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IAWA Journal 37 (2), 2016: 232–259

INTRA-ANNUAL DENSITY FLUCTUATIONS IN TREE RINGS: HOW, WHEN, WHERE, AND WHY?

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ABSTRACT

Intra-annual density fluctuations (IADFs) in tree rings are generally considered structural anomalies caused by deviations from the "normal course" of xylogenesis during the growing season. This definition is based on the bias that, under "normal conditions", cambial activity stops once a year. Each tree ring can thus be dated to one calendar year, which is one of the principles of dendrochronology. The formation of IADFs can be triggered directly by environmental changes, especially in precipitation and temperature, that affect cambial activity and cell differentiation. It can also be the result of limited photosynthesis, due to defoliation induced by biotic or abiotic constraints.

Often indicated with alternative terms, IADFs were first described in the 1930s, and recently reported for many trees and shrubs from different ecosystems throughout the world, particularly for Mediterranean species. Different types of IADFs have been detected; their formation and structural properties depend on many factors including tree genotype, age, size, rooting depth, habitat, soil, climate, photosynthetic activity, and allocation strategies. Whether IADFs affect the adaptive capability of plants remains, however, unclear.

We provide an overview of the main anatomical features of IADFs and their occurrence in tree rings from various environments and climatic regimes. We propose a simplified way of classifying them and discuss the hypotheses about their functional role and the factors triggering their formation. To understand the ecological role of IADFs better, we recommend a multidisciplinary approach,

Published by Koninklijke Brill NV, Leiden

DOI 10.1163/22941932-20160132

involving wood anatomy, dendroecology, and stable isotopes, which has already been applied for Mediterranean species. We conclude by considering that IADFs appear to be the "rule" rather than "anomalies" in some ecosystems where they help plants cope with fluctuating environmental conditions. Moreover, their anatomical structure represents a valuable proxy of past climatic conditions at a sub-seasonal resolution and may be relevant to adapt hydraulic functioning of living trees to changing climatic conditions.

Keywords: Cambial activity, double rings, false rings, intra-annual density fluctuations (IADFs), Mediterranean ecosystems, boreal climate, temperate zones, tropics.

INTRODUCTION

Climate was already known to affect tree-ring growth in the 16th century. Leonardo da Vinci observed that the number of rings in the branches of a tree indicates their age, and that the width of tree rings is related to the environmental conditions (*e.g.* abundance of precipitation) during the year of their formation. Tree rings are formed in response to genetic and environmental drivers, and are described as "well-defined increments encircling the entire stem". They should be distinguished from "growth zones", which appear as "partially faint increments which do not encircle the entire stem" (Schweingruber 2006) and can be considered as intra-ring growth bands.

By definition, in environments where a single yearly flush of growth begins in spring, as in temperate climates, tree rings appear as an alternation of light and dark bands due to the transition from the less dense earlywood (formed in spring) to the denser latewood (formed in summer) (Fritts 1976). The alternation of earlywood and latewood is more evident in softwood and ring-porous hardwoods than in diffuse-porous hardwoods (Fig. 1–3), and can be found in different plant functional types and in several climate conditions. The transition between the earlywood and latewood within each tree ring, and the boundaries between the different tree rings, are determined by genetic and environmental factors.

Fluctuations in environmental conditions, especially in temperature and water availability, affect cell formation and differentiation, which are ultimately responsible for tree rings' anatomical appearance (Schweingruber 2007). Environmental variability can have different effects on cell formation, thus on intra-ring variations in wood anatomical traits, depending on the physiological and hormonal status of the plant which regulate dormancy or quiescent phases, cambial activity, cell differentiation, and sensitivity to environmental signals (Borchert 1991; Groover & Robischon 2006; Aloni 2007).

The seasonal dynamics of cambial activity are responsible for the development of tree rings either annually or over shorter periods. In environments where cambial activity occurs during a single continuous period and stops only once a year due to limiting conditions, such as extreme low temperatures, tree rings are annual. This is frequent in forests in temperate climates at higher latitudes where trees develop one ring each calendar year. Whenever and wherever cambial activity stops more than once a year, deviations from the "normal" succession of earlywood and latewood bands occur.

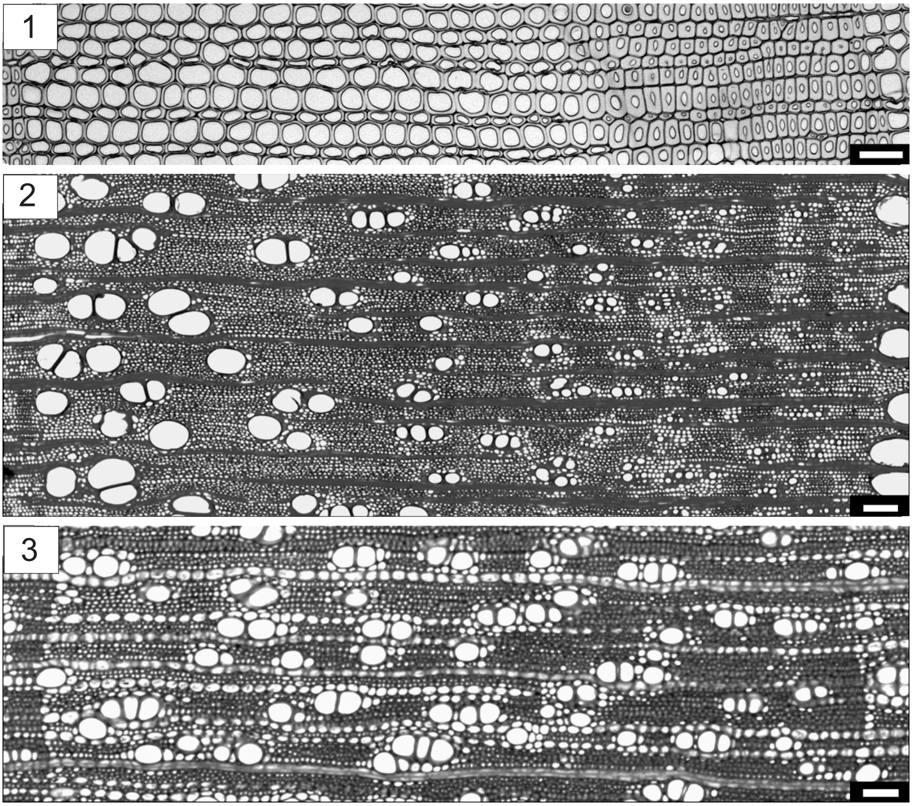

Figure 1–3. Cross sections of tree rings corresponding to one calendar year. – 1: *Pinus halepensis* (Kindly provided by Angela Balzano). – 2: *Fraxinus ornus*. – 3: *Olea europaea*. — Scale bars = 100 µm.

If the cambium remains active throughout the year, it is unlikely that distinct yearly tree rings are formed (Evert 2006). If, on the other hand, cambial activity stops more than once a year, complex tree rings are formed. These are characterised by several successive layers of earlywood and latewood, forming rings referred to as false rings, double rings, growth zones, intra-annual rings, or rings with intra-annual density fluctuations (IADFs) (Tingley 1937; Schulman 1938; Bräuning 1999; Rigling *et al.* 2001; Cherubini *et al.* 2003).

IADFs were initially considered mainly as constraints in the application of dendrochronology because they hamper the synchronisation of individual tree-ring series, the dating of ring-width curves, and the calculation of chronologies. During the last decade, IADFs have attracted more attention because they reflect variations in climatic conditions during the growing season, and can be used as proxies of past environmental conditions with intra-annual resolution. They may also be used to visually crossdate tree-ring series.

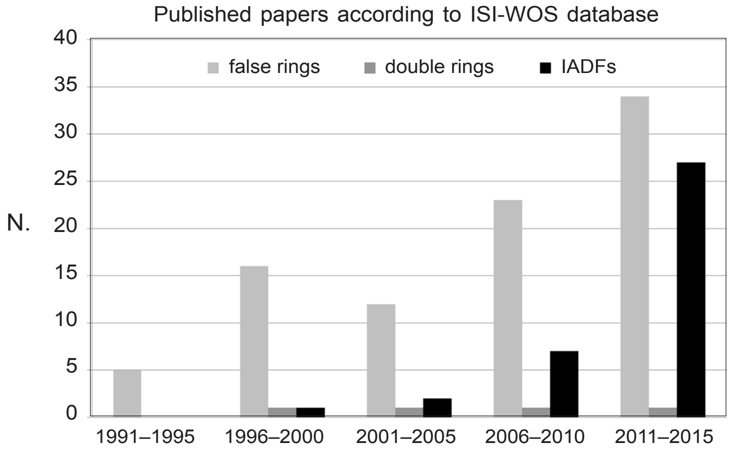

Figure 4. Number of papers published from 1991 to 2015 dealing with false rings, double rings or intra-annual density fluctuations (IADFs), as indexed in the Web of Science^{TM} database (Thomson Reuters).

According to the Web of Science^{TM} database (Thomson Reuters) (Fig. 4), the number of papers dealing with "false rings" has increased considerably since 1991, when Zhang and Romane (1991) published a paper on the relations between the occurrence of false rings, ring size and climatic parameters in *Quercus ilex* in southern France. Eight years later, the term "IADFs" appeared in a paper by Bräuning (1999), indexed in ISI-WOS, describing IADFs in *Pinus densata* trees from southern Tibet, which linked the position of IADFs within the tree ring to cold or dry events. Then, four papers were published in 2007 by three independent groups in Europe on IADFs in pine species and in *Q. ilex* growing in a Mediterranean climate (Campelo *et al.* 2007a,b; De Luis *et al.* 2007; De Micco *et al.* 2007). Several researchers have since then investigated the formation of IADFs and related their occurrence to factors to do with either such intrinsic features of the species as the genotype, sex, age, size, habit, leaf photosynthetic activity, and food reserves, or the growth environment (*e.g.* soil, climate, weather, latitude, and altitude). The number of papers on IADFs has increased markedly in the last five years (Fig. 4).

This review paper provides an overview of the literature dealing with IADFs, which are variously called also false rings, double rings, growth zones or intra-annual rings. All these terms can be considered as synonyms referring to a deviation from the condition considered "normal" in dendrochronology in which one tree ring contains two concentric sheaths of cells, earlywood and latewood, corresponding to one calendar year. We show that, although IADFs have been studied mainly in Mediterranean ecosystems, they also have been reported from other environments (*e.g.* temperate, boreal, and tropical ecosystems), and sometimes related to different environmental conditions. We also discuss the potential of different methodological approaches in analysing IADFs and for revealing the mechanisms behind the formation of different types of IADFs and their ecological role.

Anatomical description and ecological significance of IADFs

IADFs are regions within a tree ring where abrupt changes in density occur. They are detectable through quantitative wood anatomy (*e.g.* by calculating the ratio between the cell wall thickness and lumen width or the space occupied by cell walls in relation to the total wood area), or measurable as X-ray density or microdensity profiles (Kaennel & Schweingruber 1995). Viewed by the naked eye, or under the microscope at low magnification (up to about × 100), IADFs appear as either a dark band of dense wood within the earlywood (due to the formation of latewood-like cells) or a light band of less dense wood within the latewood (due to the formation of earlywood-like cells).

In softwoods, the distinction between earlywood and latewood, and consequently the identification of latewood-like or earlywood-like cells, is more straightforward than in hardwoods. Indeed, in softwood, tracheids can be unambiguously classified as latewood-type tracheids if, in radial direction, the common double cell wall thickness is equal to or greater than the cell lumen diameter (Mork 1928). In hardwoods (ring-porous, semi-ring-porous or diffuse-porous), variations in density may arise from the concurrent variation in many anatomical features, such as the lumen size and cell-wall thickness of both vessels and fibres.

The distinction between IADFs and true ring boundaries is not always easy, especially in hardwoods generally and in diffuse-porous species in particular. The transition between earlywood and latewood cells at the IADF level is, according to some authors, not as abrupt as in a true tree-ring boundary (Schulman 1939; Villalba & Veblen 1996). However, this definition is insufficient to distinguish IADFs from true tree-ring boundaries, since genuine tree-ring boundaries may also vary in distinctness. Even within one species, in some years, IADFs' transition to the neighbouring cells (*e.g.* from large, often thin-walled cells, to narrow, often thick-walled cells, or *vice versa*) may be gradual, while in other years the change in cell size is abrupt and indistinguishable from that of true tree-ring boundaries (Fig. 5–7). The abruptness of the transition probably depends on the intensity of the environmental factor triggering the IADF formation (Rigling *et al.* 2001).

In some species, the occurrence of specific anatomical features, such as the increased incidence of thin-walled parenchyma cells, narrow marginal parenchyma bands, and resin canals, can help to distinguish IADFs from true ring boundaries (Campelo *et al.* 2007a; Schweingruber 2007). Hence, if the identification of IADFs on the basis of wood anatomy is ambiguous, cross-dating with well-established reference chronologies is probably a more reliable method to identify IADFs and is commonly applied, with the detection of growth zones being easier in stem disks than in cores (Cherubini *et al.* 2003; Battipaglia *et al.* 2014).

Most studies on the relations between IADFs and climatic conditions have focused on IADF occurrence and frequency in different tree species and environments (Bräuning 1999; Rigling *et al.* 2001; Campelo *et al.* 2007b; Battipaglia *et al.* 2010; De Grandpré *et al.* 2011; De Luis *et al.* 2011a; Venegas-González *et al.* 2015). The relations between IADFs and environmental fluctuations are not always straightforward. It is therefore challenging to draw unequivocal conclusions on cause-effect relations for species growing in different environments, because how trees react physiologically to identical environmental stressors is also affected by their age, size and growth rate, as well as

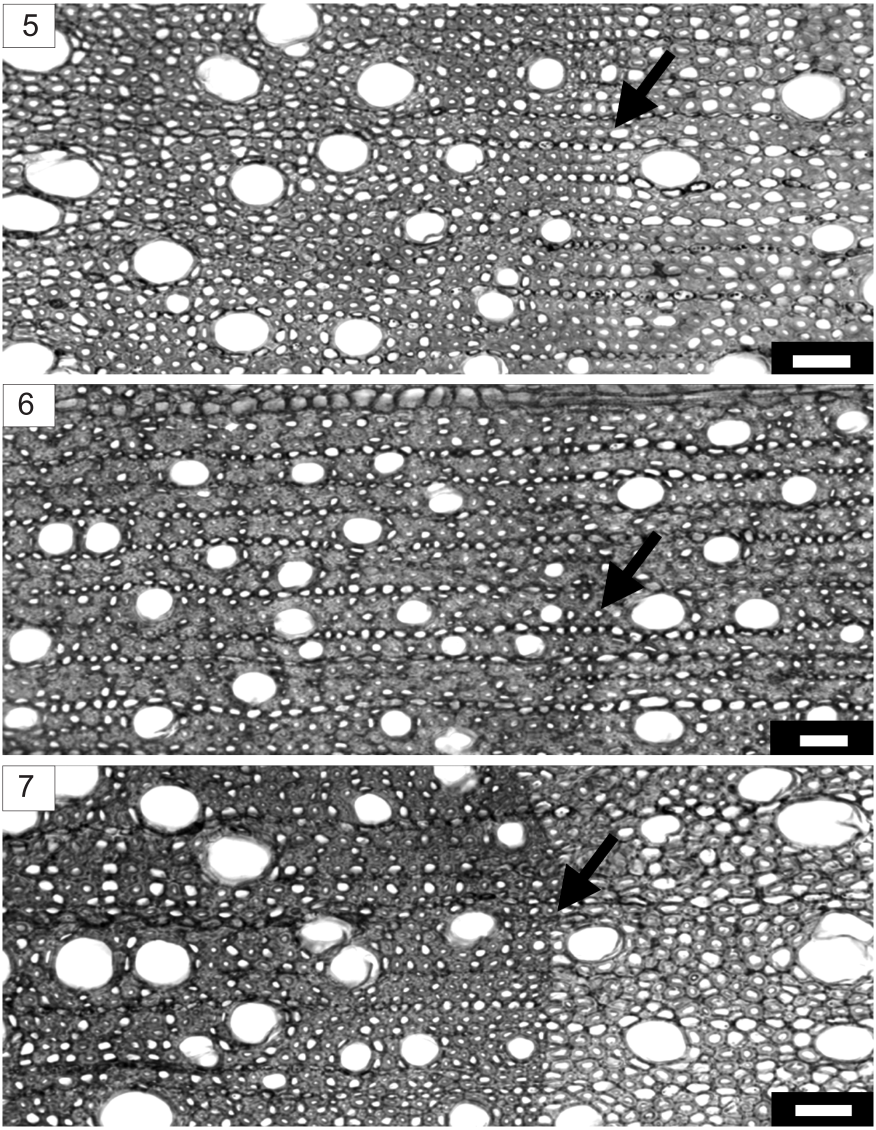

Figure 5–7. Details of cross sections of tree rings of *Erica arborea*. – 5: Faint tree-ring boundary. – 6: Gradual density fluctuation. – 7: Abrupt density fluctuation. — Scale bars = 50 μm.

genetic cues and their physiological status and morphological traits. These traits include rooting depth, which, in turn, affects the eco-physiological behaviour regulating the tree's cambial activity and cell differentiation (Schweingruber 2007; Cherubini *et al.* 2003). Moreover, different types of IADFs can be found not only in different species growing in different climates, but also in the same plant in different years, or in the same year in different species.

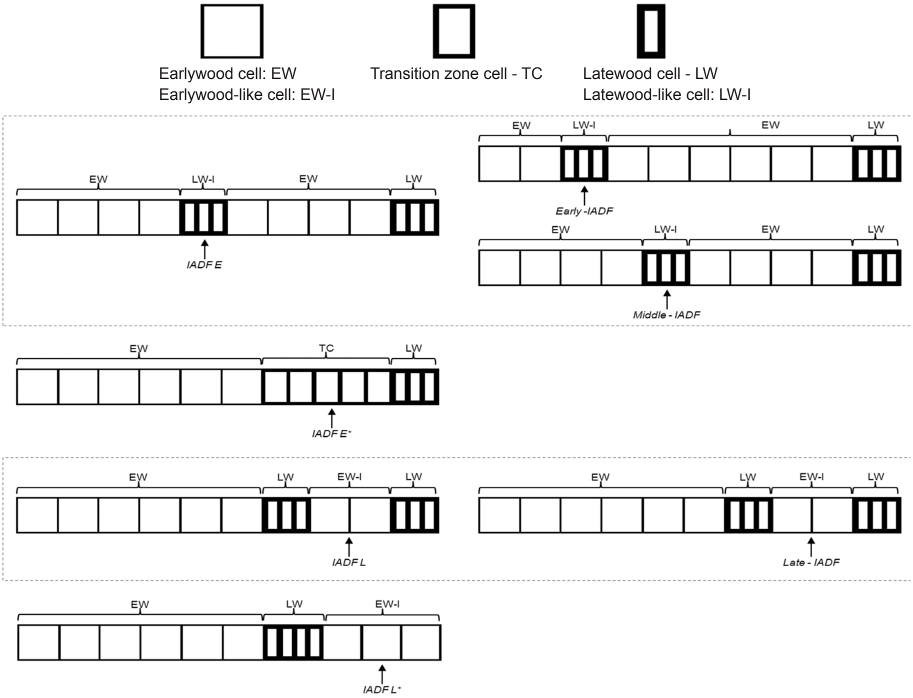

Figure 8. Classification of intra-annual density fluctuations (IADFs) illustrated schematically. On the left: earlywood (*E* and E^+) and latewood (*L* and L^+) IADFs according to Campelo *et al*. (2007b, 2013). On the right: early, middle and late IADFs according to Battipaglia *et al*. (2010) and De Micco *et al*. (2014).

Although IADFs have been found in numerous environments, they have been mostly studied in Mediterranean woods. Attempts have been made to systematically classify the types of IADFs, by considering the relative position of IADFs within the tree rings and the morphological features of the tracheids or vessels (mainly lumen size and cell-wall thickness) along a radial profile of the tree ring. IADFs in *Pinus pinea* and *Pinus pinaster* growing in Portugal have been visually classified into four types (Campelo *et al*. 2007b, 2013) according to their relative position within the earlywood (*E*- and E^+-type) and latewood (*L*- and L^+-type) (Fig. 8). More specifically: 1) type *E* occurs in the first half of the ring as a band of latewood-like cells in the earlywood; 2) type E^+ occurs at the end of the earlywood, as cells with features intermediate between true earlywood and true latewood cells, called transition cells, but are often more similar to latewood-like cells; 3) type *L* is found in the second half of the ring as earlywood-like cells in the latewood; 4) type L^+ occurs between the latewood and earlywood of the next tree ring as a band of earlywood-like cells with narrower lumen and thicker walls than true earlywood, and are similar to transition cells. This classification of IADFs has been applied to other conifer species in the Mediterranean area such as in *Pinus halepensis* growing in Spain (De Luis *et al*. 2011a,b; Novak *et al*. 2013a,b).

In *Arbutus unedo* and *Erica arborea*, IADFs have also been classified into three types according to their position within the tree ring and the morphological features of the xylem cells: early, middle and late IADFs (Battipaglia *et al.* 2010; De Micco *et al.* 2012, 2014) (Fig. 8). More specifically, each tree ring was divided into three parts and the IADFs classified as: 1) early IADFs, occurring in the first third of the annual ring as latewood-like cells in the earlywood; 2) middle IADFs, occurring in the second third of the annual ring as latewood-like cells in the earlywood; and 3) late IADFs, occurring in the third part of the annual ring as earlywood-like cells in the latewood. By comparing the two classifications, it is clear that early and middle IADFs correspond to *E*-IADFs, while late IADFs coincide with *L*-IADFs (Fig. 8). The IADF type E^+ and L^+ could be considered more as transition wood types than true IADFs, thus being accompanied by the same challenges of defining and classifying, as gradual or abrupt, the boundaries between earlywood and latewood, as well as between successive tree rings.

The formation of different types of IADFs can be triggered by multiple factors. The formation of bands of dense wood within earlywood has been associated with the interruption or reduction of photosynthesis due to environmental constraints, such as severe aridity or late frost events, or to defoliation caused by fire or pathogen attacks (De Micco *et al.* 2007; Schweingruber 2007). Precipitation and temperature are the parameters most frequently considered in relation to IADF occurrence to interpret their ecological role. Which is the main driver for IADF formation depends on the species sensitivity and on the climate of the growth environment.

IADFS IN MEDITERRANEAN ECOSYSTEMS

Mediterranean ecosystems are characterised by marked seasonal climatic fluctuations. According to Emberger (1954), the Mediterranean climate has precipitation concentrated during the cold, or relatively cold, months followed by a dry and hot season. Such conditions are responsible for the so-called “double stress” of either overly low temperatures or limited water availability which constrain plant growth (Mitrakos 1980). Such double stress is also considered responsible for the formation of IADFs as it slows down cambial activity or stops it completely, probably after stomata closure.

The process of tree-ring formation in the Mediterranean basin has been classified by Cherubini *et al.* (2003) into 4 groups. The first two groups comprise species forming annual tree rings with cambial activity stopping once a year because of either winter cold or summer aridity. The third group includes species where cambial activity stops twice, once in winter and once in summer, triggering the formation of IADFs. The last group consists of species that can maintain their cambial activity all year round without the formation of clear annual growth rings. This classification follows the one by Liphschitz and Lev-Yadun (1986), who categorised Mediterranean species according to the annual rhythm of cambial activity into two classes: 1) the temperate-Mediterranean type, in which cambial activity starts in spring and continues throughout the summer with one winter stop, as in temperate regions, and 2) the adapted Mediterranean-type, in which the cambium is activated after the first autumn rains and lasts until the beginning of summer when drought stress causes the reduction in cambial activity. Species whose cambial activity halts for a second time, due to low winter temperatures, or is continuous under favourable conditions are, according to these authors, cases of adapted Mediterranean-type vegetation.

The annual rhythm of cambial activity of a given species varies according to not only intrinsic features (*e.g.* genetic factors, ecophysiological and phenological traits, rooting depth), but also environmental conditions. Indeed, the cambial activity rates of different species sharing the same environment can be very different, whereas the annual rhythm of the cambial activity of the same species tends to depend on the specific growing conditions of the site and year (Cherubini *et al.* 2003).

The adaptive capacity of a woody species to cope with the highly seasonal Mediterranean conditions probably depends on its ability to adjust its cambial activity to the prevailing environmental conditions, thus forming IADFs. Trees that lack the capacity to promptly adjust their wood properties in response to climatic fluctuations are likely to be more vulnerable to drought (Martinez-Meier *et al.* 2008). *Pinus pinaster* trees can rapidly adjust their cambial activity to variations in soil water availability during the growing season, and thus seem to be able to adapt to seasonal droughts (Wilkinson *et al.* 2015). However, the physiological mechanisms triggering the formation of different types of IADFs are still unknown, but seem to be similar in softwood and hardwood species. IADFs' intra-ring radial position can be used to determine, for example, when the triggering factor occurred during the growing season (Campelo *et al.* 2007b; De Micco *et al.* 2014; Hetzer *et al.* 2014). More specifically, the formation of latewood-like cells within earlywood (*E*-IADFs) in Mediterranean woods has been considered the consequence of less cell expansion during a summer drought, which induces the formation of tracheids or vessels with narrow lumens (Battipaglia *et al.* 2014; Vieira *et al.* 2010; De Luis *et al.* 2011a,b; Novak *et al.* 2013a). This type of IADF is formed in response to stomatal closure under drought stress, when the tree appears to make a sort of hydraulic adjustment to reduce its vulnerability to cavitation, at the cost of lower hydraulic conductivity (De Micco *et al.* 2007; Campelo *et al.* 2013; Battipaglia *et al.* 2014). Conversely, the formation of earlywood-like cells within latewood (*L*-IADFs) has been related to the return of favourable conditions for tree growth after the start of latewood formation, *i.e.* more water availability due to autumn rainfall after a summer drought (Abe *et al.* 2003; Battipaglia *et al.* 2010; De Luis *et al.* 2011a,b; Novak *et al.* 2013a,b). In *L*-IADFs, the presence of conducting cells with lumens larger than those of true latewood would increase the hydraulic conductivity or the available volume of wood for water storage (Battipaglia *et al.* 2010; Campelo *et al.* 2013).

The physiological and ecological role of IADFs has been evaluated by correlations between chronologies of IADF frequency and monthly temperature and precipitation data for different tree species. Such relations appear to be species- and site-specific (Battipaglia *et al.* 2010; De Luis *et al.* 2011b; Novak *et al.* 2013a,b; Nabais *et al.* 2014).

IADFs in Mediterranean conifers

Evergreen conifers growing in a Mediterranean climate can be physiologically active almost all year round taking advantage of temporarily favourable conditions for growth (Corcuera *et al.* 2011; De Luis *et al.* 2011b; Sperlich *et al.* 2014; Vieira *et al.* 2014).

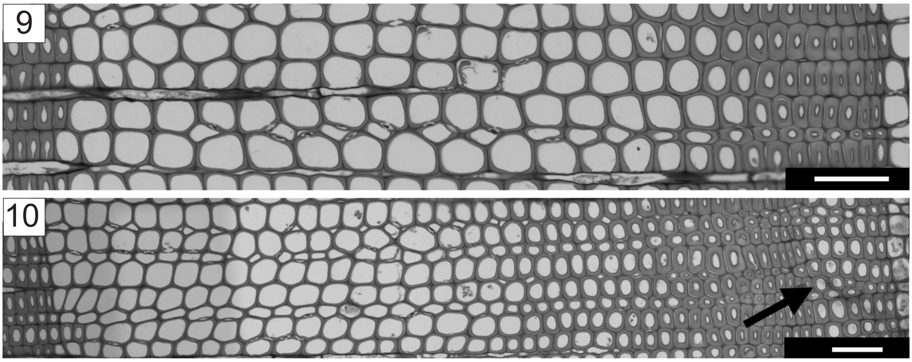

Figure 9 & 10. Cross sections of tree rings of *Pinus pinaster* growing in Portugal. – 9: Tree ring without intra-annual density fluctuations (IADFs). – 10: Tree ring with an L^+-type IADF (arrow indicates the boundary between the latewood and the beginning of the IADF). — Scale bars = 100 μm.

Their cambial activity does not always become fully dormant during the cold season, unlike in colder areas (Cherubini *et al.* 2003). Additionally, the cambium in some species can go through a quiescent period imposed by water stress during the summer, and resume activity in autumn whenever favourable conditions return (De Luis *et al.* 2007; Linares *et al.* 2009; Camarero *et al.* 2010; De Luis *et al.* 2011a,b; Vieira *et al.* 2013). Indeed, most of Mediterranean conifers show a bimodal pattern of growth, with two peaks of cambial activity, one in spring and one in autumn (De Luis *et al.* 2007; Camarero *et al.* 2010; De Luis *et al.* 2011a; Vieira *et al.* 2014). As a consequence of the bimodal pattern of xylogenesis, the wood of Mediterranean species often forms a tree-ring pattern different from the one typically found in temperate species, and is characterised by the formation of frequent IADFs in response to short-term climatic variations during the growing season (Fig. 9 & 10) (Campelo *et al.* 2007b; De Luis *et al.* 2007; De Micco *et al.* 2007).

The frequency of IADFs varies greatly in the rings of evergreen conifers growing in the Mediterranean area, such as *Pinus pinea* (Campelo *et al.* 2007b), *P. halepensis* (De Luis *et al.* 2007, 2011a; Olivar *et al.* 2012; Novak *et al.* 2013a,b; Moreno-Gutiérrez *et al.* 2015), *P. pinaster* (De Micco *et al.* 2007; Vieira *et al.* 2009; Rozas *et al.* 2011; Campelo *et al.* 2013), and *Juniperus thurifera* (Olano *et al.* 2015) (Table 1). The frequency of IADFs among these species is highest in *Pinus pinaster*, where IADF formation is more the rule than the exception (Rozas *et al.* 2011). In contrast, IADF frequency in *Pinus halepensis* in the mountain areas is extremely low, especially in the northern part of its distribution range, but higher at sites near the coast, where the summer drought is more intense and the growing season longer due to moderate temperatures (Cherubini *et al.* 2003; Novak *et al.* 2013a,b, 2016). This variability in the IADF frequency suggests that the cambial activity in Mediterranean conifers may vary greatly depending not only on the tree species (Nabais *et al.* 2014), but also on the site conditions (*e.g.* exposition and soil water-holding capacity) (Rigling *et al.* 2001), population structure (Copenheaver *et al.* 2006), and inter- and intra-annual variability

Table 1. Summary of IADFs frequency in 4 evergreen conifers growing in the Mediterranean area and an indication of the two months with the highest correlations between IADF frequency and climate variables (monthly mean temperature and monthly precipitation), based on published studies.

Species	Country	IADF (%)	Temperature		Precipitation		Author(s)
			1	2	1	2	
Juniperus thurifera	Spain	4.80–15.5	September (+)	July (+)	August (+)	September (+)	Olano *et al*. (2015)
Pinus halepensis	Spain, Slovenia	0.4–14.5	August (–)	July (–)	September (+)	August (+)	Novak *et al*. (2013a)
Pinus halepensis	Spain	0.25–58	March (+)	January (+)	August (+)	September (+)	De Luis *et al*. (2011)
Pinus halepensis	Spain	0–33					Novak *et al*. (2013b)
Pinus pinaster	Portugal	12–20	November (–)	March (–)	October (+)	September (+)	Vieira *et al*. (2009, 2010)
Pinus pinaster	Portugal	34–48	September (–)	August (+)	September (+)	June (–)	Campelo *et al*. (2013, 2015)
Pinus pinaster	Spain	6.9–18.9	August (–)	May (+)	May (–)	September (+)	Bogino & Bravo (2009)
Pinus pinaster	Spain	15.9–89.5	December (t-1)(–)	April (+)	Autumn (+)*	Annual (–)*	Rozas *et al*. (2011)
Pinus pinea	Portugal	17–32	May (+)	March (+)	October (+)	November (+)	Campelo *et al*. (2007b)

* Water Balance (Precipitation – Potential Evapotranspiration).

of environmental conditions (Novak *et al.* 2013a,b). Further comparative studies are needed to exclude any bias arising from the action of interconnected factors.

Both *E*-IADFs (related to summer drought) and *L*-IADFs (related to the increased water availability after summer) have been detected in conifers across the Mediterranean area (Bouriaud *et al.* 2005; Campelo *et al.* 2007b; De Luis *et al.* 2011a; Novak *et al.* 2013a,b; Hetzer *et al.* 2014). *E*-IADFs are less frequent than *L*-type ones, which suggests that soil water availability is less limiting during the early growing season. In contrast, many IADFs occur close to the end of the ring (*L*-IADFs) in Mediterranean species, which suggests that these structures represent an extension of the wood formation period. This assumption is supported by the correlations found between the monthly climatic variables and IADF frequency (Campelo *et al.* 2007b; De Luis *et al.* 2011a; Vieira *et al.* 2009), by the simple comparison of intra-ring density variations and sub-seasonal weather conditions (Olano *et al.* 2012), as well as by xylogenesis analysis De Luis *et al.* 2007) and combinations of different methodologies (De Luis *et al.* 2011a,b; Vieira *et al.* 2015). IADF formation thus appears to be triggered by a combination of summer drought and favourable conditions in late summer and early autumn, that promote the resumption of cambial activity extending wood formation (Carvalho *et al.* 2015). This is supported by other studies that have found more IADFs related to fast growth and wider rings (close to the pith) (Rigling *et al.* 2001, 2002; Novak *et al.* 2013b; Campelo *et al.* 2015), indicating periods of growth release (Bräuning 1999; Copenheaver *et al.* 2006).

IADFs in Mediterranean hardwoods

IADFs have been found in many Mediterranean tree and shrub hardwood species, including: *Quercus pubescens* and *Q. ilex* in Italy, France, and Spain (Maugini 1949; Zhang & Romane 1991; Cherubini *et al.* 2003; Campelo *et al.* 2007a, 2010), *Quercus ithaburensis* and *Q. calliprinos* in Israel (Fahn 1953), *Phillyrea latifolia* and *Fraxinus ornus* in Corsica (Panaïotis *et al.* 1995), *Arbutus unedo* (Cherubini *et al.* 2003; Battipaglia *et al.* 2010), *Cistus incanus* subsp. *incanus* (De Micco & Aronne 2009) and *Erica arborea* in Italy (Battipaglia *et al.* 2014). In Italy, IADFs in *Quercus ilex* were induced by one or more stops of cambial activity during spring and summer in addition to the regular brief halt of growth due to winter cold (Susmel *et al.* 1976). In the same species growing in southern France, Zhang and Romane (1991) found that the occurrence of IADFs was related to tree-ring width, with higher frequency of IADFs in wider rings. They also hypothesised that climatic factors, especially precipitation, carry more weight in the formation of IADFs than genetic predisposition. More specifically, they concluded that the presence of IADFs is related to September precipitation and that they only form if there is a dry period at the beginning of summer. The negative relation with April precipitation was explained as the consequence of reduced radial growth due to the allocation of more resources toward root growth or the formation of new shoots and reproductive structures. Additionally, Campelo *et al.* (2007a) found that precipitation after the summer drought triggers the formation of IADFs in *Quercus ilex* and the width of the IADF formed in latewood is related to the amount of precipitation.

The rhythms of cambial activity in Mediterranean environments vary probably in relation to changes in resource availability and the plants' specific rhythms of transpiration and photosynthesis, which depend on their leaf phenology, anatomy and physiology (Liphschitz & Lev-Yadun 1986; Cherubini *et al.* 2003). The seasonally dimorphic species *Cistus incanus* subsp. *incanus* has a tree-ring anatomy reflecting its leaf phenology. The presence of brachyblasts with small xeromorphic leaves in summer and dolichoblasts with large mesomorphic leaves in winter is accompanied by a seasonal dimorphism in the wood anatomy that explains the formation of IADFs (Aronne & De Micco 2001; De Micco & Aronne 2009). In southern Italy, the annual rings in branches of *Cistus incanus* subsp. *incanus* seem to be characterised by the succession of two incremental growth rings: a ring of wood formed in the brachyblast, safer (against embolism) than the ring of wood corresponding to the dolichoblast, because it is characterised by more frequent narrower and shorter vessel elements. This suggests that, although cambial activity in this species can be continuous, environmental conditions (especially water availability) affect cell enlargement and differentiation.

In *Arbutus unedo* growing in Italy, IADFs seem to be formed during summer when specific hydraulic conductivity stops (Cherubini *et al.* 2003). A detailed analysis of the anatomy of the IADFs revealed several bands of different density within each annual tree ring of *Arbutus unedo*. According to Cherubini *et al.* (2003), each annual ring can, ideally, be divided into 6 parts: 1) the first part is formed during the mild and wet spring, and is made of true earlywood with large vessels; 2) the second part appears darker than the first, probably because denser wood forms in response to dry conditions with narrower vessels and thicker cell walls in fibres; 3) the third part is more similar to the first and is produced after late-spring precipitation; 4) the fourth part is a band of very dense wood produced if limiting summer conditions halt cambial activity; 5) the fifth part includes earlywood-like vessels formed after the resumption of cambial activity, triggered by autumn precipitation; 6) the last part of the ring is the true latewood that develops before cambial activity stops due to cold. According to this model, the wood anatomical features of *Arbutus unedo* are very sensitive to fluctuations in environmental conditions, probably because of its eco-physiological traits and shallow root system. The plasticity of its cambial activity has been shown to be dependent on the environmental conditions of the growth site. Indeed, in two nearby study sites on Elba Island in Italy, *Arbutus unedo* formed two types of IADFs depending on water availability at the growth site. In *Arbutus unedo* growing in xeric conditions, Battipaglia *et al.* (2010) reported that *E*-IADFs (middle-IADFs) prevail. They are linked to low precipitation and may increase safety of water conduction against embolism under dry summer conditions. Under mesic conditions, *L*-type IADFs are formed. They are promoted by rains that restore cambial activity after aridity-induced cambium dormancy. *Erica arborea* plants at the same sites only develop *E*-IADFs if the temperature is high and little water is available in summer (Battipaglia *et al.* 2014). They lack *L*-IADFs probably because either their growing season is shorter than that of *Arbutus unedo* plants, or they are less sensitive to autumn rainfall. The presence of *E*-IADFs in *Erica arborea* also at the mesic site may be due to a higher responsiveness of this species to soil water availability during the dry summer, probably because it has a shallower root system than *Arbutus unedo*. IADF frequency also seems to be related to tree age, as younger plants are more prone to form IADFs than older ones. This relationship seems to be controlled by the duration of the growing season, as well as the plant's morphology and physiological properties which affect the availability of resources of the season (*e.g.* depth of rooting system controlling water accessibility) and of previous years (*e.g.* storage mobilisation). Indeed, the relationships between IADF properties and environmental factors can be very complex in Mediterranean angiosperms because environmental drivers interact with the intrinsic properties of the species with their different adaptive life strategies and habits.

IADFS IN REGIONS WITH TEMPERATE, CONTINENTAL AND BOREAL CLIMATES

In temperate climates, seasonal variations in temperature typically lead to warm summers and cool winters which induce cambial dormancy. In summer, droughts regularly occur, but are usually not as frequent and pronounced as in a Mediterranean climate, and the length of the growing season tends to be shorter. This could be one reason why IADFs are less frequent in temperate areas (Rigling *et al.* 2001; Rozas *et al.* 2011). On moderately dry sites, drought in the early growing season can trigger IADF formation (Schweingruber 1980; Krause 1992; Leuschner & Schweingruber 1996; Villalba & Veblen 1996; Wimmer *et al.* 2000; Grabner *et al.* 2014). Along the borders of the sub-pannonian Vienna basin, a dry region in eastern Austria, IADFs have been found in different larch species (*Larix decidua*, *L. decidua* × *kaempferi*), firs (*Abies alba*, *A. bornmuelleriana*, *A. cephalonica*, *A. cilicica*, *A. nordmanniana*, *A.* × *borisii-regis*), pines (*Pinus nigra*, *P. ponderosa*), Norway spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*) (Grabner *et al.* 2014; George *et al.* 2015).

The relationships between IADF features in softwood species and environmental parameters in temperate climates are not clear. Recently, Eilmann *et al.* (2011) found that the size of the latewood tracheids of mature *Pinus sylvestris* trees growing in a xeric site in a dry inner-alpine valley was not sensitive to irrigation. These trees appear to have a limited capacity to adjust the lumen size of their latewood tracheids to soil water availability, which would explain why they tend to have few *L*-IADFs (Wimmer *et al.* 2000). In trees growing in temperate latitudes, IADFs can occur throughout the tree ring in both the earlywood and latewood. Nevertheless, most were found in the earlywood or in the transition zone between the earlywood and latewood (Kuo & McGinnes 1973; Schweingruber 1980; Krause 1992; Wimmer *et al.* 2000) and could be possibly classified as *E*-IADFs.

In hybrid larches growing in Eastern Austria, IADFs were frequently found within the tree rings of particular years. Thus, 60 % of the samples contained IADFs in 1998, 73 % in 2000, 78 % in 2001, and 77 % in 2003 (Karanitsch-Ackerl *et al.* 2012). In these years, no or very little precipitation occurred for several days or weeks between March and May, but some rain fell in May, followed by a dry period in June. Thus, in these years there was an overall precipitation deficit in the spring months. The relationship between the IADF frequency and monthly climate variables was found to be very negative for June precipitation (R = 0.71) (Karanitsch-Ackerl *et al.* 2012; Grabner *et al.*

2014). Therefore, the climatic regime triggering IADFs in hybrid larches seems to be a dry period within March-May and then in June, with a few rain events in May. The study by Karanitsch-Ackerl *et al.* (2012) was conducted on very fast growing *Larix* hybrids in an experimental plantation, which were 25 years old at sampling time. The high frequency of IADFs found in these trees is in agreement with the finding that IADFs are likely to be more frequent in juvenile and wide tree rings (Schweingruber 1980; Rigling *et al.* 2001, 2002). During the juvenile growth phase (up to the age of 80 years), black pine trees are also more likely to form IADFs (Wimmer *et al.* 2000).

IADF frequency is influenced not only by tree age, but also by the site conditions. Trees growing at dry sites with shallow soils on solid rocks tend to have more IADFs (Rigling *et al.* 2001, 2002). Marchand and Filion (2012) found IADFs were twice as frequent on rocky outcrops than on shallow soils, probably due to the shallow root systems and the resulting differences in water availability. Wimmer *et al.* (2000) analysed black pines in the vicinity of the Vienna basin to reconstruct past climate on the basis of ring width, earlywood width and IADF frequency. They found that 72 % of years with many IADFs had low precipitation (below median) in May. If April and June were also taken into account, the pattern of wet April / dry May / wet June triggered the formation of IADFs in 50 % of the years with frequent IADFs.

The IADF frequency of Scots pine (*Pinus sylvestris*) in the Valais (Switzerland) inner-alpine dry valley was positively correlated with precipitation in July and August, and negatively correlated with August temperature (Rigling *et al.* 2001, 2002). The IADF frequency was also positively correlated with the number of drought days in February, and negatively in July and August. In *Pinus sylvestris* growing in the central Alps (Switzerland), Rigling *et al.* (2001) found that *L*-IADF formation was triggered by moist-cool conditions in the middle of the growing season (July and August), which is in agreement with results from other dry sites in the temperate zone (Schulmann 1938, 1939; Kuo & McGinnes 1973; Schweingruber 1980; Rigling *et al.* 2001, 2002).

In long chronologies of *Pinus sylvestris* growing under transitional-continental climate conditions in Bulgaria, Panayotov *et al.* (2013) observed that the formation of light, narrow and frost rings as well as of IADFs, depended on the altitude, latitude and period in which the environmental fluctuations (mainly temperature and precipitation) occurred. For example, at low altitudes, both IADFs (possibly *E*-IADFs) and light rings were found due to early summer drought followed by precipitation in the middle of summer, and to drought at the end of summer, respectively. Precipitation was also considered to be the main cause of IADF formation in tree rings of *Fagus sylvatica* growing in a semi-continental climate in south-western Germany (van der Maaten *et al.* 2012). More specifically, an analysis of the relationships between the intra-annual variations in wood density, soil water content and growth (measured with dendrometers), over a period of six years, revealed that the period of growth also plays a role as plants are more sensitive to internal factors (mainly hormonal levels) at the beginning of the growth season.

In boreal and subarctic regions, the term “false ring” rather than IADF is commonly used to describe density anomalies in tree rings. For consistency, we will continue to refer to IADF here. The growth rates of trees at higher latitudes are often compara-

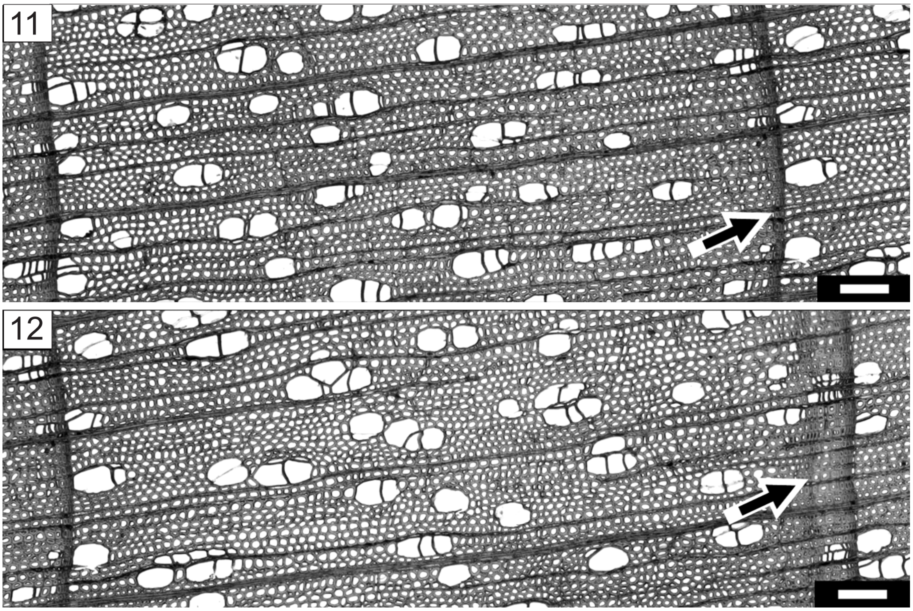

Figure 11 & 12. Cross sections of tree rings of *Betula pubescens* growing on Russian permafrost. – 11: Tree ring without IADFs (arrow indicates tree-ring boundary). – 12: Tree ring with an IADF (arrow indicates an IADF). — Scale bars = 200 µm. Kindly provided by Marina Bryukhanova.

tively low, resulting in rather small ring widths, due to the short growing season and the predominance of nutrient-poor soils. Precipitation maxima usually occur during the summer months, but the melting of sub-surface permafrost also contributes to the water supply of trees during the vegetation period. Given these conditions, trees in the sub-arctic and boreal zones are not especially prone to IADF formation. Nevertheless, on locally dry sites, such as on rocky or on well-drained sandy substrates, or in years with unusually cold summer conditions, water shortage may occur during the growing season and lead to the development of IADFs (Fig. 11 & 12).

The majority of IADFs were formed in wider and/or younger tree rings in *Pinus sylvestris* trees in boreal Siberia (Rigling *et al*. 2001). Climate and IADF formation were not clearly related, but IADFs were identified mainly in the latewood and in trees growing on shallow rocky soils. This indicates that dry conditions during the late summer season are probably important triggers for IADF formation. However, IADFs were found in *Pinus sylvestris* trees in Russia during years with unusually cold conditions in late spring and early summer (Kozlov & Kisternaya 2004), and in *Larix sibirica* forests growing in the lower and drier forest belt at the foot of mountain slopes in Mongolia (Treter *et al*. 2000). De Grandpré *et al*. (2011) observed both IADFs and light rings in *Larix sibirica*, *Pinus sibirica* and *Pinus sylvestris* growing in continental north and central Mongolia, and related IADFs to drought events at the beginning of summer and the light rings to low temperatures at the end of the summer.

IADFs have also been detected in Norway spruce (*Picea abies*) growing in southern Sweden. The position of the density bands within the tree ring seems to vary for different clones, which suggests a genetic impact on IADF formation (Rozenberg *et al.* 2002). Artificial drought experiments carried out in the boreal zone with Norway spruce resulted in greater cell wall thickness and wood density, but did not provoke the formation of IADFs (Jyske *et al.* 2010; Montwé *et al.* 2014). It may be that rain shelters used in the experiments generally reduced the amount of water available for the trees, but did not mimic the alternating pattern of dry and humid conditions thought to trigger IADF formation. However, Rossi *et al.* (2009) were able to initiate IADF formation during a 20-day drought experiment in *Abies balsamea* seedlings grown in Canada. In a mixed forest of *Pinus banksiana* and *Picea mariana* in Manitoba, Hoffer and Tardif (2009) found synchronous IADF formation in both the species in years with cool, snowy springs followed by dry summers, with more IADFs in pine. Copenheaver *et al.* (2006) analysed the occurrence of IADFs in *P. banksiana* South of the southern border of the North American boreal forests and found that the social status of trees in the stand had an influence on IADF formation and not specific climate factors. These IADFs were more likely to form in codominant and intermediate trees than in dominant or suppressed trees.

IADFs are more frequently reported from sites at the transition zone from boreal to steppe climates or from inner mountain valleys in subtropical climates. For example, *Austrocedrus chilensis* growing on rocky slopes in the steppe forests of Patagonia had IADFs in years with dry winter/spring conditions followed by wet austral summers (Villalba & Veblen 1996), while the diffuse-porous *Nothofagus pumilio* in the southern Patagonian Andes formed IADFs after rainy late summers following a dry early part of the growing season (Masiokas & Villalba 2004).

IADFS IN TROPICAL WOODS

Tree rings in tropical and sub-tropical environments have received little attention because, in many tropical plants, the cambium is active throughout the year and wood anatomical tree-ring boundaries are often absent or diffuse. However, dendrochronologists have shown renewed interest in such environments in the last 35 years (Bormann & Berlyn 1981; Baas & Vetter 1989; Worbes 2002; Rozendaal & Zuidema 2011; Harley *et al.* 2012; Battipaglia *et al.* 2015). Tropical climates are very diverse and there are many cases in which cambial activity is not continuous due to seasonal variations in hydrological conditions. Seasonally dry conditions lead to reduced cambial cell production and to the formation of tree rings with wood anatomical boundaries ranging from distinct to diffuse (Worbes & Fichtler 2010). For example, continuous growth has been reported as normal for only 75% of the plants in India, 43% in the Amazon Basin and 15% in Malaysia (Evert 2006). Recently, Tarelkin *et al.* (2016) analysed the distribution of tree-ring distinctness around the world highlighting that species with indistinct or absent tree rings account for 55–78% in the tropical regions. Teak (*Tectona grandis*) is a ring-porous species that grows naturally in monsoon climates of South Asia, where it forms clear annual rings that can be used for dendrochronological studies. However, droughts during the early growing season and other disturbances (*e.g.* insect attacks) may lead to IADF formation (Priya & Bhat 1998). When growing in other tropical climates, or when irrigated, teak may even form multiple growth zones during a single year (Priya & Bhat 1998; Dié *et al.* 2012).

Multiple tree rings have been found in *Juniperus procera* from the Ethiopian Highlands, varying greatly according to the local precipitation regime (Wils *et al.* 2011). In Ecuador, *Prumnopitys montana* has IADFs, in multiple numbers per year (Fig. 13) (Schnakenburg *et al.* 2008; Bräuning *et al.* 2009). In the Ethiopian *Podocarpus falcatus*, IADFs appear to form if the rainy season is interrupted by dry spells (Fig. 14) (Krepkowski *et al.* 2012).

IADFs in *Pinus caribaea* growing in Southeast Brazil have recently been classified as latewood-like cells in earlywood (*E*-type) and earlywood-like cells in latewood (*L*-type) (Venegas-González *et al.* 2015). In this species, tree rings were often characterised by

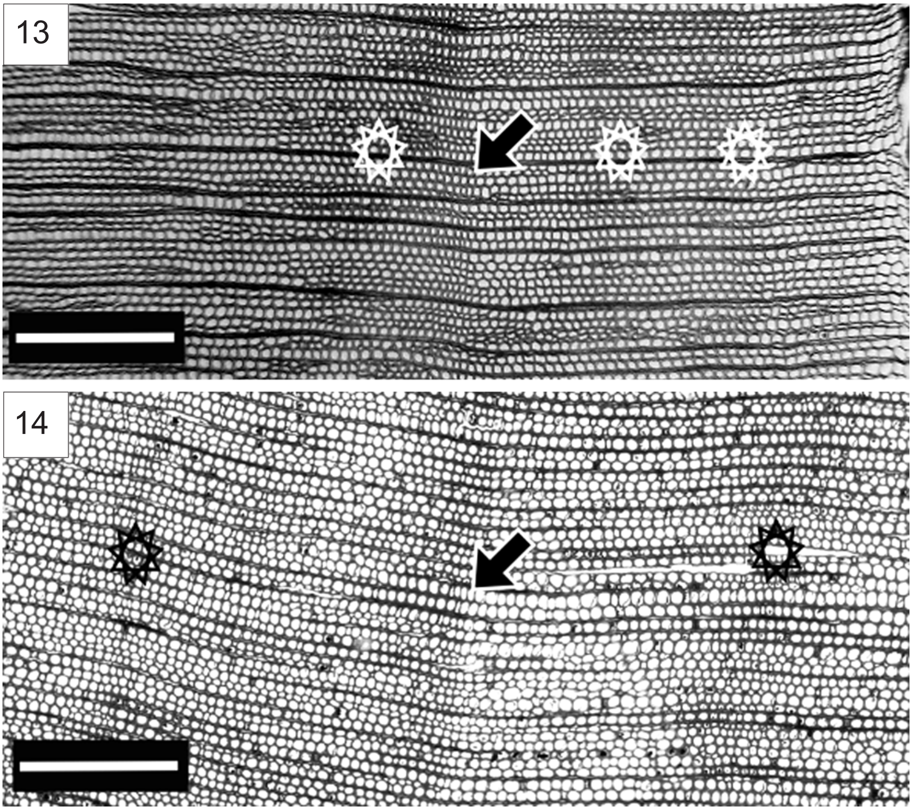

Figure 13 & 14. Cross sections of growth zones of tropical Podocarpaceae. – 13: Tree-ring boundary and IADFs in *Prumnopitys montana* growing in a mountain rainforest in southern Ecuador – 14: Tree-ring boundary and IADFs in *Podocarpus falcatus* growing in a mountain rainforest in south-east Ethiopia. The arrows indicate tree-ring boundaries and asterisks IADFs. — Scale bars = 500 μm.

the presence of more than one IADF, especially in the earlywood, and *E*-IADFs were much more frequent than *L*-types. The occurrence of *E*-type IADFs was explained either as a response to abundant precipitation (in December–February), combined with higher temperatures (especially in April) that would have significantly increased the evapotranspiration rates, or as a response to water saturation such as after a flash-flood. The occurrence of *L*-IADFs was considered to be linked with autumn precipitation (March–May): thus the authors hypothesised the same mechanisms of *L*-IADF formation as reported in Mediterranean pines, due to the growing season being extended in autumn (Campelo *et al.* 2013; Venegas-González *et al.* 2015). *L*-type IADFs have also been recorded in *Pinus elliottii* growing in south Florida and linked to amplified solar radiation during summer, which probably increases the production of photosynthates in trees (Harley *et al.* 2012).

Evergreen conifers seem to behave opportunistically in tropical climates, and regulate cambial activity and young tracheid differentiation according to the current moisture availability.

With the current global climate change, it is forecasted that tropical trees will be severely affected (Zeng *et al.* 2013). Thus, dendrochronology should be further developed and combined with the analysis of IADFs in tropical woods to comprehend seasonal variations in cambial activity and relate them to ecophysiological processes and climate variables.

COMBINING QUANTITATIVE WOOD ANATOMY AND STABLE ISOTOPE ANALYSIS TO INTERPRET THE FUNCTION OF IADFs BETTER

Traditionally, the study of IADFs has focused on the relationships between IADF frequency and tree-ring width, as well as between IADF frequency and climatic data. More recently, improved tools for digital image analysis have increased the application of quantitative wood anatomy to analyse the intra-ring variability of anatomical features and to develop long chronologies of anatomical features (Fonti *et al.* 2007, 2010). It has thus been possible to test hypotheses about the role IADFs play in the modulation of intra-annual variability of conductivity and safety against embolism, and the mechanisms triggering their formation (De Micco *et al.* 2007, 2014).

Recently, analyses of quantitative wood anatomy have been combined with analyses of the stable isotopes in IADFs, resulting in a better understanding of IADFs' ecological significance. A multidisciplinary approach, combining traditional dendroecological methods with quantitative wood anatomy and stable isotope analysis, has been applied to *Pinus pinaster*, *Arbutus unedo* and *Erica arborea* plants forming IADFs and proved to be useful to interpret their past ecophysiological behaviour with intra-annual resolution (De Micco *et al.* 2007; Battipaglia *et al.* 2010, 2014). Indeed, $\delta^{13}C$ is related to the balance between CO_2 assimilation rate and stomatal conductance, and can therefore be analysed to evaluate intrinsic water use efficiency (WUE) (Osmond *et al.* 1980; Saurer *et al.* 2004). Data on $\delta^{18}O$ in combination with $\delta^{13}C$ help to determine whether changes in $\delta^{13}C$ are due to modifications in photosynthetic levels or in stomatal conductance (Scheidegger *et al.* 2000; Barbour 2007).

In *Arbutus unedo* and *Erica arborea* tree rings with IADFs in earlywood, the wood in the IADF region was found to have narrower vessels and higher WUE (less negative $\delta^{13}C$) than earlywood, which suggests that these IADFs were triggered by stomatal closure. The correlations with climate data confirmed that the IADFs were induced by drought stress events (Battipaglia *et al.* 2010, 2014), and indicated that the drivers of IADFs could be species- and site-dependent. The analysis of $\delta^{13}C$ in tree rings of *Pinus pinaster* also revealed that narrower tracheids are coupled with higher $\delta^{13}C$ in the IADF region in comparison with other wood zones (De Micco *et al.* 2007). In contrast, the larger vessels in IADFs in *Arbutus unedo* latewood were accompanied by lower WUE (lower $\delta^{13}C$), which suggests photosynthesis had increased due to the stomata re-opening after autumn precipitation following a summer dry period (Battipaglia *et al.* 2010).

Analysing anatomical and isotopic traits with intra-annual resolution can yield valuable information on the response of each species to fluctuating environmental conditions of the current and previous years. However, so far the isotopic approach has only been combined with quantitative wood anatomy in Mediterranean species to find out more about the ecological significance of IADFs. Combining methods in this way has great potential to interpret different types of IADFs ecologically, and should be applied to more species in a larger range of climates.

CONCLUSION AND PERSPECTIVES

Tree rings with specific anatomical and isotopic signatures are formed in response to individual genetic variation and environmental conditions. In the traditional paradigm that cambial activity stops once a year, each tree ring corresponds to one calendar year. Thus, the first IADFs observed were defined as anomalies deviating from the "normal anatomical pattern" where the wood density increases from the earlywood to the latewood in tree rings; IADFs, in contrast, indicate abrupt and unexpected changes in density. Thus, the adjustment of cambial activity and xylem differentiation to changes in environmental conditions throughout the growing season has been considered the main mechanism for IADF formation in tree rings.

IADFs have been observed in many softwood and hardwood species in different environments around the world in boreal, temperate, Mediterranean and tropical climates, but the main focus of research to date has been in Mediterranean tree and shrub species. Different types of IADFs form in response to different environmental triggers. IADFs occurring as latewood-like cells in earlywood (*E*-IADFs) are probably related to conditions of extreme aridity with very little precipitation and high temperatures during active vegetative growth. In contrast, IADFs occurring as earlywood-like cells in latewood (*L*-IADFs) are probably formed when cambial activity starts again once favourable conditions for growth have been restored, during a period when vegetative growth is otherwise generally inactive. The extremely unfavourable conditions that induce *E*-IADFs and the unexpectedly favourable conditions that induce *L*-IADFs can occur at different periods more than once during the calendar year, depending on the ecosystem. Moreover, depending on the species and environment, the main triggering factor can be temperature, precipitation, or a combination of the two during the growing season. Other biotic or abiotic factors that cause defoliation during the normal course of vegetative growth may also induce IADF formation. The climate conditions before the period of intense vegetative growth can also affect a tree's predisposition to form IADFs.

Many studies deal with the frequency of IADFs, while far fewer have analysed the anatomical features of conducting cells at the IADF level. Although quantitative wood anatomy is time-consuming, knowing the intra-ring variability of the anatomical parameters of xylem cells has proved valuable in identifying why they form, which is linked to environmental changes, as well as in evaluating the physiological consequences for the plant. Here, hardwoods probably provide richer "archives" than softwoods because their anatomical structure is more complex and contains more cell types. Numerous parameters in hardwoods can be analysed, such as vessel frequency, lumen size and the cell-wall thickness of vessels, fibres and tracheids, which are useful for evaluating how the balance between efficiency and safety of water transport varies along the tree-ring width (De Micco *et al.* 2015).

Whatever the species and the environment, IADFs can be used as valuable proxies of past climatic conditions with higher resolution than annual tree rings. We need, however, to know more about the different types of IADFs occurring under different climatic conditions, as well as about the factors that can bias data comparisons and interpretations. More specifically, it is still not clear whether IADFs are the "normal case" or the "anomaly", and whether their occurrence in tree rings is a sign of stress or a signal of the plant's capacity to adapt to fluctuating environmental conditions. The answers probably depend on the species and ecosystem. Considering the wide range of climatic and geographical conditions under which IADFs occur, IADF formation seems to belong to the normal range of wood plasticity of many tree species (at least of conifers). It may have adaptive value as a way for a tree to cope with water-stress periods during the growing season. For example, the high frequency of IADFs in some Mediterranean species supports the idea that the occurrence of IADFs is the rule and indicates high plasticity of the plants to changing environmental conditions. In other environments, the climatic conditions that trigger IADF formation occur only seldom and IADFs are much less frequent. This is one reason why the frequency and type of IADFs is also a valuable source of information for palaeoclimatic studies. However, further extensive comparative studies are still needed for IADF formation to be interpreted unequivocally in different environments.

Due to climate change, extreme climatic events (*e.g.* drought, intense rainfall) are expected to become more frequent and intense in the near future. This could have a great impact on the survival of trees, which depends, among other things, on their ability to preserve stem hydraulic conductivity and water storage capacity. We hypothesise that the presence of IADFs could potentially affect the plant survival in two different ways. First, if latewood-like cells in IADFs have a conductive role, then an increase in hydraulic safety could be attained during drought periods (Wilkinson *et al.* 2015). Second, earlywood-like tracheids forming IADFs would store water that could be used by trees during drought events. The capacity of trees to adjust the tracheid features during the growing season indicates an important adaptation to maintain an equilibrium with respect to their water conducting capacity, mechanical stability, and resistance to cavitation (Domec & Gartner 2002; Martinez-Meier *et al*. 2008).

The adaptive value and ecological significance of IADFs is still under debate, but combining different types of analysis can help to understand their functionality. Indeed, combining the analysis of stable isotopes with quantitative wood anatomy at the IADF level has proved valuable in reconstructing the ecophysiological behaviour of Mediterranean species during the growing season. However, to better comprehend the mechanisms behind the formation of different types of IADFs and the ecological role they play, cambial activity should be further investigated through pinning, punching or microcoring techniques (De Luis *et al*. 2011b; Vieira *et al*. 2015). Moreover, new standardised methodologies are needed to analyse IADFs (De Micco *et al*. 2012, 2014), since the methods used to analyse the intra-annual variation in wood traits and the choice of anatomical parameters can affect their ecological interpretation.

ACKNOWLEDGEMENTS

This study profited from discussions within the COST Action STReESS (COST-FP1106). The authors thank Mrs. Silvia Dingwall for the language revision.

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Accepted: 30 December 2015