biomasy sú pre uvedené druhy drevín vzácne, alebo neboli vôbec zostrojené. Navyše to sú všetko rovnice vhodné iba pre dospelé stromy (jednak tým, že v mladosti je iný pomer komponentov biomasy stromu, ale aj tým, že hlavnou nezávislou premennou je DBH, ktorá sa u stromov menších ako 1,30 m nedá odmerať). Ďalším pozitívom tejto práce je, že sa zaoberá aj kvantifikovaním podzemnej biomasy, čo nie je vždy bežné a prispieva tak ku rozšíreniu poznatkov o koreňovej biomase, ktoré sú nevyhnutné na zlepšenie našich vedomostí o alokácii uhlíka a jeho zásobách v terestrických ekosystémoch.

Modely pre biomasu mladých jedincov listnatých drevín umožnia, napr. odhadnúť zásoby biomasy, resp. uhlíka v porastoch vzniknutých po veľkoplošných kalamitách. Takéto kalamity spôsobujú výrazný pokles uhlíkových zásob (jednak v biomase drevín ako aj v pôdnom prostredí) v krajine. Avšak chýbajú objektívne informácie o následnej kompenzácii uhlíkových strát prostredníctvom vývoja následných porastov. Ako príklad môžeme uviesť situáciu na území Vysokých Tatier, kde došlo v dôsledku dvoch rozsiahlych vetrových kalamít (2004 a 2014) a premnoženiu podkôrneho hmyzu (najmä počas rokov 2008-2011) k výraznej redukcii plochy starých porastov s prevahou smreka. V súčasnosti sú tieto postdisturbančné plochy pokryté mladými lesnými porastmi, ktoré predstavujú relatívne malú zásobu biomasy, avšak sú typické dynamickým prírastkom (významná medziročná akumulácia uhlíka).

Novátorské prístupy tejto práce sú aj vo vedeckej implementácii regresných modelov stromových komponentov pre odvodenie produkčno-ekologických charakteristík sledovaných drevín (úroveň jedinca a porastu). Z hľadiska fixácie a obehu uhlíka je dôležité poznať nielen celkovú kvantitu biomasy, ale aj jej štruktúru. Treba si uvedomiť, že drevné časti stromov (hrubé korene, kmeň a konáre) viažu uhlík dlhodobo, asimilačné orgány a jemné korene uhlíka fixujú krátkodobo – sú teda v lesnom ekosystéme „cestami“ pre obeh uhlíka. Preto modely biomasy z produkčno-ekologického hľadiska musia vyjadrovať nielen celkovú stromovú biomasu, ale aj jednotlivé komponenty. Ukazovateľmi akými sú, napr. rastová účinnosť a alokačný koeficient sa na území Česka a Slovenska takmer nikto nezaoberal. Taktiež nie sú v našich krajinách dostupné odhady čistej primárnej produkcie pre lesné ekosystémy.

Ďalším priekopníckym prvkom dizertačnej práce je využitie alometrických vzťahov pre exaktné stanovenie biomasy drevín zožratej raticovou prežúvavou zverou, ako aj odhad potravinového potenciálu pre túto skupinu zveri. Pre tento účel sa vytvorili modely rôznej úrovne, t.j. stromový komponent (konáre, listy, kmeňová kôra), celý strom a lesná porast. Takéto poznatky môžu v kombinácii s niektorými ďalšími údajmi (napr. potravinový potenciál krov a prízemnej vegetácie, resp. exaktná kvantifikácia „únosného“ poškodenia lesných drevín) poslúžiť ako podkladový materiál pre odhad úživnosti jednotlivých poľovných revírov a následne pomôckou pri plánovaní početnosti jelenej zveri. Keďže jelenia zver je v súčasnosti najzávažnejším škodlivým činiteľom v mladých lesných porastoch, harmonizácia záujmov lesného hospodárstva a poľovníctva je jednou z priorít lesníckej praxe v Česku a na Slovensku.

Vytvorené alometrické rovnice na odvodenie množstva biomasy v mladých lesných porastoch môžu poslúžiť pri spresnení údajov o zásobách uhlíka pre medzinárodné reportovanie. Taktiež prispievajú k lepšiemu pochopeniu procesov alokácie biomasy v týchto porastoch a jej vplyvu na fixáciu (drevné časti) a obeh (asimilačné orgány, resp. jemné korene) uhlíka. Na ich základe je možné stanoviť potravinový potenciál slúžiaci následne na odvodenie ekologicky únosných stavov zveri v lesných oblastiach.

Problematika dizertačnej práce nadväzuje na projekty riešené v Národnom lesníckom centre, Lesníckom výskumnom ústave Zvolen, predovšetkým APVT-27-023504 „Kvantifikácia biomasy lesných porastov I. vekového stupňa“ (roky realizácie: 2005-2007) a APVV-0268-10 „Komparačné štúdie štruktúry primárnej produkcie v porastoch buka a smreka“ (roky realizácie: 2011-2014). Ďalej vznikla aj v súčasnosti riešeného projektu APVV-0584-12 „Matematické modely alokácie biomasy v mladých porastoch vybraných druhov listnatých drevín“. Uvedené projekty financovala Agentúra na podporu výskumu a vývoja v Bratislave. Do týchto projektov sa zapojil širší kolektív riešiteľov, a to hlavne z Národného lesníckeho centra, Lesníckeho výskumného ústavu Zvolen. Pri riešení úloh uvedených projektov sa využíva medzinárodná spolupráca, napr. doc. Dr. Martin Lukac (Univerzita v Readingu, Veľká Británia), a to hlavne pri konzultáciách čiastkových výsledkov.

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9 PRÍLOHY

Príloha 1	Štatistické charakteristiky alometrických rovníc na výpočet biomasy pre buk lesný
Príloha 2	Štatistické charakteristiky alometrických rovníc na výpočet biomasy pre dub zimný
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Príloha 5	Štatistické charakteristiky alometrických rovníc na výpočet biomasy pre jarabinu vtáčiu
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Príloha 1 Štatistické charakteristiky alometrických rovníc na výpočet biomasy pre buk lesný

Regresné koeficienty b_0, b_1, b_2, ich štandardné chyby (S.E.), p-hodnoty (P), koeficienty determinácie (R^2), stredné štvorcové chyby rezíduí (MSE), logaritmické transformačné biasy (λ) a ich štandardné odchýlky (S.D.) pre nezávislé premenné (N.P.) d_0 (v mm), h (v m), a ich vzájomnú kombináciu

N. P.	Frakcia stromu	b_0	S.E.	P	b_1	S.E.	P	b_2	S.E.	P	R^2	MSE	λ	S.D.
d_0	Kmeň	-4,034	0,164	<0,001	2,852	0,063	<0,001				0,923	0,167	1,0836	0,438
	Konáre	-5,982	0,218	<0,001	3,117	0,084	<0,001				0,891	0,295	1,142	0,592
	Listy	-3,750	0,183	<0,001	2,375	0,071	<0,001				0,871	0,207	1,102	0,486
	Korene	-2,960	0,179	<0,001	2,361	0,069	<0,001				0,874	0,199	1,098	0,495
	Nadz. časť	-3,288	0,144	<0,001	2,777	0,056	<0,001				0,937	0,129	1,063	0,364
	Celý strom	-2,521	0,132	<0,001	2,639	0,051	<0,001				0,941	0,108	1,053	0,336
h	Kmeň	3,108	0,043	<0,001	2,302	0,073	<0,001				0,854	0,318	1,166	0,672
	Konáre	1,833	0,069	<0,001	2,324	0,117	<0,001				0,703	0,803	1,474	1,671
	Listy	2,206	0,058	<0,001	1,712	0,098	<0,001				0,643	0,573	1,308	1,068
	Korene	2,964	0,061	<0,001	1,651	0,102	<0,001				0,607	0,620	1,298	0,949
	Nadz. časť	3,669	0,048	<0,001	2,161	0,082	<0,001				0,806	0,396	1,216	0,855
	Celý strom	4,094	0,050	<0,001	2,000	0,085	<0,001				0,767	0,427	1,226	0,853
d_0, h	Kmeň	-1,530	0,163	<0,001	1,848	0,065	<0,001	1,015	0,054	<0,001	0,975	0,054	1,026	0,222
	Konáre	-4,768	0,364	<0,001	2,630	0,144	<0,001	0,423	0,121	<0,001	0,901	0,270	1,130	0,560
	Listy	-3,286	0,317	<0,001	2,188	0,126	<0,001	0,188	0,105	0,076	0,873	0,205	1,100	0,479
	Korene	-2,898	0,314	<0,001	2,336	0,124	<0,001	0,025	0,104	0,809	0,874	0,200	1,098	0,493
	Nadz. časť	-1,486	0,186	<0,001	2,054	0,074	<0,001	0,731	0,062	<0,001	0,966	0,070	1,034	0,266
	Celý strom	-1,236	0,197	<0,001	2,124	0,078	<0,001	0,521	0,065	<0,001	0,957	0,079	1,038	0,285

Príloha 2 Štatistické charakteristiky alometrických rovníc na výpočet biomasy pre dub zimný

Regresné koeficienty b_0, b_1, b_2, ich štandardné chyby (S.E.), p-hodnoty (P), koeficienty determinácie (R^2), stredné štvorcové chyby rezíduí (MSE), logaritmické transformačné biasy (λ) a ich štandardné odchýlky (S.D.) pre nezávislé premenné (N.P.) d_0 (v mm), h (v m), a ich vzájomnú kombináciu

N. P.	Frakcia stromu	b_0	S.E.	P	b_1	S.E.	P	b_2	S.E.	P	R^2	MSE	λ	S.D.
d_0	Kmeň	-4,311	0,224	<0,001	2,959	0,071	<0,001				0,942	0,240	1,121	0,544
	Konáre	-6,025	0,215	<0,001	2,963	0,068	<0,001				0,947	0,221	1,107	0,496
	Listy	-5,954	0,221	<0,001	2,768	0,070	<0,001				0,936	0,234	1,106	0,459
	Korene	-1,954	0,150	<0,001	2,066	0,046	<0,001				0,941	0,124	1,065	0,401
	Nadz. časť	-3,952	0,206	<0,001	2,931	0,065	<0,001				0,950	0,203	1,099	0,469
	Celý strom	-2,612	0,175	<0,001	2,646	0,005	<0,001				0,956	0,146	1,070	0,382
h	Kmeň	3,471	0,045	<0,001	2,516	0,046	<0,001				0,965	0,147	1,074	0,419
	Konáre	1,839	0,086	<0,001	2,388	0,089	<0,001				0,871	0,535	1,271	0,896
	Listy	1,370	0,074	<0,001	2,269	0,077	<0,001				0,891	0,398	1,190	0,700
	Korene	3,511	0,053	<0,001	1,719	0,051	<0,001				0,898	0,213	1,112	0,553
	Nadz. časť	3,769	0,050	<0,001	2,468	0,052	<0,001				0,954	0,186	1,095	0,483
	Celý strom	4,369	0,051	<0,001	2,207	0,053	<0,001				0,942	0,189	1,099	0,503
d_0, h	Kmeň	-0,066	0,170	0,698	1,324	0,063	<0,001	1,491	0,053	<0,001	0,993	0,029	1,014	0,171
	Konáre	-4,263	0,432	<0,001	2,284	0,161	<0,001	0,619	0,135	<0,001	0,956	0,186	1,092	0,473
	Listy	-3,577	0,412	<0,001	1,852	0,153	<0,001	0,835	0,129	<0,001	0,954	0,169	1,077	0,399
	Korene	-0,226	0,289	0,436	1,398	0,107	<0,001	0,611	0,091	<0,001	0,956	0,092	1,047	0,333
	Nadz. časť	-0,201	0,194	0,303	1,486	0,072	<0,001	1,317	0,061	<0,001	0,991	0,038	1,019	0,199
	Celý strom	0,389	0,201	0,056	1,490	0,075	<0,001	1,054	0,063	<0,001	0,989	0,040	1,020	0,209

Príloha 3 Štatistické charakteristiky alometrických rovníc na výpočet biomasy pre javor horský

Regresné koeficienty b_0, b_1, b_2, ich štandardné chyby (S.E.), p-hodnoty (P), koeficienty determinácie (R^2), stredné štvorcové chyby rezíduí (MSE), logaritmické transformačné biasy (λ) a ich štandardné odchýlky (S.D.) pre nezávislé premenné (N.P.) d_0 (v mm), h (v m), a ich vzájomnú kombináciu

N. P.	Frakcia stromu	b_0	S.E.	P	b_1	S.E.	P	b_2	S.E.	P	R^2	MSE	λ	S.D.
d_0	Kmeň s kôrou	-4.169	0.150	<0,001	2.914	0.046	<0,001				0.976	0.112	1.064	0.421
	Kmeň bez kôry	-4.700	0.156	<0,001	3.011	0.048	<0,001				0.976	0.132	1.070	0.443
	Konáre	-8.107	0.342	<0,001	3.351	0.101	<0,001				0.926	0.443	1.225	0.800
	Listy	-2.650	0.173	<0,001	1.950	0.053	<0,001				0.933	0.162	1.082	0.473
	Kôra	-4.607	0.146	<0,001	2.528	0.045	<0,001				0.970	0.115	1.060	0.396
	Korene	-2.595	0.153	<0,001	2.226	0.047	<0,001				0.960	0.119	1.060	0.370
	Nadz. časť	-3.342	0.127	<0,001	2.755	0.039	<0,001				0.981	0.088	1.044	0.324
	Celý strom	-2.432	0.115	<0,001	2.583	0.035	<0,001				0.983	0.067	1.034	0.276
h	Kmeň s kôrou	3.194	0.051	<0,001	2.273	0.040	<0,001				0.971	0.149	1.077	0.435
	Kmeň bez kôry	2.906	0.052	<0,001	2.348	0.041	<0,001				0.971	0.157	1.081	0.448
	Konáre	0.386	0.135	0.005	2.583	0.101	<0,001				0.882	0.708	1.335	0.959
	Listy	2.329	0.079	<0,001	1.459	0.062	<0,001				0.853	0.357	1.182	0.705
	Kôra	1.773	0.044	<0,001	1.977	0.034	<0,001				0.971	0.111	1.056	0.360
	Korene	3.109	0.085	<0,001	1.648	0.066	<0,001				0.868	0.391	1.205	0.753
	Nadz. časť	3.632	0.056	<0,001	2.133	0.044	<0,001				0.960	0.1832	1.0942	0.482
	Celý strom	4.140	0.066	<0,001	1.969	0.051	<0,001				0.941	0.234	1.120	0.552
d_0, h	Kmeň s kôrou	-0.832	0.174	<0,001	1.577	0.068	<0,001	1.094	0.053	<0,001	0.996	0.023	1.011	0.153
	Kmeň bez kôry	-1.223	0.178	<0,001	1.617	0.069	<0,001	1.140	0.054	<0,001	0.996	0.024	1.012	0.157
	Konáre	-5.912	0.775	<0,001	2.463	0.301	<0,001	0.741	0.237	0.002	0.934	0.402	1.195	0.709
	Listy	-2.626	0.466	<0,001	1.941	0.181	<0,001	0.008	0.142	0.956	0.934	0.164	1.082	0.473
	Kôra	-1.490	0.194	<0,001	1.278	0.076	<0,001	1.022	0.059	<0,001	0.993	0.029	1.014	0.167
	Korene	-2.797	0.404	<0,001	2.307	0.157	<0,001	-0.066	0.122	0.589	0.960	0.120	1.059	0.367
	Nadz. časť	-0.783	0.194	<0,001	1.729	0.075	<0,001	0.840	0.059	<0,001	0.994	0.028	1.014	0.167
	Celý strom	-0.784	0.241	0.002	1.923	0.094	<0,001	0.539	0.073	<0,001	0.989	0.043	1.021	0.218

Príloha 4 Štatistické charakteristiky alometrických rovníc na výpočet biomasy pre jaseň štíhly

Regresné koeficienty b_0, b_1, b_2, ich štandardné chyby (S.E.), p-hodnoty (P), koeficienty determinácie (R^2), stredné štvorcové chyby rezíduí (MSE), logaritmické transformačné biasy (λ) a ich štandardné odchýlky (S.D.) pre nezávislé premenné (N.P.) d_0 (v mm), h (v m), a ich vzájomnú kombináciu

N. P.	Frakcia stromu	b_0	S.E.	P	b_1	S.E.	P	b_2	S.E.	P	R^2	MSE	λ	S.D.
d_0	Kmeň s kôrou	-4.374	0.229	<0,001	2.997	0.075	<0,001				0.954	0.140	1.072	0.430
	Kmeň bez kôry	-5.129	0.247	<0,001	3.147	0.081	<0,001				0.951	0.163	1.088	0.516
	Konáre	-9.108	0.624	<0,001	3.738	0.197	<0,001				0.835	0.562	1.256	0.792
	Listy	-3.969	0.255	<0,001	2.388	0.083	<0,001				0.912	0.174	1.085	0.435
	Kôra	-4.658	0.204	<0,001	2.630	0.066	<0,001				0.952	0.111	1.053	0.331
	Korene	-3.301	0.243	<0,001	2.454	0.079	<0,001				0.925	0.146	1.077	0.452
	Nadz. časť	-3.839	0.209	<0,001	2.925	0.068	<0,001				0.959	0.117	1.057	0.360
	Celý strom	-2.999	0.200	<0,001	2.769	0.065	<0,001				0.959	0.099	1.049	0.332
h	Kmeň s kôrou	3.523	0.056	<0,001	2.206	0.061	<0,001				0.944	0.171	1.096	0.601
	Kmeň bez kôry	3.160	0.059	<0,001	2.317	0.065	<0,001				0.942	0.193	1.119	0.773
	Konáre	0.698	0.168	<0,001	2.785	0.189	<0,001				0.753	0.841	1.433	1.174
	Listy	2.345	0.070	<0,001	1.721	0.077	<0,001				0.864	0.270	1.129	0.554
	Kôra	2.271	0.047	<0,001	1.942	0.052	<0,001				0.946	0.124	1.060	0.358
	Korene	3.171	0.075	<0,001	1.780	0.084	<0,001				0.853	0.288	1.156	0.719
	Nadz. časť	3.874	0.057	<0,001	2.140	0.062	<0,001				0.938	0.178	1.093	0.522
	Celý strom	4.279	0.062	<0,001	2.048	0.069	<0,001				0.920	0.193	1.100	0.525
d_0, h	Kmeň s kôrou	-0.906	0.372	0.017	1.667	0.139	<0,001	1.052	0.103	<0,001	0.980	0.060	1.038	0.399
	Kmeň bez kôry	-1.460	0.409	<0,001	1.739	0.153	<0,001	1.113	0.114	<0,001	0.978	0.073	1.052	0.535
	Konáre	-6.807	1.152	<0,001	2.830	0.431	<0,001	0.795	0.339	0.022	0.847	0.529	1.244	0.782
	Listy	-2.219	0.596	<0,001	1.717	0.223	<0,001	0.531	0.165	0.002	0.923	0.156	1.075	0.411
	Kôra	-1.502	0.321	<0,001	1.419	0.120	<0,001	0.958	0.089	<0,001	0.981	0.045	1.022	0.222
	Korene	-2.043	0.056	<0,001	1.968	0.211	<0,001	0.394	0.160	0.016	0.931	0.137	1.073	0.450
	Nadz. časť	-0.795	0.355	0.028	1.757	0.133	<0,001	0.923	0.099	<0,001	0.981	0.055	1.031	0.315
	Celý strom	-0.589	0.372	0.117	1.838	0.140	<0,001	0.754	0.106	<0,001	0.976	0.060	1.032	0.301

Príloha 5 Štatistické charakteristiky alometrických rovníc na výpočet biomasy pre jarabinu vtáčiu

Regresné koeficienty *b_0, b_1, b_2*, ich štandardné chyby (S.E.), p-hodnoty (P), koeficienty determinácie (R^2), stredné štvorcové chyby rezíduí (MSE), logaritmické transformačné biasy (λ) a ich štandardné odchýlky (S.D.) pre nezávislé premenné (N.P.) *d_0* (v mm), *h* (v m), a ich vzájomnú kombináciu

N. P.	Frakcia stromu	b_0	S.E.	P	b_1	S.E.	P	b_2	S.E.	P	R^2	MSE	λ	S.D.
d_0	Kmeň s kôrou	-2.515	0.088	<0,001	2.412	0.025	<0,001				0.990	0.028	1.014	0.171
	Kmeň bez kôry	-3.218	0.094	<0,001	2.546	0.027	<0,001				0.990	0.033	1.016	0.183
	Konáre	-7.336	0.312	<0,001	3.334	0.090	<0,001				0.943	0.280	1.138	0.596
	Listy	-3.383	0.161	<0,001	2.237	0.046	<0,001				0.962	0.096	1.047	0.322
	Kôra	-2.591	0.092	<0,001	1.966	0.027	<0,001				0.984	0.032	1.016	0.179
	Korene	-3.396	0.169	<0,001	2.476	0.049	<0,001				0.966	0.105	1.056	0.382
	Nadz. časť	-2.423	0.099	<0,001	2.499	0.029	<0,001				0.989	0.034	1.017	0.190
	Celý strom	-2.067	0.104	<0,001	2.485	0.030	<0,001				0.987	0.038	1.019	0.198
h	Kmeň s kôrou	2.861	0.078	<0,001	3.066	0.073	<0,001				0.951	0.142	1.074	0.441
	Kmeň bez kôry	2.453	0.080	<0,001	3.242	0.075	<0,001				0.953	0.149	1.078	0.450
	Konáre	-0.018	0.193	0.927	4.332	0.182	<0,001				0.871	0.632	1.393	1.443
	Listy	1.651	0.109	<0,001	2.792	0.103	<0,001				0.890	0.278	1.154	0.704
	Kôra	1.790	0.067	<0,001	2.501	0.063	<0,001				0.946	0.104	1.053	0.358
	Korene	2.188	0.122	<0,001	3.076	0.116	<0,001				0.886	0.352	1.196	0.798
	Nadz. časť	3.186	0.094	<0,001	3.135	0.090	<0,001				0.934	0.202	1.112	0.584
	Celý strom	3.522	0.100	<0,001	3.104	0.095	<0,001				0.924	0.227	1.125	0.615
d_0, h	Kmeň s kôrou	-1.317	0.161	<0,001	1.857	0.071	<0,001	0.749	0.092	<0,001	0.994	0.017	1.008	0.129
	Kmeň bez kôry	-1.843	0.164	<0,001	1.909	0.072	<0,001	0.859	0.093	<0,001	0.995	0.017	1.008	0.130
	Konáre	-6.976	0.690	<0,001	3.162	0.308	<0,001	0.244	0.416	0.560	0.943	0.282	1.137	0.592
	Listy	-3.389	0.390	<0,001	2.240	0.171	<0,001	-0.004	0.222	0.987	0.962	0.097	1.047	0.322
	Kôra	-1.575	0.191	<0,001	1.495	0.084	<0,001	0.635	0.109	<0,001	0.988	0.023	1.011	0.153
	Korene	-3.684	0408	<0,001	2.610	0.179	<0,001	-0.181	0.232	0.438	0.966	0.106	1.056	0.379
	Nadz. časť	-1.666	0.220	<0,001	2.149	0.096	<0,001	0.470	0.124	<0,001	0.990	0.030	1.015	0.178
	Celý strom	-1.586	0.243	<0,001	2.262	0.106	<0,001	0.299	0.137	0.032	0.988	0.036	1.018	0.196

Príloha 6 Štatistické charakteristiky alometrických rovníc na výpočet biomasy pre vŕbu rakytovú

Regresné koeficienty b_0, b_1, b_2, ich štandardné chyby (S.E.), p-hodnoty (P), koeficienty determinácie (R^2), stredné štvorcové chyby rezíduí (MSE), logaritmické transformačné biasy (λ) a ich štandardné odchýlky (S.D.) pre nezávislé premenné (N.P.) d_0 (v mm), h (v m), a ich vzájomnú kombináciu

N. P.	Frakcia stromu	b_0	S.E.	P	b_1	S.E.	P	b_2	S.E.	P	R^2	MSE	λ	S.D.
d_0	Kmeň s kôrou	-3.178	0.189	<0,001	2.479	0.061	<0,001				0.945	0.107	1.048	0.306
	Kmeň bez kôry	-3.886	0.202	<0,001	2.601	0.065	<0,001				0.943	0.122	1.055	0.331
	Konáre	-5.018	0.236	<0,001	2.807	0.075	<0,001				0.935	0.166	1.078	0.403
	Listy	-2.409	0.206	<0,001	2.015	0.066	<0,001				0.906	0.127	1.061	0.360
	Kôra	-3.510	0.177	<0,001	2.166	0.057	<0,001				0.937	0.094	1.043	0.290
	Korene	-3.537	0.193	<0,001	2.346	0.062	<0,001				0.937	0.111	1.052	0.330
	Nadz. časť	-2.305	0.149	<0,001	2.425	0.047	<0,001				0.965	0.066	1.029	0.232
	Celý strom	-2.035	0.146	<0,001	2.406	0.047	<0,001				0.965	0.064	1.029	0.231
h	Kmeň s kôrou	2.542	0.066	<0,001	3.063	0.086	<0,001				0.928	0.140	1.069	0.390
	Kmeň bez kôry	2.106	0.065	<0,001	3.230	0.086	<0,001				0.935	0.138	1.068	0.386
	Konáre	1.613	0.125	<0,001	3.237	0.164	<0,001				0.801	0.505	1.269	0.944
	Listy	2.335	0.094	<0,001	2.344	0.124	<0,001				0.786	0.289	1.153	0.650
	Kôra	1.515	0.070	<0,001	2.636	0.092	<0,001				0.893	0.160	1.080	0.430
	Korene	1.953	0.091	<0,001	2.780	0.120	<0,001				0.846	0.271	1.135	0.573
	Nadz. časť	3.360	0.080	<0,001	2.907	0.105	<0,001				0.889	0.206	1.105	0.508
	Celý strom	3.589	0.080	<0,001	2.879	0.105	<0,001				0.886	0.208	1.104	0.501
d_0, h	Kmeň s kôrou	-0.809	0.212	<0,001	1.414	0.088	<0,001	1.457	0.110	<0,001	0.980	0.039	1.019	0.195
	Kmeň bez kôry	-1.254	0.207	<0,001	1.417	0.086	<0,001	1.619	0.107	<0,001	0.983	0.037	1.018	0.192
	Konáre	-4.569	0.442	<0,001	2.605	0.184	<0,001	0.275	0.229	0.233	0.936	0.165	1.079	0.412
	Listy	-1.939	0.382	<0,001	1.803	0.159	<0,001	0.290	0.199	0.148	0.908	0.125	1.061	0.363
	Kôra	-1.834	0.263	<0,001	1.413	0.109	<0,001	1.031	0.136	<0,001	0.961	0.060	1.029	0.246
	Korene	-2.441	0.336	<0,001	1.854	0.140	<0,001	0.674	0.175	<0,001	0.945	0.097	1.048	0.322
	Nadz. časť	-0.912	0.025	<0,001	1.801	0.094	<0,001	0.854	0.117	<0,001	0.977	0.043	1.021	0.206
	Celý strom	-0.705	0.225	0.002	1.810	0.094	<0,001	0.815	0.117	<0,001	0.977	0.043	1.021	0.207