



## Patterns of larch establishment following deglaciation of Ventina glacier, central Italian Alps

Matteo Garbarino<sup>a,\*</sup>, Emanuele Lingua<sup>b</sup>, Thomas Andrew Nagel<sup>c</sup>, Danilo Godone<sup>d</sup>, Renzo Motta<sup>a</sup>

<sup>a</sup> Department of Agronomy, Forest and Land Management, University of Torino, Via Leonardo da Vinci 44, I-10095 Grugliasco, TO, Italy

<sup>b</sup> Department of Land and Agro-Forestry Systems, University of Padova, Agripolis, Viale dell'Università, 16, I-35020 Legnaro, PD, Italy

<sup>c</sup> Department of Forestry and Renewable Forest Resources, University of Ljubljana, Vecna Pot 83, SI-1000 Ljubljana, Slovenia

<sup>d</sup> Department of Agricultural, Forestry and Environmental Economics and Engineering, University of Torino, Via L. da Vinci 44, I-10095 Grugliasco, TO, Italy

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### ABSTRACT

Rapid glacier retreat often results in extensive areas of deglaciated terrain where primary successional processes occur. We studied biotic and abiotic factors underlying the invasion of larch (*Larix decidua* Mill.) on a glacier foreland and tested the hypothesis that the pattern of its establishment was controlled primarily by terrain age.

The time span between deglaciation and establishment of larch and the importance of the position and shape of the glacier on the forest structure were studied over ~150 years of glacial retreat. We related three data sets (forest structure, topography and spatial position) using ordination methods. Simple and partial Mantel tests and kriging interpolation were used to map and identify the key factors underlying the spatial patterns of larch establishment.

The elapsed time between deglaciation and the germination of the larch trees was estimated between 14 and 34 years, with lower values found closer to the glacier terminus. Sparse and young stands developed near the glacier terminus and Mantel tests indicated significant correlations between spatial distance and ecological distance. The kriging interpolation showed strong agreement between tree age and the spatial pattern of the retreating glacier.

The most influential factors in determining stand density and age were proximity to the glacier terminus and seed sources, as well as litter cover and elevation. The age of trees was strongly influenced by terrain age or time since deglaciation, but as succession progressed forest structure became more complex.

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### 1. Introduction

The global retreat of glaciers during the last 150 years is considered a sign that climatic warming has occurred since the end of the Little Ice Age (LIA—c. 1850) (Kuhn, 1981; Jones and Henry, 2003; Oerlemans, 2005). Rapid glacier retreat is generally more pronounced in mountainous landscapes with steep slopes (Haeberli, 1995; Raffl et al., 2006), resulting in extensive areas of deglaciated terrain where primary successional processes occur (Walker and del Moral, 2003; Raffl et al., 2006). These recently deglaciated forelands provide valuable opportunities to study primary succession (Matthews, 1992).

Environmental factors that typify the foreland, such as topographical features, distance from seed sources and microsite conditions, have an important influence on primary successional pathways (Matthews, 1992; Fastie, 1995; Helm and Allen, 1995;

Houle, 1997; Jumpponen et al., 1999). At the same time, the biotic interactions of colonizing plants, including processes such as facilitation and inhibition, may be important mechanisms of successional change (Grime, 1977; Chapin et al., 1994; Callaway and Walker, 1997). For example, numerous studies have demonstrated the importance of nitrogen-fixing plants for facilitating the establishment of other plant species (Crocker and Major, 1955; Walker and Chapin, 1987; Vitousek and Walker, 1989; Walker, 1993; Chapin et al., 1994; Bellingham et al., 2001). Other studies have shown that site modification through facilitation is not an important mechanism of establishment, and that plants can colonize bare moraine till (Blundon et al., 1993; Chapin et al., 1994; Schlag and Erschbamer, 2000; Mong and Vetaas, 2006). Finally, the life history attributes of colonizing plants, especially seed dispersal ability, may contribute to determining vegetation composition during primary succession (Walker and Chapin, 1987; Chapin et al., 1994; Fastie, 1995; Jones and Henry, 2003; del Moral and Ellis, 2004).

An important aspect of primary succession involves the parallel development and feedbacks between vegetation and the physical environment, especially soil (Crocker and Major, 1955; Borman

\* Corresponding author. Tel.: +39 011 6705535; fax: +39 011 6705556.  
E-mail address: [matteo.garbarino@unito.it](mailto:matteo.garbarino@unito.it) (M. Garbarino).

and Sidle, 1990; Caccianiga et al., 2001). As primary succession progresses, biotic and abiotic factors became more and more entangled (Whittaker, 1987; van Andel et al., 1993; Haugland, 2006). In particular, while the early dynamics of primary succession are strongly influenced by abiotic factors (Houle, 1997; Jumpponen et al., 1999; Walker et al., 2006), the importance of site conditions relative to biotic conditions may decrease with time (Titus and del Moral, 1998). Therefore, simultaneously examining both environmental and biotic factors allows a broader and more inclusive perspective for evaluating landscape-scale successional processes (Matthews, 1992; Matthews et al., 1998).

A common methodology used to study succession on glacial forelands is a chronosequence approach, a space-for-time substitution where the distance from the margin of a retreating glacier is treated as a temporal sequence (Cooper, 1923; Crocker and Major, 1955; Matthews, 1992; Chapin et al., 1994; Fastie, 1995; Helm and Allen, 1995; Jones and del Moral, 2005a). Since glacier forelands are often minimally disturbed by anthropogenic factors, the position with respect to the glacier can be considered an accurate surrogate for terrain age (Matthews, 1992). However, several authors criticized the use of the chronosequence approach in ecological studies (Collins and Adams, 1983; Pickett, 1988) highlighting that its key assumption (i.e. that all sites used to represent various stages of succession have experienced the same history) should be validated through the use of other data sources (Johnson and Miyanishi, 2008), such as dendrochronological methods (Chapin et al., 1994; Fastie, 1995) or historical data (Bleuler, 1986; Vetaas, 1997; Jones and del Moral, 2005a,b).

In this study, we use a chronosequence approach, coupled with dendroecological data, historic records, and interpretation of aerial photographs, to evaluate the simultaneous influence of biotic and abiotic factors on landscape-scale successional processes following deglaciation on the Ventina glacier, Italian Alps. Extreme site conditions such as rocky, bare terrain lead to the presence of sparse, nearly pure larch (*Larix decidua* Mill.) dominated forests on glacier forelands in this landscape. Specifically, we addressed the following questions: (1) Is facilitation an important factor for tree establishment or are trees able to colonize bare moraine till? (2) Do landscape effects, including the distance from the glacier terminus (or terrain age), site conditions, and proximity to seed sources, influence larch establishment? and (3) Do the factors that influence the development of larch stands change as succession progresses?

## 2. Methods

### 2.1. Study area

The Ventina glacier (WGI I4L01122009; National Snow and Ice Data Center, 2007) is located in an 1124 ha watershed of the western Valmalenco (45°26'N; 28°33'E), a lateral valley of Valtellina (Central Alps, Lombardy, Italy). Moraines and glaciers cover most of the watershed. Geology in the region is comprised of silicate bedrock and serpentine is the predominant rock. Ventina is an inner valley of the “endalpic district” (Del Favero, 2002) characterized by a continental climate. Annual precipitation from 1921 to 1990 varied from 668 mm to 1551 mm, and averaged 974.9 mm with a standard deviation of 191.6 mm (Lanzada, 1000 m a.s.l.). There are approximately 170 ha of forest in the watershed, where European larch is the dominant tree species with Norway spruce (*Picea abies* L. Karsten), Swiss stone pine (*Pinus cembra* L.) and mountain pine (*Pinus mugo* subsp. *uncinata* (Ramond) Domin (Christensen, 1987; Montealeone et al., 2006)) as co-dominant species throughout the subalpine zone. Two common subalpine shrub species, dwarf mountain pine (*Pinus mugo* subsp. *mugo* Turra) and green alder (*Alnus viridis* (Chaix)

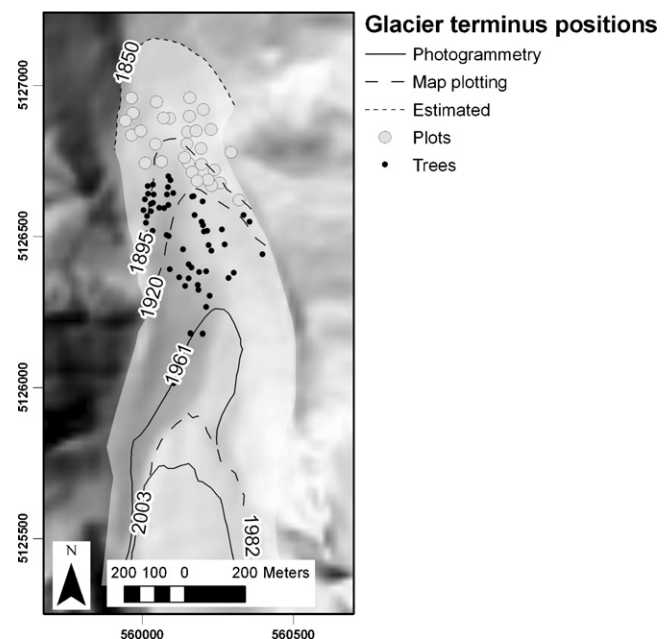
D.C.), are also locally abundant. Several larch forests in the study area were used as wood pastures until the 1970s, but grazing declined in the region and ended in the Ventina Valley. There, previously grazed open stands that have developed without grazing pressure for decades coexist with newly established forests on the glacial moraines (Garbarino et al., 2009).

The Ventina glacier is a simple basin valley glacier with a normal front (Haerberli et al., 1989). The glacier is about 3.3 km long and descends about 1300 m from the Disgrazia Massif (3678 m a.s.l.). The terminus has been retreating at an average rate of 13.7 m/year since 1923 (Smiraglia and Diolaiuti, 2006) and the rate of the retreat has increased since 1990 (Servizio Glaciologico Lombardo, unpublished data), although an expansion of 0.170 km<sup>2</sup> during the 1975–1980 period was documented (Della Ventura et al., 1983; Serandrei Barbero and Zanon, 1993). The valley includes several moraines and an active foreland that is still being colonized by larch trees, but only the lower part of the moraine is occupied by a sparse forest.

### 2.2. Sampling design and data collection

#### 2.2.1. Forest structure

Forest structure was examined in the lower part of the glacier moraine, where the stand density was higher than 50 trees/ha between an elevation of 1990 m and 2050 m a.s.l. Thirty circular plots (12 m radius) were established using a stratified random sampling design, such that a similar number of plots were distributed across the glacial chronosequence (Fig. 1). In each plot, we measured the diameter at breast height (DBH) of all trees  $\geq 5$  cm DBH, and cored the four largest (DBH) larch trees as close as possible to the ground to estimate the earliest dates of tree establishment following the glacial retreat. To characterize the regeneration layer, we counted the number of individuals (DBH  $< 5$  cm and height  $> 10$  cm) of each species in subplots (6 m radius) placed in the center of each plot. Seedlings smaller than 10 cm were not measured due to their high mortality and turnover (Lampainen et al., 2004). We also harvested four larch saplings over a range of heights to examine temporal patterns of regeneration establishment. For each larch sapling, cross-sections



**Fig. 1.** Ventina glacier and its glacier terminus positions showing the sampling scheme used in the study. Map reference system is UTM-WGS84 Zone 32N, and map coordinates are expressed in meters.

were cut at the root–shoot interface, sanded to a high polish and aged to the pith. After harvest, seedling age was determined by counting annual rings at the base of the shoot (Chapin et al., 1994). Finally, we visually estimated the percent cover for litter, herbs, shrubs and small (diameter <10 cm) and large (diameter ≥10 cm) rocks in each subplot.

### 2.2.2. Spatial patterns of larch establishment

In the upper part of the moraine, between an elevation range of 2050 m and 2170 m a.s.l., where the stand density was less than 50 trees/ha, we measured the DBH and extracted cores from all larch trees ( $N = 104$ ). In the laboratory, all cores were sanded to a high polish and the age of the innermost ring was determined.

## 2.3. Data analysis

### 2.3.1. Forest structure

Three data sets were used for the forest structure analysis: (i) forest structure data collected in the field, (ii) topographic variables derived from a 10 m resolution digital elevation model (DEM), and (iii) spatial data collected in the field using a Global Positioning System. Geographic coordinates of forest patches and the glacier terminus were located using a recent aerial orthophotograph (Provincia di Sondrio, 2003). The proximity to forest patches (Garbarino et al., 2009) and the glacier terminus were calculated in ArcGIS using Euclidean distances. Topographic variables included elevation, aspect, slope steepness and curvature. Circular aspect data (degrees) were transformed to linear data following a method based on the interaction of slope and aspect to indicate the relative solar insolation (Clark, 1990). Classical stand structure measures and diversity indices were used to classify different stand types (Table 1). Stand structural diversity was measured by means of diameter standard deviation (Neumann and Starlinger, 2000) and regeneration diversity was measured through relative dominance of larch and the nonparametric Brillouin index. This alpha diversity metric does not require any statistical test for significance differences (Magurran, 2004).

Forest structure and environmental datasets were relativized by the standard deviation in order to improve grouping and ordination analyses, as well as to place variables measured in different units on an equal footing (McCune and Grace, 2002). A cluster analysis was performed on the stand structure data by means of Ward's clustering method based on a Euclidean distance matrix. The 30 sample plots were grouped according to similarity in stand structure using cluster dendrograms and a 50% threshold for total variance explained. A comparison between groups was performed through a Multi-response Permutation Procedure (MRPP) in order to evaluate differences between groups and homogeneity within groups (Zimmerman et al., 1985).

Indirect (PCA) and direct (RDA) gradient analyses on two data matrices including eight stand structure variables (Table 1) and 10 topographic-site variables (elevation, aspect, slope, curvature, rockiness, shrubs, herbs, litter, proximity to glacier terminus and

proximity to forests) were processed. We first used principal components analysis (PCA), an unconstrained ordination method focused on the assessment of the variability of the response variables (forest structure). PCA is an empirical method to characterize the correlation structure of variables (Smith and Urban, 1988; McCune and Grace, 2002; MacKenzie et al., 2004; Garbarino et al., 2009). We used redundancy analysis (RDA) (Rao, 1964; ter Braak and Prentice, 1988) to carry out direct gradient analysis of forest structure as a function of environmental variables. RDA is a constrained ordination method complementary to PCA that provides a way to investigate the variability explained by the explanatory (environmental) variables and their correlation with spatial patterns of stand structure variation (Wimberly and Spies, 2001).

To assess the influence of spatial distribution on similarity between plots, a Mantel test was performed (Mantel, 1967; Urban et al., 2002) comparing two dissimilarity matrices (stand structure vs. spatial data) based on Euclidean distances.

### 2.3.2. Spatial patterns of larch establishment

The age structure data from both the plots in the lower part of the moraine and the individual trees in the upper moraine were used to examine the spatial pattern of larch establishment following the retreat of the glacier. Additionally, an estimate of the elapsed time between deglaciation and the germination of the trees (ecesis) was obtained using the age at coring height (McCarthy and Luckman, 1993). A threshold of 10 cm above ground level was kept as maximum coring height, in order to reduce the error of the age estimation (McCarthy et al., 1991; Koch, 2009). Historical maps, field surveys (Servizio Glaciologico Lombardo, unpublished data) and repeat aerial photography (I.G.M., 1961 and Provincia di Sondrio, 2003) were used to map the glacier tongue positions during the 1895–2003 period. Four groups of trees emerged by subdividing the glacier moraine in four bands (Jones and del Moral, 2005a,b) reflecting the position of the glacier in different years (1961, 1920, and 1895). Differences between groups and homogeneity within groups were analyzed through a MRPP test.

A partial Mantel test on six predictor variables (spatial position, elevation, slope, aspect and distance to the glacier terminus and forests) was performed to assess the relative importance of environmental variables in controlling the age of trees (Mantel, 1967; Urban et al., 2002). In this case, each predictor was employed into the analysis as an individual distance matrix and the Mantel test provided not only an overall test for the relationships among distance matrices, but also tested the contribution of each predictor variable for its pure partial effect on the dependent variable (Manly, 1986; Smouse et al., 1986; Urban et al., 2002). A kriging interpolation method was used to map our point data, converting them to continuous data (Goovaerts, 1997), in order to compare glacier retreat and larch establishment patterns.

All the ordination analyses and grouping (cluster analysis, MRPP and PCA) were performed using the PC-ORD statistical

**Table 1**

Mean values of the eight descriptors (De, density of trees and saplings; BA, basal area; DBH-SD, standard deviation of DBH; Do, proportion of larch (LD), spruce (PA), cembra pine (PC), and mountain pine (PM); HB, Brillouin diversity index, and age, maximum age of trees and saplings) for each structure type obtained by cluster analysis at the Ventina site.

Stand structure types	Plots ( $n$ )	Trees				Regeneration				HB	Age (years)	
		De ( $n/ha$ )	BA ( $m^2/ha$ )	DBH-SD (cm)	Age (years)	De ( $n/ha$ )	Do (%)					
							LD	PA	PC			PM
1	6	313	0.15	6.46	86	140	85	6	3	6	0.22	65
2	10	312	0.05	3.54	62	387	81	3	13	3	0.37	52
3	12	182	0.06	4.91	68	133	100	0	0	0	0.00	50
4	2	77	0.05	4.28	53	0	0	0	0	0	0.00	15

package (McCune and Mefford, 1999); simple and partial Mantel tests were executed through zt software (Bonnet and Van de Peer, 2002) with 10,000 randomizations for each test and kriging was done using the geostatistical software GS+ (Gamma Design Software, 2001).

### 3. Results

#### 3.1. Forest structure

Four structural types were identified from the cluster analysis performed on the stand structure data set (Table 1). The MRPP showed strong and significant ( $T = -8.22$ ;  $p < 0.0001$ ) separation between groups and high ( $A = 0.3$ ) within-group homogeneity. Larch was the only species in the tree layer, but stone pine, mountain pine and spruce were locally present in the regeneration layer (types 1 and 2). The occurrence of species other than larch was significant especially at lower elevations in denser and structured stands. Structural types varied from dense mature stands at low-elevations (type 1) to younger, sparse forests at higher elevations (type 4). Within each plot, the mean age of the tree layer was similar to the mean age of the saplings that were sampled, which indicates substantial variability in growth conditions at small scales.

PCA was used to explore the correlation structure of the sample plots based on the stand structure data. The first and second principal component accounted for 33% and 29% of the total variation, respectively. The ordination of plots revealed a clear separation of groups and a strong negative correlation of elevation ( $r = -0.55$ ) and proximity to forests ( $r = -0.60$ ) with the dominant axis (Fig. 2). The first component (axis 1) was related to tree density, basal area and age of trees and saplings; the second was related to diameter standard deviation, sapling density and diversity (Table 2). A perpendicular position of the elevation vector relative to rockiness indicated that these variables were uncorrelated.

RDA was used to relate stand structure data to environmental data. The first and second axes accounted for 21.3% and 17.3% of the total variation, respectively (Table 3). RDA-I reflected a gradient from low-elevation sites surrounded by mature larch forests to high-elevation sites near the glacier terminus. The low-elevation sites were characterized by dense and old stands with

**Table 2**

Principal component loadings for the first five principal components for the Ventina study area. Loadings greater than 0.4 are indicated in bold.

	Axis				
	PC1	PC2	PC3	PC4	PC5
	33.19 <sup>a</sup>	28.52 <sup>a</sup>	15.92 <sup>a</sup>	8.93 <sup>a</sup>	6.60 <sup>a</sup>
Trees density	<b>-0.46</b>	-0.21	-0.06	-0.40	<b>-0.62</b>
Basal area	<b>-0.42</b>	0.35	-0.39	-0.11	-0.17
Diameter SD	-0.12	<b>0.51</b>	-0.25	-0.40	<b>0.52</b>
Age of trees	<b>-0.49</b>	0.21	0.03	<b>0.46</b>	0.03
Regeneration density	-0.21	<b>-0.54</b>	0.06	-0.22	0.35
Proportion of larch	-0.17	0.17	<b>0.72</b>	<b>-0.47</b>	0.11
Regeneration diversity	-0.27	<b>-0.45</b>	-0.37	-0.07	0.38
Age of regeneration	<b>-0.47</b>	-0.02	0.35	<b>0.42</b>	0.18

<sup>a</sup> % of variance.

high litter depth and regeneration density. The second axis (RDA-II) represented a gradient of ground cover from the herbaceous layer. The sites completely covered by herbs were dominated by larch stands with low DBH variability and high sapling density (Fig. 3).

Simple Mantel tests indicated significant ( $p < 0.05$ ) correlations between spatial distance and ecological distance for all the plots, but not for the single structural types. However, the Mantel statistic ( $r = 0.12$ ) showed a weak relationship between position and stand structure (Table 4).

#### 3.2. Spatial patterns of larch establishment

Larch seedlings in the upper part of the moraine were sparsely distributed and they generally established on till substrate characterized by sand and rocks.

Dividing the glacier foreland into four bands resulted in four clearly separated ( $T = -27.43$ ;  $p < 0.0001$ ) groups of trees. Within-group homogeneity was high (MRPP test;  $A = 0.36$ ), but groups at low-elevation showed higher variability (Table 5). Maximum age increased from 30 years in band 1 to 103 years in band 4 and mean diameter showed a similar pattern.

An ecesis of 14–34 years was calculated from the difference between the estimated germination year (age at coring height) and the date of glacier disappearance from a certain site. This was computed using the mean age of all the trees within a 10 m large buffer zone corresponding to the exact terminus positions during the 1895–2003 period.

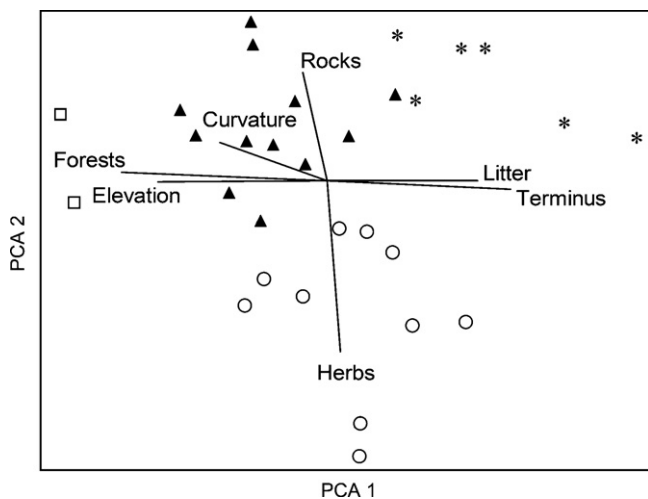
**Table 3**

Correlation of environmental variables with the first four axes of the forest structure RDAs. Boldface numbers represent the correlations greater than 0.4 between explanatory variables and the ordination axes. A  $p$  value of 0.001 on the significance of all canonical axes is derived from a Montecarlo test with 9999 permutations.

	Axis			
	RDA-1	RDA-2	RDA-3	RDA-4
	21.3 <sup>a</sup>	17.3 <sup>a</sup>	6.5 <sup>a</sup>	4.2 <sup>a</sup>
	21.3 <sup>b</sup>	38.6 <sup>b</sup>	45.1 <sup>b</sup>	49.3 <sup>b</sup>
Elevation	<b>0.51</b>	0.20	0.21	-0.03
Slope	0.16	0.09	0.31	-0.26
Slope aspect	-0.13	0.07	0.18	0.02
Slope curvature	<b>0.51</b>	-0.13	-0.16	0.18
Forest distance	<b>0.62</b>	0.11	-0.18	-0.21
Terminus distance	<b>-0.58</b>	-0.05	-0.18	0.16
Rockiness	0.34	-0.38	0.32	-0.03
Litter	<b>-0.49</b>	-0.18	-0.28	-0.14
Herbs	-0.33	<b>0.51</b>	0.21	0.08
Shrubs	-0.28	0.16	-0.15	-0.24

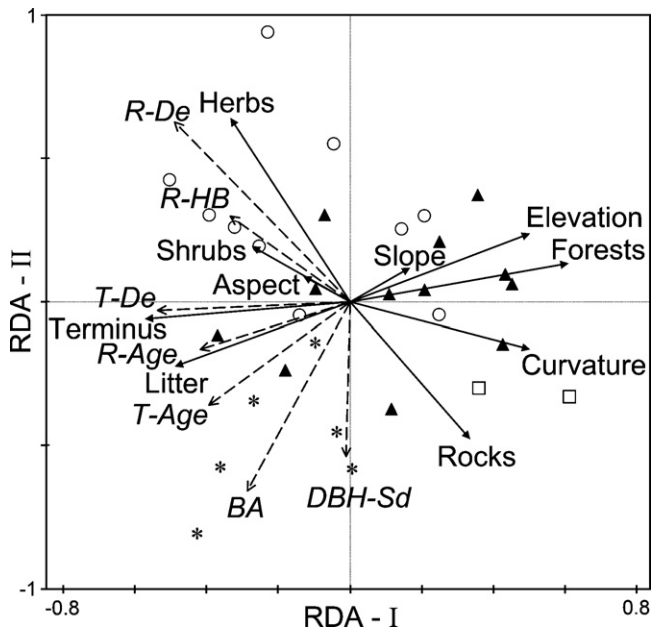
<sup>a</sup> % of variance.

<sup>b</sup> Cumulative % of variance.



**Fig. 2.** Biplot from principal components analysis of 30 plots at Ventina. Site scores are shown divided by stand structure type (\* = 1, ○ = 2, ▲ = 3, □ = 4). Correlations of environmental variables with PCA axes are shown as linear vectors. The first and second principal component accounted for 33.19% and, 28.52% of the total amount of variation, respectively.





**Fig. 3.** RDA ordination biplot of 30 plots at Ventina. Dashed arrows are the stand structure variables (T, trees layer; R, regeneration layer; De, density; BA, basal area; HB, Brillouin diversity index; age, maximum age; and DBH-Sd, standard deviation of DBH). Full-line arrows represent the “biplot scores of environmental variables”. Dots are the sampling sites divided by stand structure type (\* = 1, O = 2, ▲ = 3, □ = 4).

Partial Mantel tests indicated significant ( $p < 0.001$ ) simple and partial correlations between age (age) of trees and spatial distance (space) (Table 6). The only significant correlation between environmental predictors involved elevation and distance from forests. Space was obviously strongly correlated ( $r = 0.9$ ) to both the distance to the terminus and forests.

A Gaussian variogram model was inferred ( $r^2 = 0.987$ ) from the sample data set and was used to construct an isotropic grid of kriged estimates (Fig. 4). A comparison between measured and predicted values was performed by means of cross-validation. A relatively high ( $r^2 = 0.614$ ) correlation expressed a good overall fit of the kriged map to the observed data, which indicated the agreement between tree age and the spatial pattern of the glacier retreat.

**Table 4**  
Effects of distance on similarity between plots. The Mantel statistic was calculated by comparing matrices of spatial distance with ecological distance.

Groups	Mean distance (m)	$r$ (Mantel statistic)	$p$
1	97.87	0.054	0.862
2	125.71	0.230	0.132
3	192.32	0.197	0.158
4	103.32	–	–
All	177.33	0.120	0.018

**Table 5**  
Summary statistics for age and DBH computed for each moraine band.

Bands	Time span	Survey type	N	Age max	Age mean	Age SD	DBH mean
1	After 1961	Photogrammetry	3	30	26	5.29	0.5
2	1961–1920	Map plotting	30	53	36	8.87	5.6
3	1920–1895	Map plotting	38	81	54	11.56	12.7
4	Before 1895	Map plotting	33	103	72	15.15	14.7

**Table 6**  
Simple and partial Mantel correlations between age dissimilarity, spatial distance and dissimilarity on five individual environmental predictors. Mantel coefficients are simple correlations with age dissimilarity, space (autocorrelation), partials with age controlling for space, with space controlling for age. In the last column partial correlations between age and space controlling for all environmental variables ( $Y_s$ ) are reported. Bold numbers indicate highly significant ( $p < 0.001$ ) values, based on, 10,000 permutations.

	$Y \times \text{age}$	$Y \times \text{space}$	$Y \times \text{age} \mid \text{space}$	$Y \times \text{space} \mid \text{age}$	$\text{Age} \times \text{space} \mid Y_s$
Elevation	<b>0.339</b>	<b>0.730</b>	–0.042	0.000	<b>0.389</b>
Slope	0.415	0.163	–0.046	0.164	<b>0.498</b>
Aspect	–0.022	0.014	–0.034	0.029	<b>0.498</b>
Terminus prox.	<b>0.474</b>	<b>0.942</b>	0.018	<b>0.925</b>	<b>0.173</b>
Forests prox.	<b>0.406</b>	<b>0.881</b>	–0.078	<b>0.855</b>	<b>0.324</b>

**4. Discussion**

During early stages of succession near the glacier terminus, larch seedlings were found growing on till substrates, which suggests that facilitation by other trees is not necessary for larch establishment on our study site. These findings are compatible with the microsite requirements for *L. decidua* seedlings; initial establishment is inhibited by thick litter and herb layers, and consequently, depends on mineral soil availability (Risch et al., 2003; Lingua et al., 2008). Other studies have also found that tree species established on bare moraine till without a prior facilitation mechanism (Blundon et al., 1993; Chapin et al., 1994; Schlag and Erschbamer, 2000; Mong and Vetaas, 2006). Given that the environmental conditions are very severe on the site, the lack of interspecific interactions during early stages of succession may not be surprising (del Moral et al., 1995; Houle, 1997).

The establishment of larch on the Ventina glacier foreland occurred 14–34 years after deglaciation. Seedlings that established in the lower part of this time interval were growing closer to the current glacier terminus. During recent decades, the retreat was faster than in the past (Servizio Glaciologico Lombardo, unpublished data), which may be due to climatic warming. These warmer conditions, together with a faster glacial disappearance favored the shorter ecesis interval (14 years) for seedlings found close to the current terminus position. Our results generally confirmed the time span between deglaciation and establishment of trees documented in some other studies. The ecesis interval was estimated between 6 and 30 years on Coleman Glacier, Mount Baker, USA (Heikkinen, 1984) and between 10 and 20 years in the Canadian Cordillera (McCarthy and Luckman, 1993). In the Swiss Alps, establishment of larch on a glacier foreland has been estimated between 10 and 20 years on Morteratsch Glacier (Bleuler, 1986; Burga, 1999).

The landscape-scale approach taken in this study revealed multiple factors that influence the establishment and development of larch stands following deglaciation. Proximity to the glacier terminus and seed sources, litter cover, and elevation were the leading factors that influenced stand density and age. However, it is important to note that some environmental factors were autocorrelated. Proximity to the glacier was positively spatially autocorrelated to elevation, but negatively autocorrelated to distance from other forests. This spatial pattern strengthens the underlying terrain age gradient. Sparse and young stands developed close to the glacier terminus. Other variables such as rockiness and herb cover strongly affect stand diversity, but were uncorrelated to the glacier position. Bare soils were associated with diverse stands, whereas herbaceous cover was positively related to homogeneous stands with high regeneration density. The patchy distribution of rock and herb cover is likely related to soil depth, which may be further influenced by the frost action that

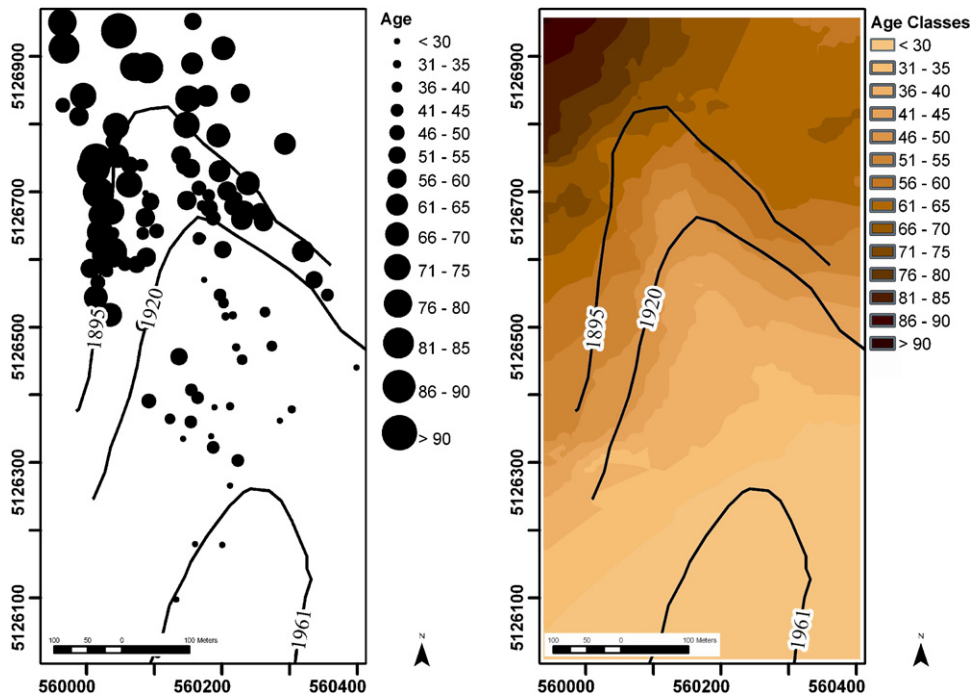


Fig. 4. Kriged map of age of trees around the Ventina foreland. Lines indicate the position of the glacier in the year reported. Points indicate locations of the 104 cored trees.

affects the creation and stabilization of patterned ground features (Haugland, 2006). Our findings generally supported the geocological concept (Troll, 1971; Matthews, 1992, 1999) in that the forest structure is a product of the parallel development of soil and vegetation (Haugland, 2006). The availability of propagules has also been emphasized as a key factor for succession on glacier forelands, and the dispersal ability of species may be more important than facilitation in determining a particular successional sequence (Chapin et al., 1994; Fastie, 1995).

It is widely accepted that physical environmental factors are more important than biotic factors during the early stages of succession in determining the distribution and abundance of plants (Reader and Buck, 1986). Biological processes become more important later in succession when development of the vegetation begins to transform the microenvironment (Matthews, 1992; Vetaas, 1994; Totland et al., 2004). Consequently, safe sites such as large rocks and depressions tend to lose their importance for ecis as succession advances (Jones and del Moral, 2005a; Raffl et al., 2006). Our results suggest that the establishment of larch on the Ventina foreland is mainly controlled by terrain age, but later in succession other factors such as litter amount, elevation and herb cover become more important in shaping the forest structure. For example, while successful establishment of larch seedlings was not conditioned by facilitation in the early succession phases, it was positively associated with herb and shrub layers later in succession, when a structured forest is well established. Moreover, the ordination of forest structure and environmental variables showed a negative correlation between seedlings and stand density.

Biotic and environmental factors are both subjected to change during succession, but physical disturbances such as avalanches can interrupt the process (Turner et al., 1998; Caccianiga et al., 2006; Raffl et al., 2006). When natural and/or anthropogenic disturbances affect the history of a certain area the series of sites used in a chronosequence cannot represent necessary stages of some successional sequence (Johnson and Miyanishi, 2008). For this reason the chronosequence approach is an oversimplification of the successional process because the distribution of vegetation

usually reflects a more complex deglaciation pattern (Matthews, 1992; del Moral and Ellis, 2004; Walker et al., 2007). Thus, the space-for-time substitution needs strong validation of its key assumptions through other methods of study (Rode, 1961; Johnson and Miyanishi, 2008). In this research we used remotely sensed data and field surveys to derive the relative time since deglaciation. No assumptions on a particular sequence of vegetation succession were addressed and only empirical evidence of larch establishment and its causes were evaluated.

At the Ventina glacier foreland the spatial and ecological (age of trees) patterns were interrelated. The kriged map showed strong agreement between the larch establishment pattern and the “tongue” shape of the retreating glacier. The proximity to the glacier terminus is a proxy for terrain age, but is probably also correlated with two main features: the presence of the glacier wind and the so-called “ice box effect” (Holmeier, 2003). Therefore, climatic conditions close to the glacier front are unfavorable both for seed dispersal and establishment.

The Ventina main foreland was largely dominated by larch in the tree layer, but a different pattern was observed in the regeneration layer. The lower part of the moraine was more diverse in the sapling composition, although the newly denudated terrain of the upper moraine was only occupied by larch saplings. This multi-specific process can be explained by the early-successional behavior of larch, a light-demanding species that is easily out competed by late-successional species as the community becomes denser.

Forest structure at Ventina was controlled by several factors that act together to form a complex mosaic of structural types. Other studies highlighted that time, expressed as terrain age, appeared to be the principal factor conditioning species and community distribution (Whittaker, 1987; Matthews, 1992; Caccianiga et al., 2001), even stronger than elevation and distance from seed sources. However, factors such as solar radiation, moisture and disturbances alter the influence of terrain age (Mizuno, 1998), so various stages in primary succession could coexist simultaneously (Raffl et al., 2006; Dolezal et al., 2008). The landscape-scale, spatially explicit approach used in this study

provided valuable insight into successional processes on recently deglaciated terrain. This study suggests that woody species development along a chronosequence may be more strongly influenced by terrain age than herbaceous ground cover. Facilitation was not necessary for successful establishment of larch seedlings at these sites.

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