CLIMATE SIGNALS DERIVED FROM DAY-TO-DAY ANALYSIS: CLIMATE SENSITIVITY OF *PICEA ABIES* IN TRENTINO

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Climate changes directly affect tree growth. Tree performance under changing conditions is maintained by xylem structure that determines the hydraulic and mechanical properties of a stem. The interest for the understanding of how trees grow during the climate change has led to the development of efficient methods for measuring and monitoring growth. Xylogenesis and annual radial increments of Norway spruce (*Picea abies* (L.) Karst.) in Trentino (Eastern Italian Alps) were monitored between 2010 and 2012 with automatic dendrometers and cell analysis. The analyses of intra-annual dynamics of wood formation were used to describe seasonal changes in xylem differentiation phases and to calculate the timing of cell development in Norway spruce. The investigation was conducted in two sites at different elevation, Savignano (650 m a.s.l.) and Lavazè (1800 m a.s.l.), to detect the effect of climate signals in the day-to-day dynamics of wood formation. Dendroclimatological analysis was performed to examine the relationship between the formation of tree rings of Norway spruce and climatic parameters in two contrasting sites. Climate–growth relationships were analyzed using correlation function analysis and moving correlation function, detecting relations between phenological phases of wood formation and seasonal patterns of temperature and precipitation. Effects of climatic variables on stem diameter variation and cell structure were examined, respectively, daily and each 15 days .The results were interpreted according to the dynamics of forest vegetation and synchronicity of cambial activity with meteorological parameters. Models of cambial and tree growth are required to improve the predictive power of ecosystem process models, in which tree growth is often an essential and complex component.

Keywords: cell structure, tree-ring, dendroclimatology, tree growth response, moving correlation analysis.
Parole chiave: struttura cellulare, anello annuale, dendroclimatologia, risposte di crescita, analisi di correlazione.

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1. Climate disturbances and effects on tree growth and survival

European forests are continuously exposed to increasing disturbances due to ongoing climatic changes. These changes impact the forest carbon budget and are suggested to contribute to the recently observed carbon sink saturation in European forests throughout the twentieth century (Seidl *et al*., 2014). The exponential increase of vapor pressure deficit (VPD) with warming air temperature, at constant absolute humidity, may trigger changes in the sensitivity and vulnerability to disturbances, which in turn may increase the risk of tree mortality once the threshold of tree resilience is over-come (Fig. 1).
We generally think of gradual linear changes in climate and ecosystem status. However, abrupt climatic change can lead to abrupt ecosystem change, while gradual climatic change may also trigger abrupt ecosystem change. Forests will, therefore, have to adapt to non-linear risk of erratic and extreme weather events, such as prolonged drought, heat waves, storms and floods (Lindner *et al*., 2010). In particular, increasing droughts and warm temperatures are supposed to induce "physio-logical stress" (because of water and carbon imbalance), determining "forest mortality" under a changing climate (Allen *et al*., 2010), contributing to abrupt ecosystem changes.
Tree mortality constitutes a major element of forest dynamics, influencing species distributions, energy fluxes, hydrological processes, and carbon fluxes (Adams *et al*., 2009). However, the processes of tree death are poorly understood, since they often result from a complex of multiple abiotic and biotic environmental factors that

occur consecutively in time. Tree mortality can be descrybed in terms of *growth-dependent* mortality factors, which affect tree vigor, sometimes for decades prior to death, also due to opportunistic pathogens of host chronic weakness, and *growth-independent* factors, which directly lead to tree death, often without being detectable in tree growth pattern. The critical importance of understanding climate sensitivities of forests is associated with the mechanisms that trigger plant mortality and drive vegetation change and their implications for assessments of climate change impacts and consequent land surface-atmospheric feedbacks (Anderegg *et al*., 2013). For instance, drought has been frequently discussed as a trigger for forest decline (Eilmann *et al*., 2011), causing directly mortality via hydraulic failure in extreme events (Bréda *et al*., 2006), or indirectly as a persistent weakening of trees by reducing carbon storage (McDowell *et al*., 2008; Deslauriers *et al*., 2014). At an increase of drought stress corresponds a reduction of tree tolerance to stress factors (Rebetez and Dobbertin, 2004), as well as phyllophagous insects, pathogenic fungi, frost, air pollutants and mechanical injury, which may lead to a strongly decrease in tree vigor. Consequently, the impacts of regional tree die-off can produce change in forest growth conditions acting as a combination of abiotic stress (e.g., drought spells and heat waves) and amplifying biotic agents able to reduce ecosystem resilience (Van Leeuwen *et al*., 2000). For instance, the reduction of habitat for wildlife and ecosystem potential to sequester carbon can induce the enhancing of opportunities for invasion by exotic species and formation of novel communities, with consequences in alterations of hydrologic cycle and temporal disruptions in ecosystem goods and services (Adams *et al*., 2009). Water shortage, in particular, is likely to become a major factor limiting species distribution and establishment in the near future (IPCC, 2007), leading to increased forest decline and rapid decline-induced vegetation shifts (Eilmann *et al*., 2011).

2. Tree adaptation detection

Emerging drought risks for trees have effects on the anatomical structure, as well as on the physical and chemical properties of wood. However, trees have evolved phenological, morphological and physiological adaptation systems to cope with drought conditions (Battipaglia *et al*., 2010; Pineda-Garcia *et al*., 2013), inducing specific patterns of cambial activity and changes in xylem-hydraulic conductivity and vulnerability to cavitation (Sperry, 2011).

Climate change has been also implicated in shifting phenological patterns of wood formation and bud burst, such as the timing and duration of the growing season across a wide variety of ecosystems (Rossi *et al*., 2013). However, biological processes frequently follow more complex and non-linear response patterns, according to limiting factors that generate shifts and discontinuities (Rossi *et al*., 2013). Thus, the shift of one phenological phase is associated with synchronous and comparable shifts of the following phases. However, small increases in the duration of xylogenesis could correspond to a substantial increase in cell production. These findings suggest that changes of the length of the growing season could be substantial in terms of cell production and carbon uptake by trees, and consequently forest productivity (Rossi *et al*., 2013). Modifications of the environmental conditions that affect plant phenology could potentially engender disproportionate responses in plant growth mechanisms (Fig. 2). Tree performance under changing conditions is maintained by the xylem structure, that determines the hydraulic functionality and mechanical properties of a stem. In this sense, tree ring anatomy and stem diameter monitoring can provide a mechanistic and functional understanding of xylem plastic responses, which can differ in times and fulfill differing functions that define climate-growth relationships (Fonti *et al*., 2013).

The cause-effect relationships between xylogenesis, structure and function of the xylem can be linked through a concerted effort involving multiple disciplines, as functional ecology, wood anatomy, plant genetic, physiology and dendrochronology (Battipaglia *et al*., 2014). The activation and cessation of plant growth during the seasonal course has been mainly related to temperature and water availability (Eilmann *et al*., 2011; Cocozza *et al*., 2012).

The complexity of the interaction between environmental conditions and growth dynamics is indicated by the varying degree of temporal correspondences between stem radius variations and specific climate variables (e.g., Zweifel *et al*., 2010).

The irreversible radial growth and the reversible living-cell dehydration-rehydration processes are related to the depletion and replenishment of stem water stored in woody tissues, and they are detectable through stem diameter variations obtained from daily dendrometer measurements (Steppe *et al*., 2006). Turgor pressure drives irreversible cell expansion and deposition of wall polymers, that define cellular enlargement and, consequently, radial growth, as water-dependent processes (Deslauriers *et al*., 2007).

For instance in conifers, the tissue water-content-related stem diameter variations are largely determined by soil water availability and atmospheric VPD (Zweifel *et al*., 2005). Whereas, phase duration, taken as an indicator of the reversible changes in stem radius, depends mainly on transpiration and sap flow (Steppe *et al*., 2006).

3. A study case: high-resolution analysis of stem growth in *Picea abies* in Northern Italy

Significant interest in how trees grow has led to advances in several methods for measuring and monitoring stem diameter variation, each of them with their own advantages and disadvantages. Timing and dynamics of xylogenesis are crucial aspects for understanding the effects of climate changes on forest ecosystems because they represent the time “window” in which environmental factors directly affect growth (Rossi *et al*., 2007). Dynamics of wood formation are similar in all species; the onset of cell production occurs in the first part of the growing season, while cambial activity, synchronized with photoperiod, reaches maximum rates during summer solstice (Rossi *et al*., 2007). Intra-annual high-resolution stem growth analysis is a first attempt to better understand mechanisms of tree growth processes in relation to the environment. A general hypothesis is that changes in cambium phenology with increasing temperature will be more consistent at higher elevations, with significant variation in rate and duration of the cell division, enlargement and lignification, than at mid-low elevation.

Although the complex interactions between environmental conditions and plant traits are non linear responses and dendrometric records remain often difficult to interpret, the sensitivity of signal recording in the present experiment enabled to determine synchronisation between plant signals and environmental variables.

The sensitivity of tree growth components (change from each measured value to the next) to environmental conditions was tested through high-resolution approaches capable to detect changing in time (dendrometers) and space (cambium anatomy). These tools gave us the possibility to detect (i) stem radius variations (irreversible and reversible radius variation), and (ii) the seasonal course of cambium activity, as a result of the ability of Norway spruce (*Picea abies* (L.) Karst.) to adapt to local conditions. We expected that the changing temperature affects the timing and capacity of cell production of cambium, allowing at lower elevation a longer growth season, and resulting in increased cell production and radial growth. In order to detect temperature-dependent growth strategies of Norway spruce, adult trees of similar age in two sites of Trentino, differing in altitudes, were chosen as model system for an integrated approach of monitoring stem diameter variation and cambial cell production. Tree growth at different altitudes was continuously monitored through dendrometers for three years. On the same trees, microcores were sampled bi-weekly throughout one growing season for examining cambial activity. The strong interest in monitoring forest health is well justified by the importance of forests that in Trentino cover more than 60% of land, characterizing economy, landscape and culture. Since changing disturbance regimes are increasingly challenging for sustainable forest management, they can influence the choices of close-to-nature management aiming to enhance forest ecosystem services, saving ecological specificity and environmental resilience.

Sampling sites were: Pomarolo (45° 56' 41" N; 11° 03' 28 E) and Lavazè (46° 21' 37" N; 11° 29' 42" E). The first one is representative of deciduous forest (*Quercetum pubescentis*) at low altitude (680 m a.s.l.), dominated by *Quercus pubescens*, *Quercus robur*, *Fraxinus ornus* and *Ostrya carpinifolia*, with secondary presence of *Castanea sativa*, *Pinus silvestris*, *Larix decidua* and *Picea abies*. The second, located at 1780 m a.s.l., is representative of the association *Picetum subalpinum* mainly formed by *Picea abies* with rare presence of *Pinus cembra* and *Larix decidua*. The climate in Pomarolo is mild continental with sub-Mediterranean influences; mean annual temperature is around 11 °C and mean annual precipitation is 1150 mm. This site is located on cambisol, in a limestone area. In Lavazè the climate is alpine-continental and the annual mean temperature is 4 °C, while the mean annual precipitation are 1100 mm. The stand grows on podsolic soil above quarz porphyric rocks.

In both sites, a meteorological automatic station was placed in a nearby open area (WMO 1998). Precipitation, air temperature, relative humidity and global radiation were recorded several times per hour and all these values were hourly averaged. In order to follow the seasonal progression of cambial cell development and stem diameter variation, two methods, dendrometers and microcoring, were used. Stem radius variations were daily monitored from January 2010 to December 2012 using automatic point dendrometers (Label *et al*., 2000) on five individual Norway spruce trees in each site. We posed attention in selecting healthy and vigorous trees within 25-30 m of distance to each other, with similar diameter ranging from 35-40 cm at breast height. The used dendrometers measure the linear displacement of a sensing rod pressed against the bark. The operating principle of the linear variable transducer (AB Electronics Ltd., Romford, Essex, UK) that responds to stem radius variation is described elsewhere (Giovannelli *et al*., 2007; Cocozza *et al*., 2009). Trees were monitored with these high-resolution automated dendrometers installed on the trunk at 130 cm from the soil surface. Raw data were recorded every 15 min, and hourly and daily averages were then calculated.

The sampling for the analysis of wood formation in three replicate plants of Norway spruce was performed from 16 April to 13 October 2010 every fifteen days, and repeated the 23 November for control. The sampling consisted in the collection of two microcores (1.8 mm in diameter, 15 mm in length) containing the bark, cambium and the last formed tree-rings from each of the selected stems using Trephor corer (Rossi *et al*., 2006a). Immediately after the sampling, the microcores were put in Eppendorf vials with 75% ethanol and 25% acetic acid for 24 h and then stored in 70% alcohol solution to preserve forming cells from degradation. Transversal microsections 10-12 μm thick were cut by a sliding microtome, restraining the microcores with a special holder. The microsections were stained with Safranin and Astra-blue, dehydrated with graded series of ethanol, and fixed to microscope slides with Canada balsam. Ring formation was assessed by anatomical observations with an Olympus BX 40 light microscope at a magnification of 400x. Observations consisted in counting the number of cells in the cambial zone and tracheids in enlargement, wall thickening and mature phases along three radial files on each microsection (Rossi *et al*., 2006b).

Both the methodologies stressed a distinct growth pattern throughout the season in each of the two sites, which was related to altitude and temperature. Correlations between parameters derived from dendrometers (maximum daily shrinkage and stem increment) and environmental variables highlighted the effects of climate on stem diameter fluctuations and radial growth patterns. The onset of radial growth and intra-annual variations of stem diameter were differently defined at each elevation. In trees at higher elevation (Lavazè), intra-annual variations in stem diameter revealed weaving peaks of radial increment, which may be the consequence of distinct stem rehydration/dehydration

cycles. Whereas, at lower elevation tree growth was more regular, showing a constantly increasing trend (Fig. 3).
The vegetative season, with the formation of enlargement cells, occurred starting from May (DOY 123) in Pomarolo and from June (between DOY 137 and 151) in Lavazè, while the last developing cells were detected in September (DOY 256) in Pomarolo and at the end of August (DOY 242) in Lavazè. The mean number of cells produced in 2009 was 163 in Pomarolo and 27 in Lavazè. Trees showed different timing of wood formation at the two altitudes, with a longer xylogenesis in Pomarolo (≈150 d) than in Lavazè (≈70 d). The onset of cambial activity was earlier and ended later in trees at lower elevation (Pomarolo), confirming that the start of cell division is a key factor determining the duration of xylogenesis and differences in tree ring widths.

4. Conclusion and perspectives

Under global warming, energy-limited forests, like those at higher elevation (Lavazè), can decease productivity and more easily reach and overcome the threshold of mortality because of increasing water deficit. Again, it is not clear whether plasticity in xylogenesis or disproportionate increases in xylem cell production might occur in low-elevation trees (water-limited forests), with lengthening of the period of cell division. Research gaps and key questions need to be filled and answered for predicting how trees will respond to projected climate change.
The development of mechanistic models can provide a more complete picture of forest resilience to environmental disturbance (Fig. 4).
Indeed, at the regional level, a mechanistic understanding of the connections between the hydrological and carbon cycles in different species is needed to elucidate the impacts of climate change on tree growth or tree mortality. As an example, Scots pine under drought stress has been found to build a more effective water-conducting system (e.g., larger tracheids) in a shorter period of wood formation, at the cost of a probably higher vulnerability to cavitation (larger tracheids with thinner cell walls), but without losing the capability to recover (Eilmann *et al*., 2011). The shortening of the growth period in trees under increasing dry conditions would indicate that the period in which wood formation takes place could become much shorter, under the projected climate scenario for the Alpine environment, than the potential and actual phenological growth period.
Although several tree-ring studies have been carried out in *P. abies*, how its radial growth at intra-annual resolution is influenced by weather conditions has scarcely been explored. In this study, technology advancements have contributed to the ability to collect information at high spatial and temporal resolution and to store large amounts of data (Battipaglia *et al*., 2014).
Attempting to isolate a growth signal from large amounts of data has proven challenging, though feasible. Many researchers have used daily weather variables to explain variability of the "isolated growth" (Deslauriers *et al*., 2003). Further work involving simple physiological and functional models will also expand our understanding of tree water deficits, providing insight into the efficiency of species-specific response to drought conditions (Zweifel *et al*., 2005).
In this sense, cambium growth models, which inherently require a thorough understanding of influences on cambium activity, may provide a more complete basis for data interpretation, when using tree rings as an archive of environmental information (Breitenmoser *et al*., 2013).

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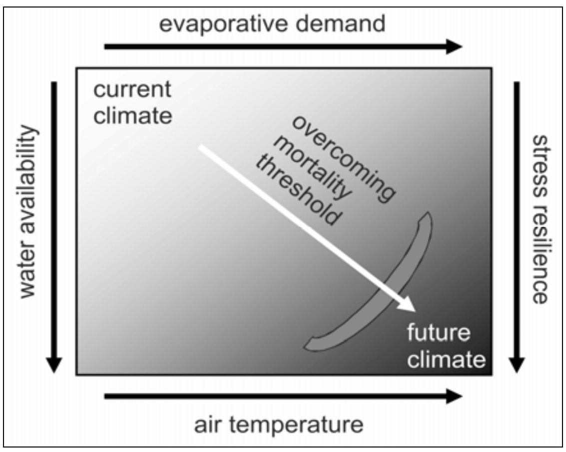

Figure 1. Scheme of the ecological factor drivers of stress resilience and tree mortality.

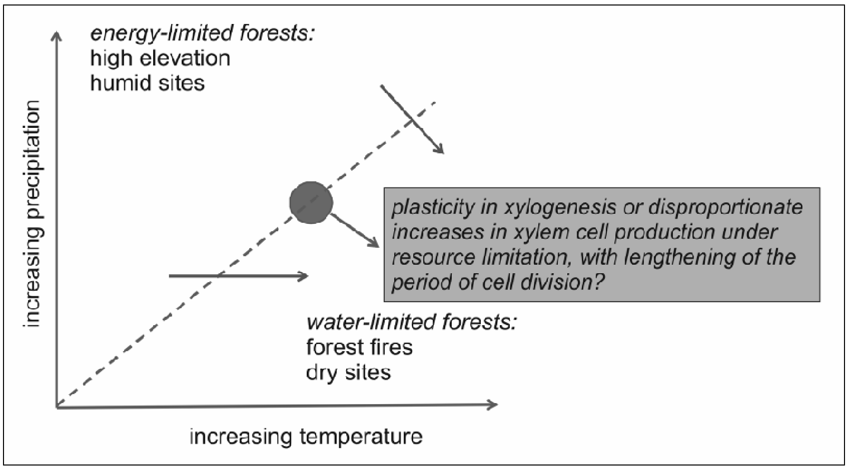

Figure 2. In a global warming scenario, it is questioned whether trees will adapt and adjust structurally and functionally in order to maintain growth performance or if they will reduce productivity and eventually overcome the threshold of mortality.

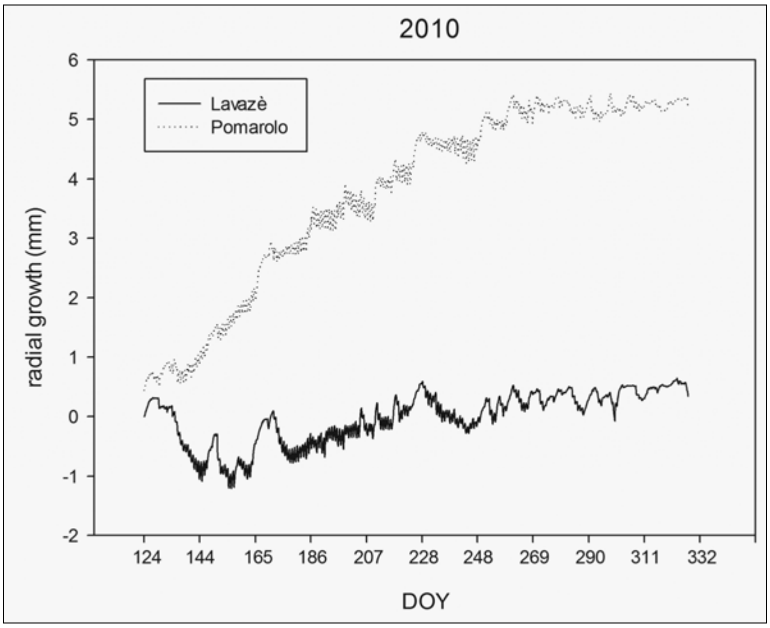

Figure 3. Radial growth of Norway spruce detected trough dendrometers in Lavazè (high elevation) and Pomarolo (low elevation) in the 2010 growing season.

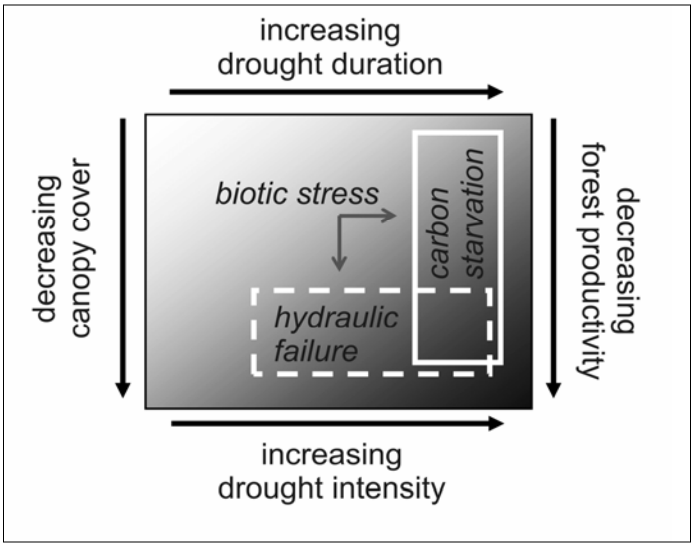

Figure 4. Potential trajectories of abiotic constraints with global warming, as amplified by biotic agents, and consequent damages to tree functionality and forest ecosystem.

RIASSUNTO

Segnali del clima dall'analisi giorno per giorno: sensitività al clima di *Picea abies* in Trentino

I cambiamenti climatici influenzano direttamente l'accrescimento delle piante. Le performance degli alberi in risposta ai cambiamenti climatici sono definite dalla struttura dello xilema che determina le proprietà idrauliche e meccaniche del fusto. L'interesse per i processi che regolano la crescita degli alberi ha definito diversi metodi di misura e monitoraggio. Le dinamiche della xilogenesi e di accrescimento del fusto di abete rosso (*Picea abies* (L.) Karst.) in Trentino sono state monitorate tra il 2010 e il 2012 mediante l'uso di dendrometri automatici e analisi cellulare. Le dinamiche annuali della formazione del legno sono state utilizzate per descrivere le variazioni stagionali delle fasi di differenziazione dello xilema e per calcolare lo sviluppo cellulare dell'abete rosso. Lo studio è stato condotto in due siti differenti per altitudine, Savignano (650 m s.l.m.) e Lavazè (1800 m s.l.m.), per identificare il segnale climatico, giorno per giorno, nella dinamica di formazione del legno. La relazione clima-crescita è stata studiata al fine di definire la possibile azione delle variabili climatiche sulla formazione del legno dell'abete rosso ed è stata analizzata mediante funzione di correlazione, rilevando relazioni tra la formazione del legno e gli andamenti stagionali di temperature e precipitazioni. Gli effetti delle variabili climatiche sulla variazione del diametro del fusto e sulla struttura cellulare sono state analizzate, rispettivamente, a scala giornaliera. I risultati sono stati interpretati seguendo le dinamiche forestali e la sincronicità dell'attività cambiale. Lo sviluppo di modelli di attività cambiale e di crescita degli alberi è necessario per migliorare la modellistica dei processi di ecosistema, dove una componente essenziale e complessa è proprio la crescita dell'albero.

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