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Analysis of intraspecific competition in two subalpine Norway spruce (*Picea abies* (L.) Karst.) stands in Paneveggio (Trento, Italy)

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Abstract

As a consequence of the recent change in human land-use intensity in mountain territories in the Italian Alps, many Norway spruce (*Picea abies* (L.) Karst.) subalpine forests have recently developed without significant anthropogenic disturbance. Even so, their structure and dynamics are still influenced by past human activity. In order to analyze the interactions between past management and current stand dynamics, competition among trees was studied in two 1-ha permanent plots in the Valbona Forest Reserve, located within the Paneveggio-Pale di San Martino Natural Park (eastern Italian Alps). The plots were established in 1993 in two stands with similar age, density and structure but different management history. Tree measurement was repeated in 2005.

We carried out the analysis both on the stand- and on the individual tree scale. We computed maximum Stand Density Index (SDI) for Norway spruce in Paneveggio Park (SDI_{max} 1380) based on an ancillary sample plot network. The intensity of stand-level competition and its course through time was assessed in each study area computing percent relative SDI (SDI%) for the two inventory years.

Competition at individual level was studied using known individual-based competition indices (CIs) as well as a new set of Crown Area Indices (CAI), all of them based on tree variables such as dbh, height, crown area and inter-tree distance. We assessed the performance of each index by evaluating its explanatory power in forecasting individual tree basal area growth (Δg) in a 10-year period.

In the more recently thinned plot, competition did not induce mortality rates comparable to the second plot, that has been unmanaged for the last 60 years. We expect the intensity of competition-induced mortality of the two stands to increase its similarity in the next future.

Individual CIs based solely on tree diameter produced the best performance in plot 1 (e.g., Daniels' CI, $R^2_{adj} = 0.580$). In plot 2 different CIs, including tree height, crown area and inter-tree distance as base variables also, proved the most explanatory ones, including CAI₆ ($R^2_{adj} = 0.553$), which not consider dbh.

We attributed the differential role of tree spatial location and dominance-related descriptors in predicting growth to the time when the stand experienced the last anthropogenic disturbance. The competition relationships still experience the effect of the artificial alteration of forest structure: after human disturbance, mature Norway spruce subalpine forests need several decades to approach more natural dynamics.

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1. Introduction

Competitive dynamics between trees is a key factor in shaping forest stand evolution (Tilman, 1982; Brand and Magnussen, 1988). This process arises when neighboring plants share limited resources, leading to a reduction in survivorship and/or growth rate (Clements, 1929; Grime, 1979; Begon et al., 1996; Oliver and Larson, 1996). For this reason, competition has long been known as a primary process governing population

size, community structure and diversity (Oliver and Larson, 1996; Newton and Jolliffe, 1998; Simard and Sachs, 2004; Simard and Zimonick, 2005).

In order to understand competitive dynamics, several competition indices (CI) have been developed through time to assess the competitive intensity taking place either in whole stand or acting on individual trees. Stand-level competition indices reflect the degree of tree crowding per unit area (Husch et al., 1982), allowing to compare competitive status in different stands (Hynynen and Ojansuu, 2003). Individual-based CIs reflect the local density of competitors interacting with an individual tree (Tomé and Burkhart, 1989). They quantitatively assess the intensity of competition experienced by focal trees

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and allow to quantify the influence of neighboring individuals on the growth of the subjects (Hynynen and Ojansuu, 2003). They may or may not rely on spatial tree location, hence they are usually classified as distance-dependent or distance-independent (Biging and Dobbertin, 1995). The interpretation of the outcome of competition can depend critically on the way competition is measured (Freckleton and Watkinson, 1999). No index has been found universally superior, but rather CIs need to be tested on local species and conditions to determine their applicability (Burton, 1993; Weigelt and Jolliffe, 2003). Moreover, the natural course of competition through time is often influenced by exogenous disturbance events, either natural or anthropogenic. All forest stands in the Italian Alps have been affected by humans in some way, either through direct periodic harvesting or by more subtle forms of land-use. Nevertheless, in the last decades there has been a noticeable reduction of the anthropogenic disturbance and, as a consequence, many forest stands have developed naturally even if their composition and structure still reflect past human activity (Guisan and Theurillat, 2000; Bachofen and Zingg, 2001; Motta and Lingua, 2005).

The Norway spruce (*Picea abies* (L.) Karst.) forest in Paneveggio-Pale di San Martino Natural Park (Trentino Alto Adige, Italy) represents an example of the aforementioned process. Historical evidence shows that the forest has been intensively managed for centuries. Following World War II, the frequency of silvicultural operations decreased and, in the Valbona valley, came to a complete end in 1990, when a forest reserve was established (Motta et al., 2006). The present study focuses on two long-term forest monitoring plots located inside the reserve, characterized by a varying time since last disturbance. Our aim was to analyze interactions between past management and current stand dynamics. We expected competition dynamics to be still influenced by past human activities in the more recently disturbed plot. This effect was expected to be observed both at stand and at individual level, i.e., on mortality rate and on individual growth rate respectively. The objectives of this work were: comparing competitive dynamics at the stand level (1) and at the individual level, analyzing the influence of competition on tree growth using existing individual-based CIs (2) and new competition indices (3), devised using biologically represen-

tative variables, i.e., the variables determining the competitive ability of the trees and shaping the outcome of inter-tree relationships.

2. Methods

2.1. Study site

The study is focused on two stands in the Valbona Forest Reserve (latitude 46°18'N, longitude 11°45'W), a 123 ha subalpine Norway spruce forest included in the Paneveggio-Pale di San Martino Natural Park (Trentino, Italy). The phytocoenosis is classified as *Homogyno-Piceetum subalpinum myrtilletosum* (Di Tommaso, 1983).

Rainfall is 1157 mm/year at Passo Rolle (2002 m a.s.l.), approximately 3 km from the study site, and 1104 mm/year at Paneveggio (1508 m a.s.l.), approximately 2 km from the study site. Annual mean temperature is 2.7 °C at Passo Rolle and 3.7 °C at Paneveggio. The bedrock is porphyry and sandstone, and soils are podsols and rankers.

Both stands are pure and monolayered; spatial pattern of adult tree stems is random (Motta, 2002). The first stand was established after a logging that removed parts of the previous stand around year 1820. This stand was affected by moderate and major disturbances during 19th century, and again during the period 1915–1924. The plot is located a few hundreds meters from a forest road, and was quite accessible for thinning and harvesting operations, that lasted until 1980–1984. The second stand was established after a logging around year 1790. This stand is relatively faraway from forest roads and has developed without anthropogenic influence since the 1940s, when all thinning and harvesting operations were over (Motta et al., 1999) (stand characteristics on Table 1).

2.2. Field measurements

During 1993, two 1-ha (100 × 100 m) sample plots were established and all live and dead standing trees with diameter at breast height (dbh) >7.5 cm, logs, and stumps were identified, labelled with numbered tags and mapped. Dbh was measured for each tree. The inventory was repeated in 2005. We measured diameter at 50 cm height, dbh, total height, crown radii in the

Table 1
Stand characteristics

	Plot 1 (1993)	Plot 1 (2005)	Variation %	Plot 2 (1993)	Plot 2 (2005)	Variation %
Elevation (m a.s.l.)	1695			1815		
Slope (%)	30			47		
Aspect	North			North		
Trees ($n \text{ ha}^{-1}$)	484	476	-1.7%	557	510	-8.4%
Basal area ($\text{m}^2 \text{ ha}^{-1}$)	55.9	64.6	+15.6%	65.9	73.7	+11.8%
Quadratic mean dbh (cm)	38.4	41.6	+8.3%	38.8	42.9	+10.6%
Mean height (m)		31.1			29.6	
Volume ($\text{m}^3 \text{ ha}^{-1}$)	820	946	+15.4%	874	977	+11.8%
Snag density ($n \text{ ha}^{-1}$)	0	9	^a	53	101	+90.6%
Snag volume ($\text{m}^3 \text{ ha}^{-1}$)	0	5.5	^a	21.9	59.9	+173.5%

^a For Plot 1 it was not possible to calculate Snag density and Snag volume percent increment.

four cardinal directions, and height of the lowest living branches (upslope and downslope).

The trees chosen for competition analysis (focus trees) were taken in a 60 × 60 m subplot placed at the center of the permanent plot in order to avoid edge effects. A stratified random sampling was carried out in each subplot by splitting the trees ($n_1 = 179$, $n_2 = 157$) in three equal groups based on dbh class. A random sample of 20 trees was selected from each size class.

An increment core was taken upslope from focus trees at a height of 50 cm. In the lab, following optimization of surface resolution, we measured radial increments of the last 40 years to the nearest 0.01 mm. Data were collected and stored using a LINTAB device and the TSAP package (Rinn, 1996). All the cores were cross-dated against available site chronologies (Motta, 2002; Motta et al., 2002) in order to ensure the assignment of the correct year to each annual ring. We successfully cross-dated 58 cores from plot 1 and 55 from plot 2.

2.3. Stand-level competition analysis

We used Reineke's Stand Density Index (SDI) (Reineke, 1933) to analyze competition intensity in the two stands. SDI describes stand density as the number of 25 cm-dbh stems per hectare required to express an equivalent degree of crowding. We calculated SDI in plot 1 and plot 2, using the summation method proposed by Shaw (2000) as the generalization of Reineke's formulation for all stand structures:

$$SDI = \sum_{i=1}^n \left(\frac{d_i}{25} \right)^b \quad (1)$$

where d_i is the dbh of the i th tree in the sample (cm), and b is the self-thinning coefficient. The value of the coefficient, representing the negative slope of a species' self-thinning line, has been debated (for a review see Pretzsch and Biber, 2005). Nevertheless, Reineke's suggested value of 1.6 can be considered a reasonable approximation for all species when broad ecological dynamics are investigated (Shaw, 2006).

A species' maximum SDI represents the boundary of all possible size-density combinations attained by stands of that given species. Relative density, i.e., the percent ratio between observed stand density and this theoretical maximum, describes the intensity of competition acting in the stand, and can be linked to specific stand developmental stages (Drew and Flewelling, 1979; Long, 1985). Maximum SDI values proposed in literature for Norway spruce are not consistent with one another, ranging from 1057 to 1571 in Austria (Sterba, 1981; Monserud et al., 2005), to 1609 for non-planted spruce forests in Southern and Central Germany (Pretzsch, 2005). The maximum SDI for Norway spruce in the Paneveggio-Pale di San Martino Natural Park (forested area: 2970 ha) was calculated from dataset of 291 sample plots already available. The plots have a surface area ranging from 400 to 452 m² and are located on elevations ranging from 1600 to 2200 m a.s.l. Plots with less than five sample trees, or less than 80% of total

basal area accounted for Norway spruce, were excluded from further analysis in an effort to draw plots from nearly pure stands (Long and Shaw, 2005). One hundred thirty eight plots were used for SDI calculation, based on the dbh of sample trees (Eq. (1)). The 98th percentile of the SDI distribution was assumed as maximum SDI for Norway spruce in the study area (Shaw, personal communication). We obtained percent relative density in the two permanent plots for both inventory years through the ratio between observed and maximum SDI. In order to compare stand development with the self-thinning trajectory of undisturbed stands (Long, 1985), we plotted SDI resulting from both inventories (years 1993 and 2005) on log-log axes and calculated the average self-thinning slope between the two points.

2.4. Individual-based competition indices

In order to analyze competition dynamics in the plots and find out the variables effectively determining the competitive relationships between trees, we used individual-based competition indices (CIs). The explicative power of a competition index is usually tested by how well it predicts the growth of subject tree (Stadt et al., 2002). The set of indices (Table 2) was selected from the literature in such a way to represent different combinations of tree variables (diameter, height, crown area, inter-tree distance) involved in determining a tree's competitive status.

We included both distance-dependent and distance-independent CIs. The latter can be very useful because they require less information than spatially explicit CIs, even if they are not appropriate for the analysis of tree spatial pattern in the plot (Zhao et al., 2006).

The first step to calculate individual-based competition indices was the identification of the trees actively competing with the focus tree. Many methods for competitors selection are available (for a complete review see Biging and Dobbertin, 1992; Alvarez Taboada et al., 2003; Corral Rivas et al., 2005). We recurred to the influence-zone concept proposed by Staebler (1951), i.e., the bidimensional surface within which trees compete for environmental resources (Ottorini, 1978). Competition is assumed to exist when the zones of influence of two trees overlap. Since larger trees may compete at greater distances than smaller trees (Martin and Ek, 1984), we deemed the methods that take into consideration the size of the subject and competitor trees as the most appropriate. Many authors defined the zone of influence as a circular area surrounding the tree with a radius equal to the crown radius of an open-grown tree of the same diameter (Holmes and Reed, 1991; Larocque, 2002; Corral Rivas et al., 2005) or the same height (Ek and Monserud, 1974). We chose tree height, rather than dbh, as the predictor variable because it is less influenced by the degree of crowding experienced during tree development (Assmann, 1970), and therefore it is a better expression of a tree's maximum crown size (Strand, 1972). In order to calculate the size of open-grown crowns, we used the allometric equations proposed by Hasenauer (1997) for Norway spruce in the Austrian Alps, an area both geographically and climatologically similar to the one studied

Table 2
Competition indices and corresponding equations^a

Index	Source	Variables	Equation
Daniels	Daniels et al. (1986)	dbh	$\frac{d_i^2 n}{\sum_{j=1}^n d_j^2}$
NSCIM	Corona and Ferrara (1989)	dbh	$\frac{\sum_{j=1}^n d_j^2}{d_i^2}$
CAI ₁	This work	Crown area	$\sum_{j=1}^n \frac{a_j}{a_i}$
CAI ₂	This work	Crown area	$\sum_{j=1}^n \left(\frac{a_j}{a_i}\right)^2$
CAI ₃	This work	Crown area, height	$\sum_{j=1}^n \left(\frac{a_j h_j}{a_i h_i}\right)$
CAI ₄	This work	Crown area, height	$\sum_{j=1}^n \left(\frac{a_j h_j}{a_i h_i}\right)^2$
Staebler	Staebler (1951)	Distance	$\sum_{j=1}^n l_{ij}$
Hegyí	Hegyí (1974)	Distance, dbh	$\sum_{j=1}^n \frac{d_j}{a_i(l_{ij}+1)}$
R.K. ₁	Rouvinen and Kuuluvainen (1997)	Distance, dbh	$\sum_{j=1}^n \frac{d_j d_i}{l_{ij}^2}$
R.K. ₂	Rouvinen and Kuuluvainen (1997)	Distance, dbh	$\sum_{j=1}^n \frac{(d_j/d_i)^2}{l_{ij}}$
P.K.	Pukkala and Kolström (1987)	Distance, height	$\sum_{j=1}^n \arctan \frac{(h_j-h_i)}{l_{ij}}$
CCS	Alvarez Taboada et al. (2003)	Distance, crown area	$\sum_{j=1}^n \frac{a_j}{a_i l_{ij}}$
CAI ₅	This work	Dist., crown area, height	$\sum_{j=1}^n \frac{(a_j h_j / a_i h_i)}{l_{ij}}$
CAI ₆	This work	Dist., crown area, height	$\sum_{j=1}^n \frac{(a_j h_j / a_i h_i)^2}{l_{ij}}$

^a n , number of competitors; d_i , subject tree dbh (cm); d_j , competitor tree dbh (cm); l_{ij} , distance between competitor (j) and subject (i) tree (m); h_i , subject tree height (m); h_j , competitor tree height (m); a_i , subject tree crown area (m²); a_j , competitor tree crown area (m²).

herein:

$$\ln(cw) = a_0 + a_1 \ln(h) \tag{2}$$

where cw is crown width of an open-grown tree (m), h is total tree height (m), and a_0, a_1 are respectively the intercept and the slope of the regression line. The trees whose zone of influence intersects the open-grown crown of focal tree were chosen as competitors; this selection method was applied to all the CIs used.

The explicative power of each CI was tested examining his relationship with 10-year basal area increment (Δg) of focus trees, defined by

$$\Delta g = \pi [d_{0.5h} \Delta r - (\Delta r^2)] \tag{3}$$

where Δg is individual basal area increment (cm²), Δr is the last 10-year radial increment (cm), $d_{0.5h}$ is diameter at 0.5 m height.

Δg distribution was normalized by logarithmic transformation; the logarithm of Δg is considered one of the best variables reflecting the nonlinear curve of tree growth (Cole and Stage, 1972; Zeide, 1993; Wykoff, 1990) and has got desirable properties with the error structure, e.g., homogeneous variance (Monserud and Sterba, 1996). Δg was modeled as an exponential function of tree size and competition indices by a number of studies (e.g., Cole and Lorimer, 1994).

The following linear regression model was used to investigate the performance of each competition index:

$$\ln(\Delta g) = b_0 + b_1 \ln(CI_i) \tag{4}$$

where CI_i is the value of the competition measure being used for the i th focal tree and b_0, b_1 are respectively the intercept and the

slope of the regression line. We examined overall goodness-of-fit of each regression model (RMSE and adjusted- R^2) in order to assess the most informative competition measure. The analyses were made both on all focus trees at a time and separately for each study area. All analysis were performed using the software SPSS 13.0 (SPSS Inc., Chicago IL).

To better understand the relationship between different variables and the actual competition in the two study areas, we devised a new competition index including biologically representative variables, i.e., the variables determining the aboveground competitive relationships of trees: inter-tree distance, crown area, tree height. The new index was designed excluding diameter at breast height as a predictor, since this variable is strongly related to subject tree's Δg (Holmes and Reed, 1991). Moreover, dbh is related more to the age and the past competitive status of trees (Prévosto and Curt, 2004) than to their current social position and ability to intercept light or shade other competitors.

An individual's ability to intercept light and to shade other competitors also depends on its crown area (Hatch et al., 1975; Doyle, 1983; Holmes and Reed, 1991). As suggested by Alvarez Taboada et al. (2003), we examined the role of crown cross-sectional area calculated by four crown radii, summing the ratios between the i th competitor and the subject's projected crown areas but excluding spatial information (CAI₁) (Table 2). A second index (CAI₂) was designed to reflect the asymmetry of aboveground competition (Weiner, 1990): a squared ratio enhances size differences between focus and competitor trees.

Next, we added total tree height, to explicitly consider the relative social position of the subject tree compared with its neighbors, again using a simple (CAI₃) and a squared (CAI₄)

ratio. Last, we added spatial information to these height-weighted crown area ratios, creating CAI₅, and finally, using a squared ratio, we created CAI₆.

3. Results

3.1. Site description

Plot 2 had an higher density and mean diameter compared to plot 1 (Table 1). Diameter class distributions had a Gaussian shape, supporting evidence of an even-aged structure (Fig. 1). In the last 10 years, a few trees overcame the lower dbh measurement threshold (7.5 cm) in both plots. There was an increase in frequencies of the higher diameter classes and a decrease in the medium-lower ones.

In plot 1 density had slightly decreased since the first inventory because of the death of smaller trees. In plot 2 density had clearly decreased, and mortality involved lower and medium-lower diameter classes (Fig. 1).

3.2. Stand-level competition

The maximum SDI for Norway spruce in Paneveggio-Pale di S. Martino Natural Park was 1380. Stand Density Index in plot 1 was 1051 (76.2% relative density) in 2005 and 935 (67.7%) in 1993. In plot 2, SDI values were 1178 and 1098 respectively (i.e., 85.4% and 79.6% in relative terms).

The average slope of the self-thinning trajectory was -4.802 in plot 1, and -1.139 in plot 2 (Fig. 2). Especially in plot 1, the obtained value was far from -0.6 , i.e., the suggested slope for the maximum self-thinning line (Reineke, 1933).

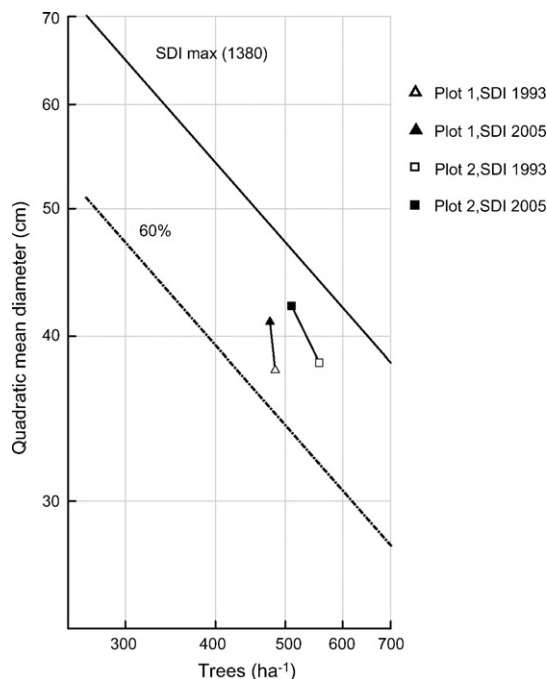


Fig. 2. Plots self-thinning trajectory in the inventory period. Solid line represents maximum SDI. Dash-dot line represents 60% of maximum SDI.

3.3. Individual-level competition

Results obtained by correlation between individual-based CIs and basal area increment (Table 3) show that spatial independent Daniels and NSCIM indices had better R_{adj}^2 in both plots (except NSCIM for plot 2).

Indices performance improved as dbh ratio was taken into greater account, i.e., from R.K.₁ to Hegyi's index to R.K.₂. R.K.₂ was the distance-dependent index having the best R_{adj}^2

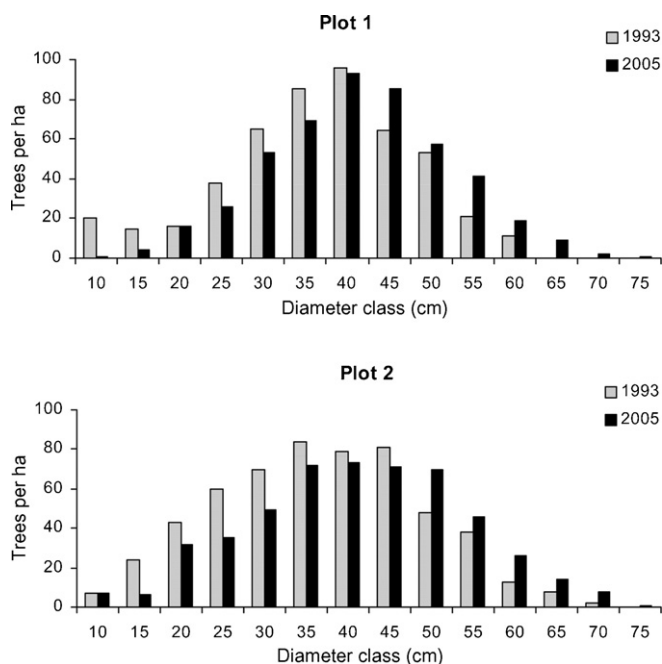


Fig. 1. Comparison between 1993 and 2005 diameter distribution in the study plots.

Table 3
Contribution of competition indices to individual tree basal area growth models (logarithmic linear regression)^a

Index	Plot 1		Plot 2	
	R_{adj}^2	RMSE	R_{adj}^2	RMSE
Daniels	0.580	0.480	0.598	0.646
NSCIM	0.531	0.507	0.537	0.693
CAI ₁	0.056	0.719	0.295	0.855
CAI ₂	0.079	0.711	0.344	0.825
CAI ₃	0.169	0.675	0.475	0.738
CAI ₄	0.188	0.667	0.499	0.721
Staebler	0.030	0.729	0.292	0.857
Hegyi	0.393	0.577	0.508	0.715
R.K. ₁	0.095	0.704	0.176	0.924
R.K. ₂	0.529	0.508	0.581	0.660
P.K.	0.387	0.580	0.503	0.718
CCS	0.082	0.709	0.384	0.799
CAI ₅	0.191	0.666	0.527	0.701
CAI ₆	0.214	0.657	0.553	0.681

^a Pukkala and Kolström's index was computed considering not only trees taller than subject as competitors (as suggested by Prévosto and Curt, 2004), but the totality of the neighboring individuals. The calculated values can be either positive or negative; therefore tree's index value was not log-transformed.

value in both plots. All the distance-dependent indices had an higher R_{adj}^2 in plot 2 than in plot 1, but also an higher RMSE, including those using crown area as a variable. The R_{adj}^2 value of Crown Area Indices proposed herein increased when accounting for competition asymmetry (CAI₂ better than CAI₁) and including the height variable (CAI₃, CAI₄ better than CAI₁ and CAI₂ in both plots). In plot 2, inter-tree distance improved index performance more than in plot 1, and CAI₅ and CAI₆ performed as the best spatial indices (a few lower R_{adj}^2 and a few higher RMSE than R.K.₂).

4. Discussion

The intensive and diversified exploitation that occurred in the past complicates the study of natural forest dynamics. Understanding the dynamics of forest stands with strong past anthropogenic disturbances is particularly difficult because the different types of human impact typically vary in time and space.

At the beginning of the study period, relative density in both plots was already above the 60% threshold, which represents complete resource exploitation and marks the onset of the self-thinning process (Drew and Flewelling, 1979). It is notable that relative density limits marking specific developmental stages are usually broad indications and are not to be considered accurate numerical estimates. Moreover, relative density has been calculated from SDI_{max} of a local sample, and may not represent the species' maximum density.

In 1993, about 10 years later the last thinning operations, SDI in plot 1 was 68% of the maximum. During the observation period, relative density increased up to 76%; the observed mortality involved mostly small size classes, in agreement with the self-thinning hypothesis (i.e., competition-induced death of suppressed trees).

Stand 2 developed in a similar way, increasing its relative density by six percentage points and showing a comparable rise of tree mean size, promoted by an active growth of the surviving trees.

Since more time has passed from the last silvicultural operation in the second stand, its current development may be considered closer to natural conditions. In the last 10 years, the unthinned plot suffered sustained competition-induced mortality; such dynamics seem to have been continuously taking place, since several standing dead trees were already found in the stand at the time of the first measurement.

Current density of plot 1 is close to the initial degree of crowding in plot 2. Even so, percent frequency of standing dead trees in the former situation is too low if compared to the latter to be imputed only to relative density differences (i.e., 2% and 10%, respectively).

The low mortality rate can be related to the effect of past thinning. Even when average size and density are equal, thinned stands do not behave the same as stands grown without thinning (Farnden, 1996). Low thinning imply that suppressed trees – that in undisturbed stands would generally lose competition and die – are removed all at once.

Plot 1 is characterized by a different diameter and height distribution as compared to plot 2. The slope of self-thinning

trajectory in plot 1 is far from the asymptotic self-thinning slope, while in plot 2 this parameter is closer to the reference -0.6 , although mean tree size is similar in the two sites. This means that the latter stand is currently experiencing a higher mortality rate than plot 1 (higher mortality per unit size increase); the self-thinning process is fully operating and involves both lower and medium size classes. According to Newton (2003), the size-density trajectory of a recently thinned stand diverges from that of a stand that had naturally evolved to a comparable density level. In the last 10 years, plot 1 was approaching the more natural trajectory plotted by plot 2. The treated stand will need some additional time to adjust its competitive relationships, i.e., to attain the natural mortality rate typical of its relative density. In absence of exogenous disturbance, we expect mortality rate in plot 1 to approach an incidence closer to the one in plot 2 in the next future.

The differences shown by stand-level measures of competition were consistent with individual CIs measurement. For each CI used in this study, we analyzed the trend in average CI value per dbh class (data not shown). We observed that competitive pressure decreased more rapidly with increasing tree size in plot 2. Here, more intense stand competition dynamics determined stronger inequalities in individual social relationships, while in plot 1 individuals belonging to different diameter classes seemed to suffer a more uniform competitive pressure.

Existing individual based distance-independent CIs (Daniels and NSCIM) use dbh squared to represent subject tree size. Since dbh is correlated with basal area increment, these indices were expected to show a strong relationship with Δg .

Even if site characteristics (climate, micromorphology) seem to be similar to plot 1, all distance-dependent competition indices showed a better R_{adj}^2 in plot 2. The higher RMSE in plot 2 was due to the higher variability. In plot 1, giving a greater weight to competitor distance (e.g., R.K.₂ to R.K.₁) or adding spatial data to the indices' formulation (e.g., CAI₃ to CAI₅) did not improve the predictive ability of the indices. Current tree spatial pattern is influenced by recent anthropogenic interference (more than in plot 2), due to recent logging activities. The likely outcome of this disturbance factor is that natural spatial structure, i.e., the one originated by natural stand dynamics as inter-tree competition, is masked, hence the little role played by spatial location of neighbouring competitors. Past studies have shown that superiority of distance-dependent competition indices is not a rule (e.g., Biging and Dobbertin, 1995). Competitive influence on spatial structure is complicated by the confounding effect of spatial micro-site variability (Fox et al., 2001), and by possible human activities, misleading interpretation of individual CIs (Fox et al., 2007).

Diameter is used in the formulation of many competition indices (e.g., Hegyi, 1974; Lorimer, 1983). Spatial indices using dbh as the main predictor variable (e.g., R.K.₂) showed a good performance in both plots, differently than the other CIs used. Success of these indices was probably due to the correlation existing between subject tree's diameter growth and its dbh, as suggested by Holmes and Reed (1991); such correlation might introduce ambiguity in the expression of the

effect of competitive stress (Brand and Magnussen, 1988; Larocque, 2002). Moreover, diameter is related to the age and past competition history of the tree (Prévosto and Curt, 2004; Fox et al., 2007), rather than to actual social position. Past competitive status was a good predictor of the current one in both plots (see also Cole and Lorimer, 1994).

Inequalities in height within a population can result in the pre-emption of resources (light) by taller individuals (D'Amato and Puettmann, 2004). In monolayered populations, relative height of the subject tree expresses his current social status compared with the neighbors (Holmes and Reed, 1991). Indices using tree height had good performance in plot 2, and quite good in plot 1. The worse performance in plot 1 is consistent with the behaviour of all spatial-dependent indices, where distance has a lower predictive power because of the recent treatments. Tree height still represents a good descriptor of competitive dynamics, retaining a close relationship to 10-year increment. This can also be seen by considering the improvement in index performance when using CAI₃ in place of CAI₁.

Logging activities could also explain the lower performance of CIs using crown area ratio in plot 1 as compared to plot 2. These activities were carried on already mature individuals (tree age averaged 160 years at the time). Ageing trees, especially softwoods (Williams, 1996), lose the ability to expand crown to fill in newly created gaps (Waller, 1986; Zeide, 1987; Piussi, 1994; Joudvalkis et al., 2005). In plot 1 the trees likely did not adapt their crown to the new canopy conditions created by thinning operations; actual crowns are not related to their current competitive status.

As Lorimer (1983) pointed out, growth cannot be predicted from stem spatial pattern alone and requires some indication of the crown class or competitive status of the subject tree, especially when predicting recovery from competition when a competitor is removed (e.g., by thinning, Vanclay, 1994).

The satisfactory performance of the Crown Area Indices proposed herein in plot 2 confirmed that crown area, tree relative height, and spatial information are useful variables to understand and describe competition in a stand experiencing natural dynamics and undisturbed by man in the recent past. The three predictors were simultaneously used in CAI₅ and CAI₆. The fairly good performance of latter indices shows their ability to adequately represent the competitive status of a tree. CAI₅ and CAI₆ might be used in future researches to test their usefulness in competition analysis of Norway spruce forests.

Not many years have passed since the interruption of forest management in the Valbona forest reserve. We found the influence of past silvicultural operation to be still determinant in shaping current competitive dynamics. The plots analyzed herein showed limited differences in stand density, tree age or environmental factors, but competition was likely influenced the most by recent thinning, that altered forest structure and tree spatial relationships. In the first study plot, that has been developing without human disturbances since 1984, the intensity of competition between trees (stand level analysis) and the role of its mediators (individual level analysis) seem to be deeply influenced by past disturbance. In this case, only CIs

using diameter as a predictor variable have the ability to reflect competitive relationships. Conversely, self-thinning dynamic in the more natural developed plot is closer to natural's, and competition can be efficiently modeled by indices based on dominance-related tree variables. These effectively represent competitive relationships between individuals when natural dynamics are the main drivers of stand development. We suggest that following human activities, including moderate logging, mature subalpine Norway spruce stands will require several decades to restore mortality rates and tree competitive relationships characterizing naturally developed forests.

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References

- Alvarez Taboada, M.F., Anta, B.M., Varala, J.G., Gonzalez, A.J.G., 2003. Influencia de la competencia en el crecimiento en seccion en *Pinus radiata* D. Don. Invest. Agrar.: Sist. Recur. For. 12 (2), 25–35.
- Assmann, E., 1970. The principles of forest yield study. Pergamon Press, New York.
- Bachofen, H., Zingg, A., 2001. Effectiveness of structure improvement thinning on stand structure in subalpine Norway spruce (*Picea abies* (L.) Karst.) stands. For. Ecol. Manage. 145, 137–149.
- Begon, M., Harper, J.L., Townsend, C.R., 1996. Ecology: Individuals, Populations, Communities. Blackwell Scientific, Oxford.
- Biging, G.S., Dobbertin, M., 1992. A comparison of distance dependent competition measures for height and basal area growth of individual conifer trees. For. Sci. 38, 695–720.
- Biging, G.S., Dobbertin, M., 1995. Evaluation of competition indices in individual tree growth models. For. Sci. 41, 360–377.
- Brand, D.G., Magnussen, S., 1988. Asymmetric, two-sided competition in even aged monocultures of red pine. Can. J. For. Res. 18, 901–910.
- Burton, P.J., 1993. Some limitation inherent to static indices of plant competition. Can. J. For. Res. 23 (10), 2141–2152.
- Clements, F.E., 1929. Plant Competition: An Analysis of Community Function. Carnegie Institute, Washington.
- Cole, W.G., Lorimer, C.G., 1994. Predicting tree growth from crown variables in managed northern hardwood stands. For. Ecol. Manage. 67, 159–175.
- Cole, D.M., Stage, A.R., 1972. Estimating future diameter of lodgepole pine. US Forest Service Research Paper INT 131. US Department of Agriculture, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Corona, P., Ferrara, A., 1989. Individual competition indices for conifer plantations. Agric. Ecosyst. Environ. 27, 429–437.
- Corral Rivas, J.J., González, J.G.A., Aguirre, O., Hernández, F.J., 2005. The effect of competition on individual tree basal area growth in mature stands of *Pinus cooperi* Blanco in Durango (Mexico). Eur. J. For. Res. 124, 133–142.
- D'Amato, A.W., Puettmann, K.J., 2004. The relative dominance hypothesis explains interaction dynamics in mixed species *Alnus rubra*/*Pseudotsuga menziesii* stands. J. Ecol. 92, 450–463.
- Daniels, R.F., Burkhart, H.E., Clason, T.R., 1986. A comparison of competition measures for predicting growth of loblolly pine trees. Can. J. For. Res. 16, 1230–1237.
- Di Tommaso, P.L., 1983. Contributo ad una tipologia floristico-ecologica della foresta di Paneveggio (TN). Versante meridionale. Annali Accademia Italiana di Scienze Forestali 32, 287–335.
- Doyle, T.W., 1983. Competition and growth relationships in a mixed-aged, mixed-species forest community. Ph.D. diss. Univ. Of Tenn., 86 pp.

- Drew, J.T., Flewelling, J.W., 1979. Stand density management: an alternative approach and its application to Douglas fir plantations. *For. Sci.* 25, 518–532.
- Ek, A.R., Monserud, R.A., 1974. FOREST: a computer model for simulating the growth and reproduction of mixed species forest stands. University of Wisconsin, College of Agriculture and Life Science. Res. Rep. R. 2635.
- Farnden, C., 1996. Stand density management diagrams for lodgepole pine, white spruce, and interior Douglas-fir. Government of Canada, Department of Natural Resources, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. Inf. Rep. BC-X-360, 37 pp.
- Fox, J.C., Ades, P.K., Bi, H., 2001. Stochastic structure and individual-tree growth models. *For. Ecol. Manage.* 154, 261–276.
- Fox, J.C., Bi, H., Ades, P.K., 2007. Spatial dependence and individual-tree growth models I. Characterising spatial dependence. *For. Ecol. Manage.* 245, 10–19.
- Freckleton, R.P., Watkinson, A.R., 1999. The mis-measurement of plant competition. *Funct. Ecol.* 13, 285–287.
- Grime, J.P., 1979. *Plant Strategies and Vegetation Process*. Wiley, London.
- Guisan, A., Theurillat, J.P., 2000. Equilibrium modelling of alpine plant distribution: how far can we go? *Phytocoenologia* 30 (3–4), 353–384.
- Hasenauer, H., 1997. Dimensional relationships of open-grown trees in Austria. *For. Ecol. Manage.* 96, 197–206.
- Hatch, C.R., Gerrard, D.J., Tappeiner, J.C., 1975. Exposed crown surface area: a mathematical index on individual tree growth potential. *Can. J. For. Res.* 5, 224–228.
- Hegyí, F., 1974. A simulation model for managing jackpine stands. In: *Growth models for tree and stand simulation*. Fries J. (ed.) Royal Coll. of For., Stockholm, Sweden, pp. 74–90.
- Holmes, M.J., Reed, D.D., 1991. Competition indices for mixed species northern hardwoods. *For. Sci.* 37, 1338–1340.
- Husch, B., Miller, C.I., Beers, T.W., 1982. *Forest mensuration*, third ed. Wiley, New York.
- Hynynen, J., Ojansuu, R., 2003. Impact of plot size on individual-tree competition measures for growth and yield simulators. *Can. J. For. Res.* 33, 455–465.
- Joudvaskis, A., Kairiukstis, L., Vasiliauskas, R., 2005. Effects of thinning on growth of six tree species in north-temperate forests of Lithuania. *Eur. J. For. Res.* 124, 187–192.
- Larocque, G.R., 2002. Examining different concepts for the development of distance-dependent competition model for red pine diameter growth using long term stand data differing in initial stand density. *For. Sci.* 48, 24–34.
- Long, J.N., 1985. A practical approach to density management. *For. Chron.* 61, 23–27.
- Long, N.L., Shaw, J.D., 2005. A density management diagram for even-aged ponderosa pine stands. *West. J. Appl. For.* 20, 205–215.
- Lorimer, C.G., 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. *For. Ecol. Manage.* 6, 343–360.
- Martin, G.L., Ek, A.R., 1984. A comparison of competition measures and distance models for predicting plantation red pine diameter and height growth. *For. Sci.* 30, 731–743.
- Monserud, R.A., Ledermann, T., Sterba, H., 2005. Are self-thinning constraints needed in a tree-specific mortality model? *For. Sci.* 50, 848–858.
- Monserud, R.A., Sterba, H., 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. *For. Ecol. Manage.* 80, 57–80.
- Motta, R., 2002. Old-growth forests and silviculture in the Italian Alps: the case-study of the strict reserve of Paneveggio (TN). *Plant Biosyst.* 136 (2), 223–232.
- Motta, R., Berretti, R., Lingua, E., Piussi, P., 2006. Coarse woody debris, forest structure and regeneration in the Valbona Forest Reserve, Paneveggio Italian Alps. *For. Ecol. Manage.* 235, 155–163.
- Motta, R., Lingua, E., 2005. Human impact on size, age, and spatial structure in a mixed European larch and Swiss stone pine forest in the Western Italian Alps. *Can. J. For. Res.* 35, 1809–1820.
- Motta, R., Nola, P., Piussi, P., 1999. Structure and stand development in three subalpine Norway spruce (*Picea abies* (L.) Karst) stands in Paneveggio (Trento, Italy). *Global Ecol. Biogeogr.* 8, 455–471.
- Motta, R., Nola, P., Piussi, P., 2002. Long-term investigation in a strict forest reserve in the eastern Italian Alps: spatio-temporal origin and development in two multi-layered subalpine stands. *J. Ecol.* 90, 495–507.
- Newton, P.F., 2003. Yield prediction errors of a stand density management program for black spruce and consequences for model improvement. *Can. J. For. Res.* 33 (3), 490–499.
- Newton, P.F., Jolliffe, P.A., 1998. Assessing processes of intraspecific competition within spatially heterogeneous black spruce stands. *Can. J. For. Res.* 28, 259–275.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. McGraw Hill, New York.
- Ottorini, J.M., 1978. Aspects de la notion de densité et croissance des arbres en peuplement. *Ann. Sci. For.* 35, 299–320.
- Piussi, P., 1994. *Selvicoltura Generale*. UTET, Torino.
- Pretzsch, H., 2005. Stand density and growth of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.): evidence from long term experimental plots. *Eur. J. For. Res.* 124, 193–205.
- Pretzsch, H., Biber, P., 2005. A re-evaluation of Reineke's rule and stand density index. *For. Sci.* 51, 304–320.
- Prévosto, B., Curt, T., 2004. Dimensional relationships of naturally established European beech trees beneath Scots pine and Silver birch canopy. *For. Ecol. Manage.* 194, 335–348.
- Pukkala, T., Kolström, T., 1987. Competition indices and the prediction of radial growth in Scots pine. *Silva Fenn.* 21, 55–67.
- Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* 46, 627–638.
- Rinn, F., 1996. *TSAP Reference Manual, Version 3.0*. TSAP, Heidelberg.
- Rouvinen, B., Kuuluvainen, T., 1997. Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scots pine forest. *Can. J. For. Res.* 27, 890–902.
- Shaw, J.D., 2000. Application of Stand Density Index to irregular structured stands. *West. J. Appl. Forest.* 15, 40–42.
- Shaw, J.D., 2006. Reineke's stand density index: where are we and where do we go from here? In: *Proceedings: Society of American Foresters 2005 National Convention*. Fort Worth, TX [published on CD_ROM]: Society of American Foresters, Bethesda, MD. October 19–23, 2005.
- Simard, S.W., Sachs, D.L., 2004. Assessment of interspecific competition using relative height and distance indices in an age sequence of serial interior cedar-hemlock forests in British Columbia. *Can. J. For. Res.* 34, 1228–1240.
- Simard, S.W., Zimonick, B.J., 2005. Neighborhood size effects on mortality, growth and crown morphology of paper birch. *For. Ecol. Manage.* 214, 251–265.
- Stadt, K.J., Huston, C., Loeffers, V.J., 2002. A comparison of non-spatial and spatial, empirical and resource-based competition indices for predicting the diameter growth of trees in maturing boreal mixedwood stands. *Sustainable Forest Management Network Project Report*, p. 32.
- Staebler, G.R., 1951. *Growth and spacing in an even-aged stand of Douglas fir*. Master's thesis. Univ. of Michigan.
- Sterba, H., 1981. *Natürlicher Bestockungsgrad und Reinekes SDI*. *Centralblatt für das gesamte Forstwesen* 98, 101–116.
- Strand, L., 1972. A model for stand growth. 3rd IUFRO Advisory Group of Forest Statisticians, Louy-en-Josas, 7–11 September 1970. *Institut National de la Recherche Agronomique Publ.*, 72–3, pp. 207–216.
- Tilman, D., 1982. Resource competition and community structure. In: *Monographs in Population Biology*. Princeton Univ Press, Princeton.
- Tomé, M., Burkhart, H.E., 1989. Distance-dependent competition measures for predicting growth of individual trees. *For. Sci.* 35, 816–831.
- Vancly, J.K., 1994. *Modelling Forest Growth and Yield: Applications to Mixed Tropical Forests*. CAB International, Wallingford, UK, XVII, 312 pp.
- Waller, D.M., 1986. The dynamics of growth and form. In: *Crawley, M.J. (Ed.), Plant Ecology*. Blackwell Scientific Publications Ltd, Oxford, pp. 291–320.
- Weigelt, A., Jolliffe, P., 2003. Indices of plant competition. *J. Ecol.* 91, 707–720.

- Weiner, J., 1990. Asymmetric competition in plant population. *Trends Ecol. Evol.* 5, 360–365.
- Williams, M., 1996. A three-dimensional model of forest development and competition. *Ecol. Model.* 89, 73–98.
- Wykoff, W.R., 1990. A basal area increment model for individual conifers in the northern rocky mountains. *For. Sci.* 36, 1077–1104.
- Zeide, B., 1987. Analysis of the 3/2 power law of self-thinning. *For. Sci.* 33, 517–537.
- Zeide, B., 1993. Analysis of growth equations. *For. Sci.* 39, 591–616.
- Zhao, D., Borders, B., Wilson, M., Rathbun, S.L., 2006. Modeling neighborhood effects on the growth and survival of individual trees in a natural temperate species-rich forest. *Ecol. Model.* 196, 90–102.