

Biomass allocation in natural regeneration of *Fagus sylvatica* and *Picea abies* trees in Italian Alps

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Abstract. Biomass allocation in seedlings and saplings at different stages of growth is important information for studying the response of species to site conditions. The objectives of the paper are: (a) to analyse the relationship between height and biomass in young Norway spruce and European beech trees, (b) to study the influence of the leaf area on ontogenetic growth stages and biomass sequestration capacity on the regeneration of these two species. 96 seedlings ($H < 30$ cm) and saplings ($31 < H < 130$ cm) were collected in different light conditions in a case study in the Alps (Trentino province, Italy). Leaf Area Index and shoot/root ratio were used as indicators of the ecological conditions (e.g. light, soil moisture, nutrient status) able to influence the seedlings and saplings growth. Two non-linear regressions were fitted to analyse the relationship between height and biomass and to develop the above-ground and below-ground allometric equations. Non-linear regressions show that sapling or seedling height is a good predictor of above-ground and below-ground biomass with a R^2_{aj} above 0.8 for all equations and a R^2_{aj} above 0.9 for above-ground biomass of Norway spruce. The results show that silvicultural practices may influence the regeneration patterns and increase the biomass allocation rate influencing stand density and canopy cover.

Key words: Norway spruce, European beech, allometric equation, saplings, seedlings, Leaf Area Index.

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Introduction

Estimates of the carbon stocks in vegetation biomass are a fundamental information by the United Nations Framework Convention on Climate Change (UNFCCC, 1992) and Kyoto Protocol (UNFCCC, 1997). These political documents recognized that forest ecosystems contribute to mitigate the anthropogenic greenhouse effect (Teobaldelli *et al.*, 2009; Durkaya *et al.*, 2013). The Intergovernmental Panel for Climate Change published the Good Practice Guid-

ance (IPCC GPG) in 2000 for reporting carbon stocks in tree above-ground and below-ground biomass in a transparent and verifiable way (Penman *et al.*, 2004).

Biomass and carbon stocks are generally estimated using biomass functions (Cienciala *et al.*, 2005; Ruiz-Peinado *et al.*, 2012), applying the biomass expansion factors (BEFs) (Levy *et al.*, 2004; Skovsgaard & Nord-Larsen, 2012) or adopting non-destructive methods based on photo imagery (Ter-Mikaelian & Parker, 2000). The international literature has mainly focused on

biomass allocation in mature and old trees, while few studies have focused on the above-ground and below-ground biomass in young and very young trees (e.g. Elliott & Clinton, 1993; Claesson *et al.*, 2001; Pajtik *et al.*, 2011; Blujdea *et al.*, 2012). Generally, allometric equations estimated for large trees are not applicable to young trees. In addition, many of these studies considered shoot growth but not root growth (Canham & Marks, 1985). Yet seedling and sapling biomass are important variables used to measure the net primary productivity, to estimate the carbon sequestration potential of forest stands, and to evaluate the performance of forest regeneration after different silvicultural treatments (Schmidt *et al.*, 2009; Øyen *et al.*, 2011). Consequently, the estimation of seedling and sapling biomass and the analysis of the relationship between shoot/root (R/S) ratio and site characteristics might help forest managers to promote the growth of desired tree species (DeLucia *et al.*, 1998).

The growth and survival of young trees is influenced by multiple site characteristics such as light, altitude, soil fertility and competition with the surrounding vegetation. In particular, light plays an outstanding role in forests, at least on mesic sites in temperate regions, and it can easily be manipulated by silvicultural treatments (Petriřan *et al.*, 2008).

Leaf Area Index (LAI) can be defined as the amount of foliage area in a canopy per unit ground surface area (m^2m^{-2}) (Watson, 1947) and it is a dynamic parameter that depends on species composition, developmental stage, prevailing site conditions, season of the year and management practices and it expresses the photosynthetic and transpiration surface of plant canopies (Jonckheere *et al.*, 2005). In the literature there are several methods for ground-based estimation of LAI (Liang *et al.*, 2012): direct methods (destructive harvesting and direct determination of one-sided leaf area, collection and weighing of total leaf litterfall), indirect contact methods (allometry,

plumb lines, point quadrat methods) and indirect optical methods (Ceptometer, LAI-2000 and hemispherical photographs).

The amount of leaf area in plant canopies influences primary production, transpiration, precipitation interception, microclimate and energy, water and carbon exchanges between vegetation and atmosphere (Pastorella & Paletto, 2013). Leaf area also influences the amount of diffuse light, which is a good predictor of plant growth (Jarčuřka, 2011). Light availability can explain growth; shade-tolerant species can survive long periods in deep shade by greatly reducing their growth in height (Petriřan *et al.*, 2008). Growth responses in individual plants are difficult to predict because the factors involved are numerous. The process of natural regeneration may be considered interactive and retroactive. Apart from numerous environmental (external) factors, the natural regeneration is also influenced by internal factors such as genetically-conditioned properties of the species (Jarčuřka, 2009).

Biomass allocation (R/S ratio) is related prevailing to the light conditions and secondarily to other ecological conditions (e.g. soil moisture, nutrient status). According to the optimum allocation theory, trees modify their allocation pattern in order to capture the resource (i.e. light, water, nutrients) that most limits growth (Claveau *et al.*, 2005). Responses to light availability differ according to the species: shade-tolerant species – e.g. European beech – allocate biomass preferentially to the foliage to optimize light capture (Wagner *et al.*, 2010). Generally, these species have a higher R/S ratio than the shade-intolerant species (i.e. Scots pine or European larch).

Starting from these preliminary considerations, the objectives of the paper are: (i) to develop the allometric equations to estimate above-ground and below-ground biomass in Norway spruce and European beech (seedlings and saplings) using total height, (ii) to analyse the influence of the leaf area on ontogenetic growth stages and

biomass sequestration capacity in the regeneration of these two species.

Materials and methods

Study sites

The study was carried out in Trentino province located in the north-east of Italy (Figure 1), which occupies 620,688 ha, of which about 56% is covered by forests (345,180 ha). The main forest types are Norway spruce (*Picea abies* (L.) H. Karst), European larch (*Larix decidua* Mill.), European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.). The Trentino province has a long tradition in the management of public and common forests; nowadays around 76% of the forest area is managed by the Forest and Wildlife Service of the Trentino province according to forest unit management plans. Furthermore, 18.6% of the forest area falls within protected areas (Natura 2000 sites, biotopes, natural reserves, national and regional parks).

Trentino province is a mountainous territory (70.5% of forests are located above 1,000 m a.s.l.). The climate is cool, temperate and mild continental with large differences in the temperature and rainfall from valley to valley. The mean annual temperature in the Adige valley is 11.5 °C, while the annual rainfall averages 883 mm with two main peak periods, in spring (May rainfall averages 94 mm) and autumn (October rainfall averages 110 mm).

Field data collection

The samples of Norway spruce and European beech seedlings and saplings were collected in the field during the main growing season (June–October 2012) in 8 study sites distributed in two forest types (Norway spruce forests and European beech forests). The sites were selected by random extraction in Quantum-GIS from the forest types map made by the Forest and Wildlife Service of the Trentino province. From the bioclimatic point of view all sites are included in the “Supratemperate-Wet”



Figure 1. Trentino province (North-East Italy) with highlighted the 8 study sites.

category of the Rivas-Martinez classification, but there are some differences in average temperature and rainfall.

A set of 47 Norway spruce (22 seedlings and 25 saplings) and 49 European beech (30 seedlings and 19 saplings) samples were collected and measured (Table 1). 60% of samples were uprooted entirely to estimate above-ground and below-ground biomass and to calculate the R/S ratio, while the remaining 40% of samples were cut at the collar to estimate only the above-ground biomass. These species are selected for two main reasons: their quantitative importance in the Alpine region, and their different responses to light conditions. Norway spruce is a mid-shade-tolerant species that dominates the boreal forest zone with Scots pine prevailing on more nutrient-rich, mesic-moist soils, in areas with a more oceanic climate and on sites with a low fire frequency (Barbati *et al.*, 2007). European beech on the other hand is considered to be the most shade-tolerant European broad-leaved woody plant (Jarčuška, 2009).

Due to the species distribution in Trentino province, samples were collected from

different altitude ranges: Norway spruce from 1,103 to 1,589 m a.s.l. and European beech between 405 and 1,630 m a.s.l. In each study site a variable number of samples were collected depending on regeneration density, species composition and site light conditions. The samples were chosen randomly, starting in the centre of the forest management unit and setting a minimum distance between samples of 10 m. The plant height was measured (to the apical bud to the nearest 0.1 cm) and a set of hemispherical photographs were used to estimate the Leaf Area Index (LAI) as described below. In the present research, plants less than 30 cm tall were considered as seedlings, while those with a height between 31 cm and 130 cm were considered as saplings.

Plant area index estimation

In this study, hemispherical photographs were used to estimate the amount of foliage area in a canopy per unit ground surface area (Leaf Area Index – LAI).

For each seedling and sapling sample a set of 16 hemispherical photographs of the canopy – one set of four photographs

Table 1. Distribution of the samples collected by study sites in Trentino province and forest stand characteristics.

Site name	N	E	Altitude (m)	Forest type	N° samples	
					European beech	Norway spruce
Ala	657147	5067368	427	European beech	2	
Castelfondo	663406	5148732	1,148	Norway spruce		19
Condino	624308	5081384	1,315	European beech	10	3
Madonna della neve	647795	5065225	1,608	European beech	14	3
Terres	654357	5130821	1,469	Norway spruce	2	5
Val Calamento	687282	5114149	1,435	Norway spruce		13
Val di Gresta	649434	5083038	1,066	European beech	15	1
Valcava	677826	5119702	1,306	Norway spruce	6	3

per cardinal point following the sequence north, east, west and south - was taken to estimate the LAI. Hemispherical photographs were taken using a Nikon Coolpix 900 camera and a Fish-eye converter Nikon FC-E8 at 1 m from the ground. The camera was used in the programme mode where exposure time and lens aperture are set automatically using the parameters fixed in FISHEYE1 lens mode (focus set to infinity, widest zoom, metering center-weighted), and the shutter speed was varied automatically by the camera.

Hemispherical photographs were processed by the Spot Light Intercept Model (SLIM) 3.02 following the guidelines given by Pastorella & Paletto (2013). LAI provided by SLIM software may be considered as "plant area index" or "vegetation area index", because some trunks and tree branches are captured in the images analysed.

Laboratory analysis

The samples of seedlings and saplings collected in the field were analysed in the laboratory in order to estimate water content and mass. The analyses were carried out within 24 hours after collection in the field to avoid changes in the water content.

Sampled seedlings and saplings were separated at the root collar into above-ground biomass (foliage, stem and branches) and below-ground biomass (stump and roots). The length of roots and shoot was measured with callipers to the nearest 0.1 cm. The sample was then oven-dried for 24 hours at 105 °C and, after cooling in a dryer with silica gel, reweighed to determine the dry weight. As suggested by the standard "EN 14774-2" (British Standard Institute, 2009), for each collected sample, fresh and dry weight were determined using an electronic analytical balance to the nearest 0.01 g.

Data analysis

The data are used to calculate for each sapling and seedling sample the following

parameters: water content (W_c), dry/fresh weight ratio (R_{df}) for above-ground and below-ground biomass, and root/shoot ratio (R/S).

The water content, defined as the weight of water in wood expressed as a percentage of the weight of oven-dry wood, was calculated with the following formula:

$$W_c = \left(\frac{M_F - M_D}{M_D} \right) \cdot 100 \quad (1)$$

where:

W_c = water content as a percentage of oven-dry weight (%);

M_F = fresh (above-ground or below-ground) weight (g);

M_D = dry (above-ground or below-ground) weight (g).

The dry/fresh weight ratio was calculated with the following formula:

$$R_{df} = \frac{M_D}{M_F} \quad (2)$$

where:

R_{df} = dry mass/fresh weight ratio ($g\ g^{-1}$);

M_F = fresh (above-ground or below-ground) weight (g);

M_D = dry (above-ground or below-ground) weight (g).

The ratio of the below-ground weight to the above-ground weight (R/S ratio) depends on plant form and changes in relation to the light conditions (Cairns *et al.*, 1997; Green *et al.*, 2007). The formula used to calculate R/S ratio were the following:

$$R/S = \frac{M_{DBg}}{M_{DAg}} \quad (3)$$

where:

R/S = dry root/shoot weight ratio ($g\ g^{-1}$);

M_{DBg} = dry root system weight (g);

M_{DAg} = dry stem, branches and foliage weight (g).

Statistical analysis

The data were analysed with R software (R core team, 2013) and two equations were developed in order to estimate Norway spruce and European beech biomass.

Two allometric equations (Eq. 4 and Eq. 5) were used to make estimates using the “lm” function from the “stats” package in R software. The first estimates biomass from height and the second estimates below-ground (root and stump) biomass from above-ground (stem, branches and foliage) biomass. In our study, scatterplots of the data indicated that the above-ground biomass of seedlings and saplings were non-linearly related to plant height for both species.

The general allometric equation widely accepted is the power equation:

$$Y = aX^b$$

where Y is oven-dry mass (kg), X is a tree dimension variable (e.g. collar diameter, plant height), a and b are parameters (Ter-Mikaelian & Korzukhin, 1997).

A second approach uses ordinary least squares estimation after logarithmic transformation of both sides of the power equation (Geudens *et al.*, 2004). Consequently, a non-linear equation by applying logarithms to both sides of the equation is fitted. The regression used is the following:

$$\ln(M_D) = a + b(\ln H) \quad (4)$$

where:

M_D = dry (above-ground or below-ground or total) weight (g);

H = height of the plant (cm);

a and b = equation parameters (intercept and slope of the relationship).

Similarly, scatterplots of the biomass distribution in the different components show that a linear log-log equation better fits the

relationship between above-ground biomass and below-ground biomass. Consequently, the following equation was used to estimate the below-ground biomass from the above-ground biomass:

$$\ln(M_{DBg}) = a + b(\ln M_{DAg}) \quad (5)$$

where:

M_{DBg} = dry below-ground biomass of the plants (g);

M_{DAg} = dry above-ground biomass of the plants (g);

a and b = equation parameters (intercept and slope of the relationship).

Results

Water content

The water content (W_c) of the Norway spruce seedlings is 77.3% for the shoots and 67.6% for the roots, while the European beech seedlings have water content of 156.0% (shoots) and 30.4% (roots) (Table 2). For the shoot the water content is higher in the European beech, while for the root it is higher in Norway spruce. These results confirm the data of McKay *et al.* (1999) which show that in seedlings of many species – such as beech and some *Picea* species – the water content in the root system is inversely proportional to the tree diameter.

Water content of the saplings is lower than that of seedlings for both species: Norway spruce 79.7% (above-ground component) and 76.9% (below-ground component), European beech 90.0% (above-ground component) and 110.3% (below-ground component).

Dry-fresh weight ratio

Analysis of the Norway spruce above-ground biomass shows a mean dry-fresh weight ratio (R_{df}) equal to 0.56 for the seedlings and 0.56 for the saplings, while for the European beech the mean dry-fresh weight

Table 2. Mean values of water content (Eq.1), fresh and dry mass (Eq.2) by Norway spruce and European beech seedlings and saplings.

		N	M _F [g]	M _D [g]	W _c [%]	R _{df}
Norway spruce						
Seedlings	Above-ground	22	43.8	24.7	77.3	0.56
	Below-ground	18	11.4	6.8	67.6	0.60
	<i>Total</i>	18	43.7	25.8	69.4	0.59
Saplings	Above-ground	25	503.8	280.3	79.7	0.56
	Below-ground	7	49.7	28.1	76.9	0.57
	<i>Total</i>	7	228.4	124.7	83.2	0.55
European beech						
Seedlings	Above-ground	30	6.4	2.5	156.0	0.39
	Below-ground	23	3.0	2.3	30.4	0.77
	<i>Total</i>	23	8.7	5.5	58.2	0.63
Saplings	Above-ground	19	51.3	27.0	90.0	0.53
	Below-ground	14	34.7	16.5	110.3	0.48
	<i>Total</i>	14	82.4	37.1	122.1	0.45

ratio is 0.39 for the seedlings and 0.53 for the saplings (Table 2). Similar differences in the mean dry-fresh weight ratio were found for the below-ground biomass: Norway spruce seedlings 0.60 and saplings 0.57, European beech seedlings 0.77 and saplings 0.48. Results seem to confirm those of Bolte & Villanueva (2006) which indicated a space sequestration efficiency and a competitive below-ground ability higher in European beech than in Norway spruce.

R/S ratio

The results show that the R/S ratio is 0.52 for Norway spruce seedlings and 0.27 for saplings, while it is 0.90 for European beech seedlings and 0.76 for saplings. The reduction of the ratio values with tree size (and consequently with age) is in agreement with other studies (Ritson & Sochacki, 2003; Konôpka *et al.*, 2010). Other authors found R/S ratio values between 1.1 and 1.5 in European beech regeneration (Fotelli *et al.*, 2001; Platt *et al.*, 2004; Curt *et al.*, 2005).

According to Schall *et al.* (2012) we can observe that the biomass partitioning to shoots and roots in Norway spruce and European beech depends on the ecological characteristics of the species.

Biomass estimation

Table 3 shows that the sapling or seedling height is a good predictor of above-ground and below-ground biomass, with a R^2_{aj} value above 0.8 for all equations and a R^2_{aj} value above 0.9 for above-ground biomass of Norway spruce. Schmidt *et al.* (2009) for the natural regeneration of lenga (*Nothofagus pumilio* Poepp. & Endl.) in Chile show R^2_{aj} values between 0.80 and 0.95. In addition, Pajtk *et al.* (2013) show – for the allometric equations for expressing above-ground biomass on the basis of the diameter – a R^2 of 0.990 in reference to Norway spruce stem and a R^2 of 0.989 for the European beech stem in Slovakia. In the present study, the equation parameters show a high significance level for both species ($p < 0.001$) and the Residual Standard Error (RSE) ranges between 0.66 and 0.77.

The regression results show that below-ground biomass allocation is strongly related to above-ground biomass. In this study, juvenile Norway spruce has a R^2_{aj} value of 0.96 and juvenile European beech a R^2_{aj} value of 0.95 (Table 4). As shown by Curt *et al.* (2005) in young plants, these two variables are closely correlated ($R^2 > 0.95$).

The equation parameters show a high significance level ($p < 0.001$) except for the intercept (a) of the equation for the European beech ($p < 0.5$). Residual Standard Error (RSE) ranges between 0.35 and 0.41 (Tables 3–4).

Some authors have indicated that light and altitude influence plant growth. Ritter *et al.* (2005) show a dependence of European beech and Norway spruce seedling and sapling growth on light in canopy gaps. In particular, beech seedlings become established under a wide range of canopy openings (Wagner *et al.*, 2010). Cunningham *et al.* (2006) found that the growth of Norway spruce saplings in Swiss forests is influenced by LAI, tree size and spring snow duration, whereas Kobe & Hogarth (2007) found that canopy openness may be used to estimate seedling growth.

Mean LAI estimates for Norway spruce were below 3.14 while for European beech they fell below 4.33. This difference agrees with the characteristics of the species, the former being moderately shade tolerant whereas the latter is very shade tolerant. The ANOVA test confirms this difference. The species show a statistical differences in LAI ($F_{1,94} = 18.9$; $p < 0.001$) suggesting a difference in the biomass allocation strategy.

Discussion

The main results concerning allometric equations and quantification of the influence of light on young plant growth can be summarized in three points.

First, our study confirms that the light beneath the canopy influences forest regeneration. Young plants may or may not survive under a specific canopy cover (LAI) range. This is usually referred to as shade or light tolerance. The results confirm the ecological characteristics of the two species. Norway spruce is a shade-tolerant species that can exist as advanced regeneration beneath the canopy of a mature forest stand (Lundqvist & Fridman,

Table 3. Parameter estimates for allometric equation (Eq. 4).

Species	Allocation (M_0)	a	b	R^2_{adj}	SE (a)	SE (b)	RSE	p-value	N
Norway spruce	Above-ground	-5.88 ***	2.73 ***	0.91	0.48	0.12	0.70	< 0.001	47
	Below-ground	-5.08 ***	2.18 ***	0.82	0.67	0.19	0.76	< 0.001	25
	Total	-4.57 ***	2.42 ***	0.86	0.64	0.19	0.72	< 0.001	27
European beech	Above-ground	-5.03 ***	2.01 ***	0.83	0.51	0.14	0.70	< 0.001	48
	Below-ground	-4.58 ***	1.81 ***	0.87	0.48	0.13	0.55	< 0.001	34
	Total	-4.57 ***	2.02 ***	0.83	0.58	0.16	0.73	< 0.001	40

Significant codes: *** < 0.001; ** < 0.01; * < 0.5.

Table 4. Parameter estimates for allometric equation (Eq. 5).

Species	a	b	R^2_{aj}	SE (a)	SE (b)	RSE	p-value	N
Norway spruce	-0.6***	0.86***	0.96	0.12	0.04	0.41	<0.001	25
European beech	-0.20 *	0.99***	0.95	0.07	0.04	0.35	<0.001	34

Significant codes: *** < 0.001; ** < 0.01; * < 0.5.

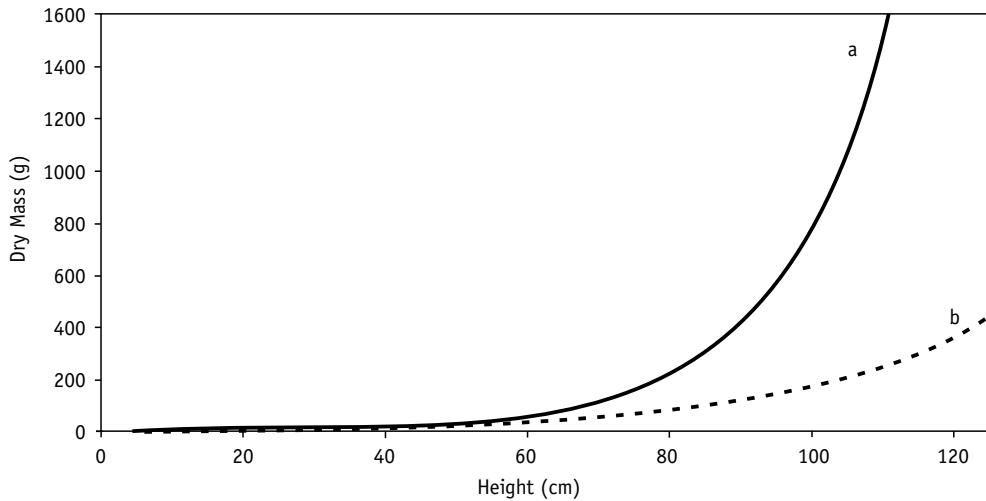


Figure 2. Comparison of height and above-ground biomass equations for Norway spruce: a – our study; b – Mitt *et al.* (2014).

1996), whereas European beech is a very shade-tolerant species (Götmark *et al.*, 2005). Madsen & Larsen (1997) found unsuccessful regeneration beneath canopies with LAI above 3.5. Seedlings and saplings of European beech become established under a wide range of canopy cover. Generally, seedlings of beech grow more slowly than most associated species (i.e. ashes and maples), and they survive better at low or intermediate light (Wagner *et al.*, 2010). Small forest gaps may provide favourable conditions for photosynthesis and growth of beech regeneration as a result of the limited ability of seedlings to acclimate to sudden increases in high irradiance (Tognetti *et al.*, 1998). Beech seedlings survive for long periods at very low light levels (Relative Light Intensity, RLI = 1%), but they grow slowly. Height and diameter growth are best in the open (RLI = 100%), but almost as good with light at 30% < RLI < 50% (Wagner *et al.*, 2010). Such seedlings may experience virtually no height growth for several years, but they can resume rapid growth by the creation of a gap in the canopy (Price *et al.*, 2001).

Second, biomass allocation shows differences related to the species characteristics and to the plant age. In particular, both biomass allocation and water content depend on species and age class. European beech shows a lower biomass accumulation rate than Norway spruce. Besides, the comparison between the allometric equation developed in this study and the one developed by Mitt *et al.* (2014) in Estonia highlights that probably the geographical latitude affects the relationship between biomass and height (Figure 2). The comparison shows that at about 50 cm height saplings growth faster in the Alps.

Third, seedling and sapling biomass allocation may be estimated from height, while below-ground biomass may be estimated from above-ground biomass with high precision. These relationships have often been analysed for adult trees, but rarely in young ones. Both the equations confirmed the results of previous studies: the first gives R^2_{aj} values between 0.8 and 0.91, while the second gives R^2_{aj} values above 0.95.

Conclusions

The study focuses on the analysis of the biomass allocation in the regeneration of European beech and Norway spruce in the Italian Alps. Biomass allocation in young trees at different stages of development is important information to study the response of species (shade-tolerant, mid-shade-tolerant, shade-intolerant) to site conditions (such as light). Generally, plant biomass estimation requires destructive methods, but the development of a robust non-destructive method of estimation using simple measurable variables would provide a useful tool for forest managers. Besides, the method should be useful to estimate the carbon sequestration rate in young forests and to forecast the biomass in forest gaps jointly with remote sensing methods.

The equations developed in this study are site-specific, their application should be restricted to site conditions similar to the basis of this study. Further analysis for validate and verify the presented models with new data from a wider range of site are recommended.

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