Tree Physiology 30, 773–781
doi:10.1093/treephys/tpq031

Flash-flood impacts cause changes in wood anatomy of *Alnus glutinosa*, *Fraxinus angustifolia* and *Quercus pyrenaica*

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Received February 6, 2010; accepted March 25, 2010; published online May 12, 2010

Summary Flash floods may influence the development of trees growing on channel bars and floodplains. In this study, we analyze and quantify anatomical reactions to wounding in diffuse-porous (*Alnus glutinosa* L.) and ring-porous (*Fraxinus angustifolia* Vahl. and *Quercus pyrenaica* Willd.) trees in a Mediterranean environment. A total of 54 cross-sections and wedges were collected from trees that had been injured by past flash floods. From each of the samples, micro-sections were prepared at a tangential distance of 1.5 cm from the injury to determine wounding-related changes in radial width, tangential width and lumen of earlywood vessels, and fibers and parenchyma cells (FPC). In diffuse-porous *A. glutinosa*, the lumen area of vessels shows a significant (non-parametric test, P-value <0.05) decrease by almost 39% after wounding. For ring-porous *F. angustifolia* and *Q. pyrenaica*, significant decreases in vessel lumen area are observed as well by 59 and 42%, respectively. Radial width of vessels was generally more sensitive to the decrease than tangential width, but statistically significant values were only observed in *F. angustifolia*. Changes in the dimensions of earlywood FPC largely differed between species. While in ring-porous *F. angustifolia* and *Q. pyrenaica* the lumen of FPC dropped by 22 and 34% after wounding, we observed an increase in FPC lumen area in diffuse-porous *A. glutinosa* of ~35%. Our data clearly show that *A. glutinosa* represents a valuable species for flash-flood research in vulnerable Mediterranean environments. For this species, it will be possible in the future to gather information on past flash floods with non-destructive sampling based on increment cores. In ring-porous *F. angustifolia* and *Q. pyrenaica*, flash floods leave less drastic, yet still recognizable, signatures of flash-flood activity through significant changes in vessel lumen area. In contrast, the use of changes in FPC dimensions appears less feasible for the determination of past flash-flood events as these two species do not react with the same intensity and clarity as *A. glutinosa*.

Keywords: anatomical changes, fibers and parenchyma cells, flash flood, growth rings, vessel, wounding.

Introduction

One of the most common hydrological processes in Mediterranean mountain ecosystems are flash floods (Roca et al. 2008) characterized by both very high discharge and important debris transport rates. In addition, an abrupt rise and fall of flood hydrographs combined with high flow velocities is normally observed during flash floods, which often results in damage or removal of the riparian vegetation.

Hydrological processes interfere with and play an important role in the establishment and survival of riparian vegetation (Sigafoos 1964, Kozlowski 1997). Hydrological and hydraulic parameters such as flood frequency, flood duration, flow regime and sediment transport often determine tree age and species distribution, as well as the morphology and anatomical structures of riparian trees (e.g., Oliveira-Filho et al. 1994, Kozlowski and Pallardy 1997).

Over the past decades, tree rings have been widely used by hydrologists for flood frequency reconstructions (Harrison and Reid 1967, Gottesfeld and Gottesfeld 1990, Zielonka et al. 2008) or peak discharge estimations of singular flood events (McCord 1996). Most of the flood events in these studies were determined using classical dendrochronological techniques (see Stoffel and Bollschweiler 2008, 2009, Stoffel et al. 2010) and events were dated based on the position of scars in the tree-ring series (Yanosky and Jarrett 2002). More recently, research started to focus on the anatomical response of conifers to flash floods (Ballesteros et al. 2010) and debris flows (Bollschweiler et al. 2008, Stoffel 2008). Wood anatomical features in broadleaved trees have, in contrast, only

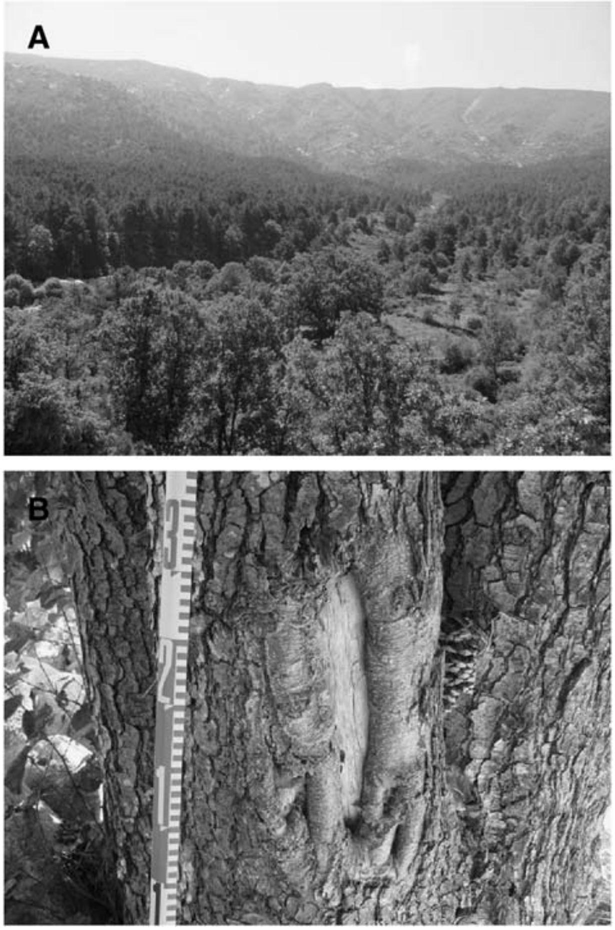

Figure 1. (A) General view of the Venero Claro catchment and the riparian trees on both sides of the main channel (foreground). (B) Stem of *A. glutinosa* L. scarred by debris transported by a flash flood.

been used in the study of large and prolonged floods so far, where the root system and lower trunk remained submerged over several days or weeks and the transport of growth hormones was interrupted as a result of lack of soil aeration (Kozlowski 1997). Moreover, experimental studies report on the anatomical effects of flooding treatments on seedling plants (Harrington 1987, Colin-Belgrand et al. 1991) or the effect of prolonged floods on the bark (Yáñez-Espinosa et al. 2008). Dendrochronological investigations of past floods include the work of Astrade and Bégin (1997), who related the presence of smaller and fewer vessels in *Populus tremula* L. (aspen) and *Quercus robur* L. (English oak) to persistent floods at the beginning of the growing season. Yanosky (1984) observed the formation of fibers with thinner cell walls and larger lumina after floods occurring at the end of the growing season. More recently, St. George et al. (2002) correlated the lumen of vessels in *Quercus macrocarpa* Michx. (bur oak) with spring floods and discussed their use for paleoflood studies.

In contrast, there is still a considerable lack of knowledge on how broadleaved trees growing in Mediterranean environments react to short-lived but much more energetic impacts of flash floods.

Our objective, therefore, is to characterize wood anatomical signatures in diffuse- and ring-porous Mediterranean broadleaved trees (European alder, *Alnus glutinosa* L.; narrow-leafed ash, *Fraxinus angustifolia* Vahl.; and Pyrenean oak, *Quercus pyrenaica* Willd.) wounded by recent flash floods. The knowledge of these anatomical signals associated with flash floods is of particular interest for the reconstruction of time series of past events and the design of future sampling strategies that can be based on non-destructive methods (i.e., increment cores). The study reports on results obtained from the measurement of earlywood vessels and fibers and parenchyma cells (FPC) of 54 micro-sections prepared from trees injured by flash floods.

Materials and methods

Study site

The study was performed with trees growing on the banks of the Arroyo Cabrera torrent (40°24′28″N; 4°39′25″W), located 3 km distant from the east of Navaluenga on the northern slopes of Sierra del Valle (Gredos Mountain Range, Spanish

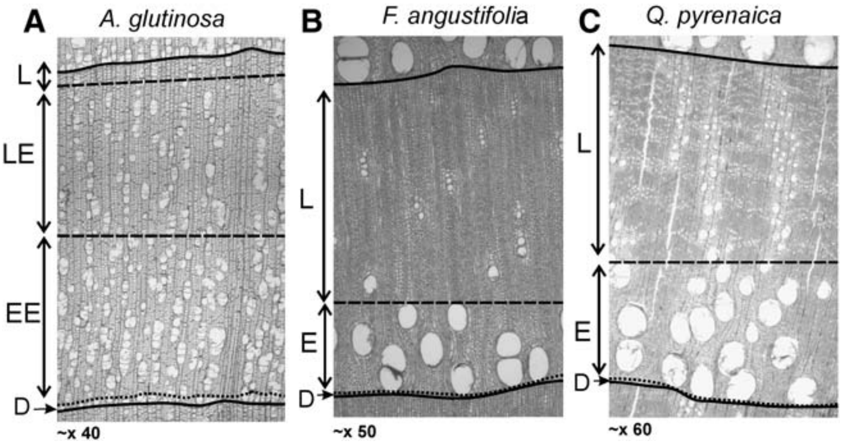

Figure 2. Subdivision of increment rings in (A) diffuse-porous *A. glutinosa*, (B) ring-porous *F. angustifolia* and (C) ring-porous *Q. pyrenaica*.

Central System; Figure 1A). The local forest stand is formed predominantly by *Pinus pinaster* Ait. (maritime pine), *Pinus sylvestris* L. (Scots pine) (81%) and *Q. pyrenaica* Willd. (13%). In addition, riparian broadleaved species (6%, *A. glutinosa* (L.), *F. angustifolia* Vhal.) colonize both banks of the river corridor. Mean annual temperature is 14.6 °C and mean annual rainfall amounts to 414 mm (AEMET 2009).

Torrential rainfall events usually occur in winter, resulting in abundant surface runoff, mobilization of sediments and related flash-flood events. At the study site, recent events occurred in the winters of 1989/90, 1997/98 and 2004/05 (Ballesteros et al. 2010). The flash flood recorded on 18 December 1997 was particularly severe and resulted in abundant damage in the riparian vegetation and the removal of *Salix* sp. and other shrubs.

Sampling design

Sampling was based on visibly injured trees located on the banks of the torrent (Figure 1B). We only considered injured trees with scars oriented in the flow direction. Trees with scars located elsewhere on the stem or with doubtful geometry such as unusually large or elongated scars were avoided since they could result from the toppling of neighboring trees. In the field, wedges were cut from the overgrowing callus with a handsaw. For each tree sampled, we took one increment core from the side opposite to the flow direction at breast height to determine tree age.

Sample preparation

Samples were air-dried, sanded and polished up to 400 grit to facilitate visibility of individual tree rings. We scanned the samples in high resolution (400 d.p.i.) before small cubes (8- to 10-mm edges) were prepared from each wedge at a tangential distance of 1.5 cm from the wound. Micro-sections (~15 μm) were obtained using a Reichert sliding microtome equipped with wedge-shaped blades. Samples were prepared following the procedure described by Schweingruber et al. (2006) and pictures taken from each micro-section with a digital imaging system (Leica DFC320) attached to an optical microscopic at 50× magnification and in 200 d.p.i. We prepared a total of 20 micro-sections from *A. glutinosa*, 18 from *F. angustifolia* and 16 from *Q. pyrenaica*.

Sample analysis

Wood anatomical analysis and microscopic observations focused on tree reactions after wounding (Stoffel and Hitz 2008). According to Stoffel et al. (2005) and Arbellay et al. (2009), annual rings of diffuse-porous *A. glutinosa* were subdivided into dormancy (D; i.e., the first cell layer formed in each ring), early (EE) and late (LE) earlywood, as well as latewood (L), as illustrated in Figure 2A. For ring-porous *F. angustifolia* and *Q. pyrenaica*, increment rings were divided into D, earlywood (E; i.e., the portion of the ring containing large vessels) and L. As all wounds were located in the very first layer of the increment rings—indicating that the wound was inflicted during D (i.e., sometime between October and March)—we restricted quantitative analysis of normal anatomical features related to flash floods to EE in *A. glutinosa* and to E in *F. angustifolia* and *Q. pyrenaica*. In addition, E layers are considered to represent a good proxy for environmental influences (García-González and Fonti 2006).

The growth ring formed immediately after the impact was assigned an ‘i’, the two tree rings preceding were defined as −2 and −1, and the two tree rings following the impact ring +1 and +2. Analyses of earlywood FPC and vessels were performed with the automated image analysis program WinCell Pro Version 5.6c (Régents Instruments 2008) in the E layers. Measurements of lumen area, radial width and tangential width of FPC and vessels were realized with a precision of 1 μm. We considered a lower error margin of 5 μm^2 for intercellular interstices, a minimum error margin of 100 μm^2 for the limit between FPC and vessels in *A. glutinosa* and an upper error margin of 50,000 μm^2 for several vessels with poorly discernible cell walls in *Q. pyrenaica*. Results underwent the Friedman test at 95% least squares difference to check median values of anatomical variables for statistical significance. This is a test analogous to the *t*-test but a nonparametric test (Sprent and Smeeton 2001) is used for more robust results when the data distribution is unknown. Assuming a normal distribution for our data would be incorrect since the number of samples analyzed is <30.

Results

General aspects

The main descriptive parameters of trees and wounds considered for the analysis are given in Table 1. Mean injury sizes in tangential orientation amount to 31.9 ± 21.2 cm for *A. glutinosa*, 26.5 ± 23.4 cm for *F. angustifolia* and 32.3 ± 8.2 cm for *Q. pyrenaica*. Injury lengths average 49.5 ± 50.8, 51.0 ± 51.2 and 28.7 ± 21.7 cm, respectively. The riparian species *A. glutinosa* and *F. angustifolia* exhibit larger injury sizes than *Q. pyrenaica* as they were located closer to the river channel. Similarly, while *Q. pyrenaica* showed single scars and only one sample with multiple scars was identified in *F. angustifolia*, 14 trees with multiple scars (1998, 2001 and 2005) were found in *A. glutinosa* trees.

Macroscopic observations

Callus tissue was the feature most commonly observed in all samples next to the injury (Figure 3A–C). At a tangential distance of 1.5 cm from the wound, however, only 25% of diffuse-porous *A. glutinosa*, but 55% and 56% of ring-porous *F. angustifolia* and *Q. pyrenaica*, samples showed this feature.

Tangential bands with smaller and flatter FPC and thicker cell walls have been observed in 35% of the *A. glutinosa* samples in the increment ring formed directly after wounding

Table 1. Descriptive parameters of the trees and wounds considered for analysis.

	Tree age (years)	Tree height (m)	DBH (cm)	Injury width (cm)	Injury length (cm)	Event years (years, no. of samples)
A. glutinosa						
Mean ± SD	55.4 ± 13.6	34.0 ± 3.5	34.0 ± 5.9	32.0 ± 21.2	49.6 ± 32.9	1997 (20); 2000 (6); 2004 (9)
Rank	49.0–8.0	18.3–22.3	44.6–22.3	91.0–10.5	109.0–5.0	
F. angustifolia						
Mean ± SD	37.8 ± 9.7	11.1 ± 3.8	26.6 ± 7.6	26.5 ± 23.5	51.0 ± 27.7	1981 (1); 1997 (18)
Rank	52.0–10.0	16.6–4.0	43.6–15.0	80.0–4.0	100.0–5.0	
Q. pyrenaica						
Mean ± SD	40.8 ± 14.2	11.9 ± 3.4	23.4 ± 5.4	30.0 ± 8.2	28.8 ± 21.7	1997 (16)
Rank	69.0–21.0	18.0–8.0	31.8–19.1	40.0–20.0	60.0–10.0	

DBH, diameter at breast height.

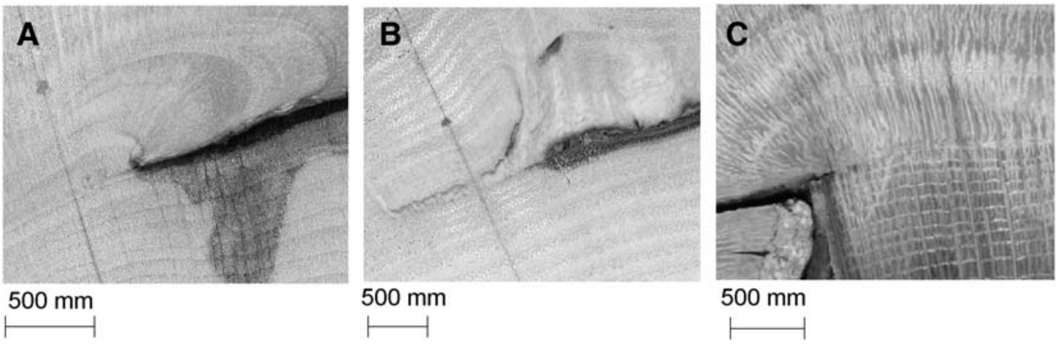

Figure 3. Macroscopic view of callus tissue in (A) *A. glutinosa*, (B) *F. angustifolia* and (C) *Q. pyrenaica*. Note the change in orientation of radial rays in the wood overgrowing the wound.

(Figure 4). These density fluctuations exhibit a gradual flattening and broadening of cells, which clearly distinguish them from latewood cells. At the edge of the injuries, these bands are located at the very beginning of the increment ring, but they move to later portions of the tree ring with increasing distance from the wound.

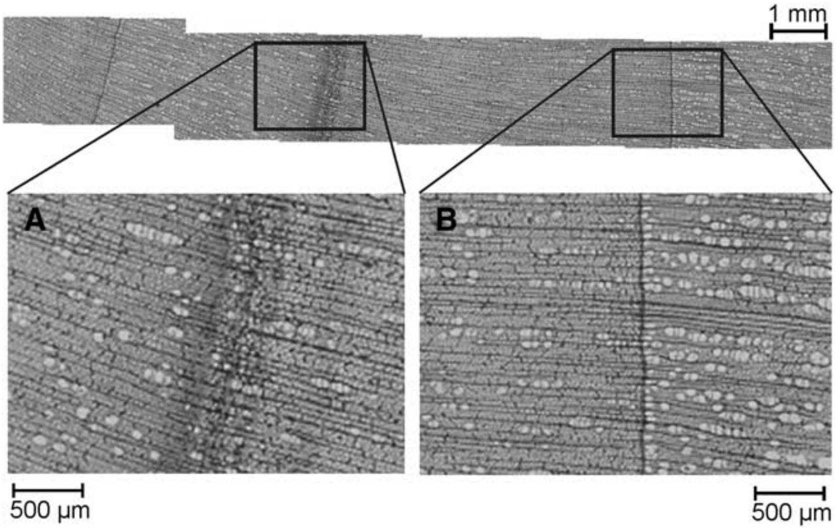

Figure 4. Tangential bands of flatter and smaller FPC with thicker cell walls, known as density fluctuations, are formed in 35% of the samples in diffuse-porous *A. glutinosa*. (A) The density fluctuation is located in EE and characterized by a gradual narrowing and re-widening of FPC. (B) in contrast, shows the sharp limit between two increment rings.

Table 2. Results obtained from the measurement of earlywood vessels. The mean of the lumen area, radial length and tangential widths of vessels are given for the year of the impact (i), 2 years before (−1, −2) and 2 years after (+1, +2) the event. Values given in bold are statistically significant (*P*-values <0.005).

Increment ring		*A. glutinosa*			*F. angustifolia*			*Q. pyrenaica*		
		Lumen area (µm^2)	Radial length (µm)	Tangential width (µm)	Lumen area (µm^2)	Radial length (µm)	Tangential width (µm)	Lumen area (µm^2)	Radial length (µm)	Tangential width (µm)
−2	Mean ± SD	1045.3± 303.6	32.2 ± 4.5	27.0 ± 3.7	3213.5 ± 836.8	70.9 ± 13.4	60.8 ± 11.8	2766.8 ± 1113.0	75.3 ± 26.1	65.8 ± 18.4
	%	162.4	113.4	114.4	247.3	162.6	150.5	179.9	126.3	122.3
−1	Mean ± SD	1048.3 ± 202.9	32.9 ± 11.4	26.7 ± 6.3	3159.9 ± 1129.6	68.0 ± 14.9	57.7 ± 9.7	3057.3 ± 1453.8	75.7 ± 18.9	67.1 ± 15.5
	%	162.9	115.8	113.1	243.2	156.0	142.8	198.8	127.0	124.7
i	Mean ± SD	**643.6 ± 171.8**	28.4 ± 8.5	23.6 ± 3.6	**1299.4 ± 559.5**	**43.6 ± 8.9**	**40.4 ± 8.8**	**1538.2 ± 655.2**	59.6 ± 22.4	53.8 ± 16.1
	%	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
+1	Mean	867.2 ± 211.7	33.9 ± 8.2	26.7 ± 4.0	1849.3 ± 973.1	52.3 ± 14.4	45.6 ± 10.9	2836.2 ± 2372.2	69.9 ± 24.8	63.4 ± 23.5
	%	134.7	119.4	113.1	142.3	120.0	112.9	184.4	117.3	117.8
+2	Mean	893.7 ± 251.4	34.1 ± 8.7	28.0 ± 6.4	2465.5 ± 946.6	62.0 ± 12.1	51.9 ± 8.8	3130.1 ± 2374.3	75.9 ± 26.7	65.6 ± 21.7
	%	138.9	120.1	118.6	189.7	142.2	128.5	203.5	127.3	121.9
F-ratio		3.49	0.55	0.92	16.45	15.01	14.17	2.53	1.46	1.66
P-value		0.018	0.700	0.460	<0.001	<0.001	<0.001	0.043	0.219	0.164
Mean number of vessels per sample			36 ± 9.7			26.9 ± 5.8			15.3 ± 7.0	

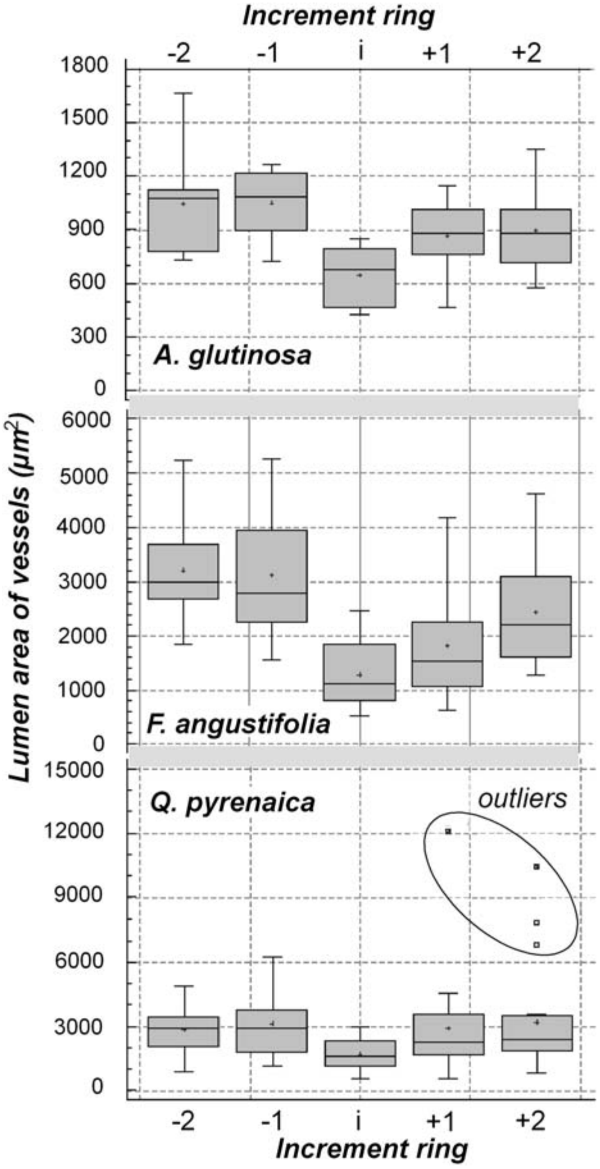

Figure 5. Boxplots representing the vessel lumen area in the increment rings preceding the wounding (increment ring −2, −1), in the increment ring of the year of the event (i) and after the event (increment ring +1, +2).

Changes in vessel dimensions after wounding

The size of vessels undergoes significant changes as a result of wounding by flash floods. Table 2 and Figure 5 summarize and illustrate results on lumen area, tangential width and radial width of vessels for the three tree species. The number of vessels identified per increment ring on an averaged sample area of almost 0.6 mm^2 (0.57 ± 0.09 mm^2) total 36 in *A. glutinosa*, 26 in *F. angustifolia* and 15 in *Q. pyrenaica*. All three species show a distinct reduction in vessel lumen area in the increment ring formed immediately after the flash-flood impact (i) as compared with the two preceding increment rings (−1 and −2). Reduction amounts to 39% in *A. glutinosa*, 59% in *F. angustifolia* and 42% in *Q. pyrenaica.* Non-parametric tests indicate that reduction is in all cases statistically significant (*P*-values = 0.018, <0.001 and 0.043, respectively).

We also observe differences in recovery rates between the species in the 2 years after wounding (+1 and +2). In *A. glutinosa* and *F. angustifolia*, vessel lumen areas attain only 84 and 64% of the pre-event values. In contrast, vessel lumen areas of *Q. pyrenaica* reach values that are comparable to or even larger than those measured in the tree rings formed before wounding (i.e., outliers in Figure 5).

The reduction of radial width and tangential width of vessels amounts to 13 and 12% in *A. glutinosa* and 21 and 19% in *Q. pyrenaica*. The highest values are observed in *F. angustifolia*, where radial width is significantly reduced by 37% and tangential width by 31%.

Changes in earlywood FPC dimensions after wounding

The dimensions of earlywood FPC were measured on a sample area of 0.06 mm^2 and yielded, on average, data on 950 FPC per growth ring and sample in *A. glutinosa*, 349 in *F. angustifolia* and 517 in *Q. pyrenaica*. Results of the measurements of lumen area, radial lengths and tangential widths are provided in Table 3 and illustrated in the form of boxplots in Figure 6.

In diffuse-porous *A. glutinosa*, wounding results in a significant increase (*P*-value = 0.012) in lumen area in FPC of 35%. Interestingly, the same impact results in a non-significant decrease in FPC lumina in ring-porous *F. angustifolia* (22%) and *Q. pyrenaica* (34%).

The changes in lumen area result from changes in radial width and tangential width. It seems that in the investigated tree species, radial width is slightly more affected by flash-flood impacts than tangential width. While the radial width in *Q. pyrenaica* and *F. angustifolia* decreased by ~18 and 19%, tangential width decreased by around 8 and 16%. In the case of diffuse-porous *A. glutinosa*, both radial length and tangential width of FPC increased by 22 and 19%, respectively.

Discussion and conclusion

In this study, 54 injuries caused by flash floods have been analyzed to identify reactions and anatomical signatures related to wounding. Among these, 20 injuries correspond to *A. glutinosa*, 18 to *F. angustifolia* and 16 to *Q. pyrenaica* trees.

Noteworthy, 14 out of the 20 *A. glutinosa* trees selected for analysis showed multiple scars. In contrast, we identified only one out of 18 injured *F. angustifolia* and none of the 16 *Q. pyrenaica* trees with more than one wound. The closer position of *A. glutinosa* trees with respect to the river channel (Brown et al. 1997) is certainly one of the reasons for the more abundant presence of injuries, as this renders them more exposed to flash floods than the other two species investigated. Another possible explanation may be the hardness of the wood and bark of each of the species and therefore their sensitivity to being injured. As a result of the vessel arrangement

Table 3. Changes in FPC dimensions as a result of wounding by flash floods. Values are given for the year of the impact (i), the 2 years preceding (−1, −2) and 2 years following (+1, +2) the event. Values in bold are statistically significant (*P*-values <0.005).

		A. glutinosa			*F. angustifolia*			*Q. pyrenaica*		
Increment ring		Lumen area (μm^2)	Radial length (μm)	Tangential width (μm)	Lumen area (μm^2)	Radial length (μm)	Tangential width (μm)	Lumen area (μm^2)	Radial length (μm)	Tangential width (μm)
−2	Mean ± SD	34.5 ± 13.8	6.5 ± 1.5	6.4 ± 1.3	26.8 ± 8.1	6.6 ± 1.2	4.9 ± 0.5	80.8 ± 18.9	11.8 ± 2.6	10.1 ± 1.8
	%	74.5	81.2	83.1	131.3	124.5	108.8	162.2	128.2	123.1
−1	Mean ± SD	34.1 ± 12.4	6.6 ± 1.3	6.5 ± 1.6	26.0 ± 10.4	6.4 ± 1.5	4.9 ± 0.8	72.0 ± 10.0	10.9 ± 1.3	9.5 ± 1.0
	%	73.6	82.5	84.4	127.4	120.7	108.8	144.5	118.4	115.8
i	Mean ± SD	**46.3 ± 16.7**	8.0 ± 1.5	7.7 ± 1.7	20.4 ± 7.4	5.3 ± 1.1	4.5 ± 0.8	49.8 ± 21.0	9.2 ± 2.2	8.2 ± 1.8
	%	100	100	100	100	100	100	100	100	100
+1	Mean ± SD	35.3 ± 10.6	6.8 ± 1.0	6.5 ± 1.3	21.9 ± 5.7	5.7 ± 0.9	4.6 ± 0.7	61.8 ± 19.8	11.6 ± 2.8	9.6 ± 1.4
	%	76.2	85	84.4	107.3	107.5	102.2	124.0	126.0	117.0
+2	Mean ± SD	35.5 ± 10.18	6.8 ± 1.1	6.4 ± 1.1	23.6 ± 2.6	5.9 ± 0.5	4.7 ± 0.4	71.4 ± 27.1	11.0 ± 2.2	9.8 ± 1.3
	%	76.6	85	84.4	107.3	107.5	102.2	124.0	126.0	117.0
F-ratio		3.5	1.05	2.01	1.04	1.57	0.3	1.55	1.33	1.5
P-value		0.012	0.387	0.104	0.400	0.203	0.800	0.215	0.213	0.226
N			950 ± 335			350 ± 121			517 ± 233	

within the increment rings and according to results on the average radial and tangential wood penetration obtained for different forest species with Janka hardness tests (Forest Products Laboratory 1999), the xylem structure of *Alnus* sp. would be much softer than that of *Fraxinus* sp. and *Quercus* sp. This implies that *Alnus* sp. would require smaller impact energies to generate sizeable scars.

The most important anatomical signature observed in our flash-flood samples was the change in vessel size after wounding. All species showed a statistically significant reduction in vessel lumina. The decrease was most important in *F. angustifolia* where a reduction of almost 59% was observed in the tree ring formed immediately after the impact as compared to the two increment rings preceding the year of wounding. In a similar way, data indicate that wounding by flash floods also causes changes in FPC size. Here, in contrast to the uniform and statistically significant response observed in vessel lumina, changes differed among the three species studied. While earlywood FPC lumen area exhibits a considerable, yet non-significant, decrease in ring-porous *F. angustifolia* and *Q. pyrenaica*, we observe a statistically significant increase in FPC lumina by >40% in diffuse-porous *A. glutinosa*.

The decrease in vessel size as a result of flash-flood impacts is in concert with data obtained for different broadleaved species after artificial wounding (Rier and Shigo 1972, Aloni and Zimmermann 1984, Kuroda 1986, Lev-Yadun and Aloni 1993, Lev-Yadun 2001). The increase in FPC lumen area in *A. glutinosa* observed in our samples is, in contrast, in contradiction with the findings of the above cited studies, which were realized under laboratory conditions and with predominantly young trees or seedlings.

For vessels and FPC, we see that radial width was more sensitive to changes than tangential width for all species. This is especially true for *A. glutinosa* where radial length decreased by almost 37%. Considerable changes in the radial length of earlywood cells appear to be a common reaction of trees to wounding and have been reported for *Larix decidua* Mill. (European larch) impacted by rockfall and snow avalanches (Stoffel and Hitz 2008) and *P. pinaster* Ait. injured by flash floods (Ballesteros et al. 2010).

While FPC dimensions and lumina almost attained pre-event values 2 years after the impact in *A. glutinosa* and *F. angustifolia*, it also becomes obvious from our data that *Q. pyrenaica* overcompensates for the decrease in FPC reduction (see outliers in Figure 5). According to Schweingruber et al. (2006), such overcompensation could result from less competition and improved light conditions after the elimination of neighboring trees and shrubs by the very large 1997 flash-flood event. On the other hand, it is also feasible that the overcompensation represents a form of reaction of *Q. pyrenaica* to the very unusual disturbance by flash floods and a stress-generated attempt to increase the efficiency of water transport (Hacke et al. 2006).

Despite the decrease in vessel size observed in all species after flash-flood impacts, there is an increase in the number of vessels (Figure 7). This increase could result from an overcompensation of conductance area and therefore be related to water transport efficiency, as a decrease in vessel sizes implies a reduction in water transport efficiency (Hacke et al. 2006).

One-third of the *A. glutinosa* samples show tangential bands of flattened and smaller FPC in the increment ring produced immediately after wounding. These bands resemble intra-annual density fluctuations and could therefore be indirectly related to the severity of the wound and the vitality of the tree, as suggested by Kozlowski and Pallardy (1997). On the other hand, it is also feasible that these intra-annual density fluctuations simply reflect changes in the water table and related drought stress (see Fritts 1976, Schweingruber

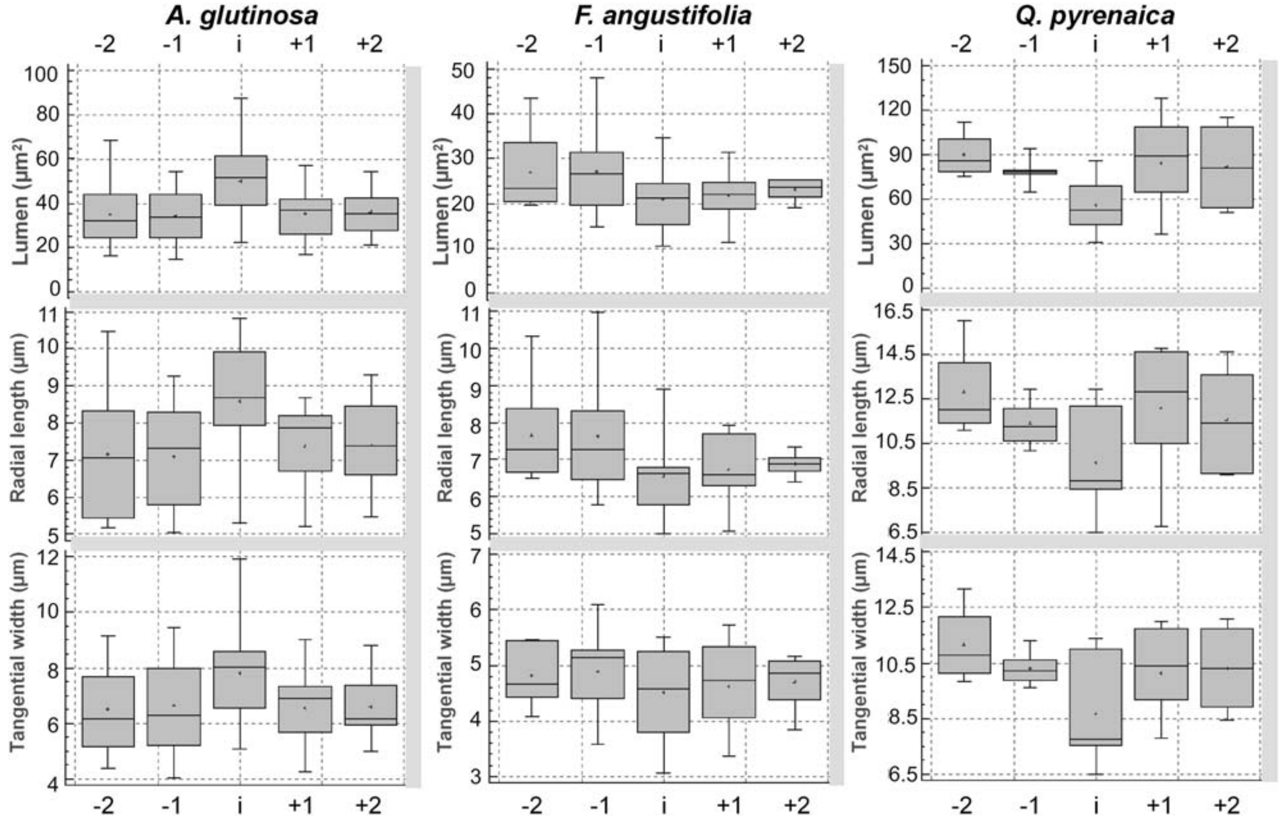

Figure 6. Boxplots representing FPC lumen area in the increment rings preceding the wounding (−2, −1), that formed immediately after the event (i) and in the two rings formed following the event year (+1, +2).

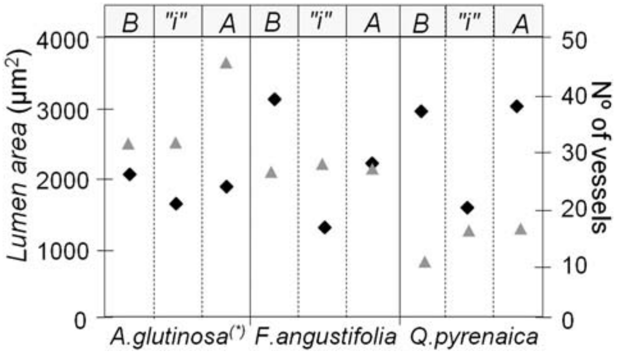

Figure 7. Number and size of vessels in *A. glutinosa*, *F. angustifolia* and *Q. pyrenaica* before the flash flood event (B), in the year of impact ("i") and after the event (A). Please note that vessel size of *A. glutinosa* has been multiplied by a factor o2.

2001) resulting from the flash flood and changes in the water course.

The present analysis has clearly shown that diffuse-porous *A. glutinosa* represents a valuable species for flash-flood research in vulnerable Mediterranean environments. It will therefore be possible in the future to gather data on past flash floods with non-destructive sampling methods (i.e., increment cores) and to reliably date past flash floods with the purpose of assessing hazards and risks in mountain catchments where systematic hydrological data are not available. In ring-porous *F. angustifolia* and *Q. pyrenaica*, flash floods leave less drastic, yet still recognizable, signatures of flash-flood activity through significant changes in vessel lumen area. A determination of past events based exclusively on changes in FPC dimensions appears, in contrast, less feasible, as they do not react with the same intensity and clarity as *A. glutinosa*.

Acknowledgments

This paper was funded in part by CICYT, the DendroAvenidas project (number CGL2007-62063 of the Spanish Ministry of Science and Innovation) and the Instituto Geológico y Minero de España (IGME). The authors acknowledge the valuable feedback of Estelle Arbellay and the kind collaboration of the Environment Department of Ávila (Castilla-Leon), in particular forester J.L. Galán.

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