



Subsidy or stress? Tree structure and growth in wetland forests along a hydrological gradient in Southern Europe

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ARTICLE INFO

Article history:

Received 25 November 2009

Received in revised form 7 February 2010

Accepted 9 February 2010

Keywords:

Alnus glutinosa

Dendrochronology

Functional traits

Salix atrocinerea

Soil waterlogging

Vegetative strategy

ABSTRACT

In forested wetlands, hydrology exerts complex and sometimes compensatory influences on tree growth. This is particularly true in semi-arid ecosystems, where water can be both a limiting resource and a stressor. To better understand these relationships, we studied hydrologic and edaphic controls on the density, growth, tree architecture and overall productivity of forested wetlands dominated by the tree species *Alnus glutinosa* and *Salix atrocinerea* in Southern Europe. We sampled 49 plots set within 21 stands in the Atlantic coastal zone of the Iberian Peninsula, and quantified woody composition, size structure (diameter and height), and radial growth using dendrochronology. Plots were grouped into three saturation classes to compare tree growth characteristics (tree density, degree of sprouting, live basal area and productivity) across levels of saturation. We used Principal Component Analysis (PCA) to create integrated explanatory factors of hydrology, soil nutrient status and soil texture for use in linear mixed models to predict stand characteristics. Increased site saturation favoured a shift in species dominance from *Alnus* to *Salix* and resulted in a higher degree of multi-stemmed tree architecture ('shrubbiness'), particularly for *Alnus*. Radial growth was negatively correlated with long-term soil saturation; however, annual productivity on a per-tree basis varied by species. *Alnus* growth and tree density were negatively correlated with waterlogging and fine-textured soils, possibly due to anaerobiosis in the rooting zone. In contrast, *Salix* growth was more influenced by nutrient limitation. Overall site productivity as measured by annual basal area increment decreased with prolonged saturation. In summary, soil saturation appears to act as a chronic stressor for tree species in this ecosystem. However, these species persist and maintain a dominant canopy position in the most permanently flooded patches through increased sprouting, albeit at a reduced rate of overall biomass accumulation relative to well-drained sites. The diversity in functional responses among wetland forest species has important implications for the conservation and management of these ecosystems. The sustainable management of these ecosystems is directly tied to their vulnerability to changing hydrological conditions. Non-equilibrium modifications to the hydrologic regime from land use and climate change, which are particularly severe in semi-arid regions, may further decrease productivity, integrity and resilience in these stress-adapted communities.

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1. Introduction

The growth and functional response of plants to resource availability and stressors is a long-standing research focus in ecology and agriculture (Chapin, 1980; Grime, 2002). In wetlands, water can be both a limiting resource and a chronic stressor (Mitsch and Gosselink, 2007). This is particularly the case for wetlands in semi-

arid or transitional climates (Gasith and Resh, 1999), where sharp ecological gradients exist between upland communities and those dominated by wetland specialists that tolerate a wider range of disturbance and hydrologic conditions (Mouw, 2003; Sieben et al., 2009). Odum et al. (1979) characterized the opposing effects of perturbations such as flooding as ends of a "subsidy-stress" gradient, and predicted that ecosystem function/performance is highest at intermediate levels along the gradient. The effects of seasonal or permanent flooding can be envisioned as influencing both individual plants as well as whole ecosystems. Flooding can create a subsidy of high water and nutrient availability to individual terrestrial plants. Conversely, long-term soil saturation induces soil anoxia, which limits nutrient availability and gas exchange for

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plants (Mitsch and Gosselink, 2007), and soil toxicity due to reducing conditions. In addition, flooding in dynamic riparian settings can scour the soil substrate disturbance or induce local sedimentation (Kozłowski and Pallardy, 2002). These negative effects are mitigated to some degree by plants' adaptive responses to prolonged flooding, including tissues to facilitate oxygen exchange such as aerenchyma and lenticel development (Blom and Voeselek, 1996; Rood et al., 2003; Walls et al., 2005). Much of the research on physiological responses to flooding is based on laboratory experiments (Gill, 1975; Pereira and Kozłowski, 1977; Conner et al., 1997; Lopez and Kursar, 2003; Li et al., 2005; Day et al., 2006; Ewers et al., 2007; Wikberg and Ögren, 2007), with less emphasis on field studies (but see Megonigal et al., 1997; Eschenbach and Kappen, 1999; Tardif and Bergeron, 1999).

Though flooding generally has negative effects on individual tree function, its effects on overall stand productivity are less clear. Understanding the net integrative effects of flooding on species and whole stands is difficult because plants may exhibit compensatory responses across the hydrological gradient (e.g., shifts between sexual and clonal reproduction), and these are generally species-specific (Tardif and Bergeron, 1999). Increased inundation frequency and duration can have various effects on aboveground net primary productivity (ANPP), ranging from negative (e.g., Mitsch et al., 1991; Megonigal et al., 1997) to slightly positive (Burke et al., 1999; Clawson et al., 2001; Hanson et al., 2001). Many factors affect productivity, including stand age (Ryan et al., 1997), growth rate (Burke et al., 1999; Anderson and Mitsch, 2008), density (Szaro, 1990), and degree of sprouting (Bellingham, 2001; Francis, 2007; Opperman et al., 2008). In recent years, there has been a growing appreciation for the role of vegetative growth in allowing woody plants to persist in a diversity of ecosystems, particularly where stressful abiotic conditions may limit organism size, lifespan, and/or recruitment opportunities (Odum et al., 1979; Klimesová and Klimeš, 2007; Nzunda et al., 2007). Sprouting may be an important strategy in particular for species that do not maintain a seed bank (Karrenberg et al., 2002; Stella et al., 2006).

The question of whether flooding is primarily a subsidy or a stress in woodlands is of particular interest in drought-prone areas, where water is limiting to the surrounding upland ecosystem for long periods of the year (Eriksson, 1996; Megonigal et al., 1997). Many studies have been conducted in flooded bottomland forests of the mesic Southeastern U.S. (Conner et al., 1997; Mitsch et al., 1991; Megonigal et al., 1997; Burke et al., 1999; Anderson and Mitsch, 2008). Studies in arid and semi-arid climates tend to focus on drought and/or water regulation impacts to riparian communities (e.g., Scott et al., 1999; Shafroth et al., 2002; Northcott et al., 2007), and dendroecological studies generally consider growth of individual trees (e.g., Stromberg and Patten, 1990). However, whole-stand productivity studies in the wetland forests of drought-prone areas are less common. In Southern Europe, where few forested wetlands remain because of intensive land use and extensive hydrologic alteration, wetland tree sensitivity to flooding is not well-understood. A large portion (86%) of wetland forests in Portugal and western Spain are dominated by *Salix atrocinerea* Brot. and/or *Alnus glutinosa* (L.) Gaertn. (Rodríguez-González et al., 2004, 2008). Though growth and yield have been studied extensively for some North American species of both *Alnus* and *Salix* (Johnson, 2000; Schaff et al., 2003; Balian and Naiman, 2005; Hultine et al., 2007; Johnston et al., 2007), studies of European wetland trees are relatively rare (but see Iremonger and Kelly, 1988; Johansson, 1999) and are non-existent for Southern Europe. The *Salix* and *Alnus* stands of Portugal and Western Spain show distinct patterns of stand structure and relative dominance by each species, but the drivers of these patterns are largely unknown. Given the importance of the remaining wetlands in semi-arid regions –for wildlife habitat, ecosystem productivity, and the regulation of biogeochem-

ical cycles, studying the controls on tree composition and structure is critical to developing a comprehensive understanding of these ecosystems' dynamics.

Our study examines the influences of hydrology and soil properties on tree species dominance, growth, and aboveground stand biomass across the natural range of wetland hydrology within the Ibero-Atlantic region of Portugal and Western Spain. This study represents the first attempt to quantify net aboveground wood production in Southern European wetland forests. Specifically, we compared tree density, shrubbiness (single versus multi-stemmed architecture), growth rate, and stand health (proportion of dead standing aboveground biomass) along the natural hydrological gradient. We hypothesized that high soil saturation and correlated edaphic factors exert differential responses based on species' flood-tolerance, resulting in shifts in woodland stand composition, structure, and aboveground biomass. Furthermore, we assessed whether the correlated trends in basal area, density, shrubbiness, and growth rate along the hydrological gradient were consistent with a stress response (i.e., lower aboveground growth and productivity with higher soil saturation), or alternatively, a positive growth response to increased resource subsidies (Odum et al., 1979).

2. Materials and methods

2.1. Tree sampling

The field sampling was carried out during the summer of 2003 and 2004 in 21 freshwater wetland forest stands along the Atlantic coastal belt of the Iberian Peninsula, from north-western to southern Portugal and western Andalusia in Spain (between 6° and 9°W longitude and 42° to 38°N latitude; Fig. 1). Sampling years were representative of long-term hydrologic conditions across the Ibero-Atlantic coastal belt, with annual precipitation during the sampling years generally falling into the middle two quartiles of annual precipitation totals since 1960 (Appendix A). Criteria for stand selection included dense tree cover (>70%), and sufficient permanence of soil water for the development of wetland species. Forests were mainly lentic systems located in depression areas, on soils subject to frequent flooding and saturation, or with markedly impeded drainage with different levels of connectivity with the fluvial network. Thus their geomorphic position

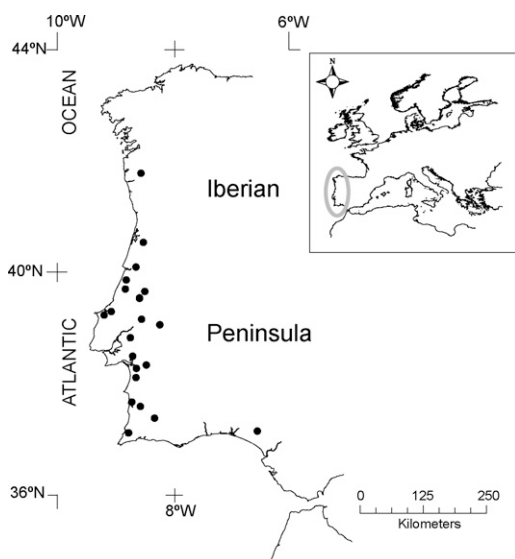


Fig. 1. Location of the sampled wetland forests along the Atlantic coastal belt of the Iberian Peninsula in Southern Europe.

within the hydrographic basin varied from the floodplain to depressional areas disconnected from the river. This means that the main sources of water were diverse and often mixed surface and groundwater sources. Stands were dominated by *A. glutinosa* and/or *S. atrocinerea*, which are the best-represented types of wetland forests along the Ibero-Atlantic latitudinal gradient (Rodríguez-González et al., 2008).

We selected only stands with little evidence of human contemporary disturbance in both the stand itself and its surrounding area.

Within each stand we located 15 m-diameter circular plots within homogeneous areas with respect to groundwater depth (consistent elevation/topography) and evidence of surface saturation (presence/absence of surface water, or visible waterlogging). Our aim was to cover the range of hydrological conditions relevant to tree development in each stand; therefore the number of plots per stand was determined depending on the variation in hydrology evident within the stand. Several plots had small portions inaccessible during sampling due to logistical difficulties and were area-adjusted; all adjusted plots conformed to the recommended range of minimum sampling area for swamp forests (100–250 m², van der Maarel, 2005). A total of 49 plots were sampled within the 21 stands.

In each plot, all trees higher than 1.5 m were identified to species and the tree height was measured with a hypsometer to the nearest 0.5 m. Breast height diameter (DBH) for all trunks ≥ 5 cm was measured to the nearest 0.1 cm at two perpendicular locations using a caliper. For trees with multiple trunks at breast height, all stems were counted, measured and recorded as dead or alive. Using the averages of the two diameter measurements per tree, basal area was calculated for all live and dead stems. Sexual reproduction within the plot was visually estimated for both tree species as the percentage cover of seedlings (individuals <1.5 m tall). A total of 245 individuals (705 stems) of *A. glutinosa* and 602 individuals (2409 stems) of *S. atrocinerea* were measured in the field.

At each of the 49 plots, we cored 3–4 of the largest individuals of the dominant species in the canopy with a standard 5-mm increment borer, taking two (three when needed) perpendicular cores at 1.3 m (Mäkinen and Vanninen, 1999). For multi-stemmed trees cores were taken from the largest stem. Cores were dried, mounted and polished. Cores were visually cross-dated (Stokes and Smiley, 1996) and ring increments were measured to an accuracy of 0.01 mm using a linear table Lintab (Frank Rinn S.A., Heidelberg, Germany) and the program TSAP-Win (Rinn, 2003). A total of 451 increment cores were taken, corresponding to 207 trees (95 *Alnus* and 112 *Salix*) from the measured stems.

2.2. Environmental variables

Soils were sampled in each plot at three depths 0–20, 20–40 and 40–60 cm using a 3-cm diameter unslotted alloy soil probe at three random locations. The three samples at each depth were composited, air dried, and the <2 mm fraction was analyzed at the Laboratório de Pedologia do Instituto Superior de Agronomia, Lisboa, to obtain estimates of percent organic matter and carbon (De Leenheer and Van Hove, 1958); nitrogen (Kjeldhal digestion); extractable phosphorus (Murphy and Riley, 1962); organic phosphorous (Saunders and Williams, 1955); magnesium, calcium, sodium, potassium (atomic absorption spectroscopy); and soil texture (percentages by weight coarse sand, fine sand, silt and clay) (Póvoas and Barral, 1992). Redox potential and pH of the soil solution were determined on site using portable field probes (WTW, MultiLine P4). Depth to water table was measured digging a hole within the plot and letting the water level stabilize (usually after sampling the rest of the parameters within the plot) and the areal percentage of the plot that was saturated in summer was visually estimated.

2.3. Data analyses

We conducted correlation analyses (Pearson) on the collected variables in order to examine existing relations within the environmental matrix. For the soil parameters, the averages of 0–60 cm values were used. Plots were stratified into three saturation classes based on the depth to the water table and the percent of the plot fully saturated at the surface during summer, which is the driest season throughout the region (Rivas-Martínez, 2004) (Appendix B-1). These classes were then used to interpret trends in the vegetation structure and growth data along the hydrologic gradient. Class 1 plots ($n=7$) were defined as unsaturated, with the water table depth ≥ 50 cm and no waterlogged surface substrate. Class 2 plots ($n=21$) were semi-saturated, with water table depth <50 cm and surface saturation $\leq 65\%$. Class 3 plots ($n=21$), which were the wettest, had surface saturation over >65% of the plot area. These divisions were based on the range of environmental variability that occurs within wetland sites throughout the region, and were designed to stratify sites by suites of correlated values of dry season hydrologic measurements (e.g. water table depth, surface saturation) indicative of short-term, acute stress as well as hydric edaphic factors (e.g. redox potential) that indicate longer term saturation status and potential enduring stress to plants.

Differences among saturation classes in the density of trees (trees/ha) and stems (stems/ha), live per-tree basal area, shrub-biness (stems per tree), and age-corrected growth rates were tested by analysis of variance (ANOVA). In order to satisfy residual assumptions, log transformations were used for tree and stem density, stems-per-tree, and live basal area; an arcsin square-root transformation was used for dead stem proportions. The Tukey's honest significance difference post hoc test assessed group-by-group differences.

We analyzed tree growth using tree-ring chronologies. First, ring widths for all cores of each stem by species were averaged by year. Samples showing pith were used to determine cambial age and to obtain a predicted growth curve for each species. Fourth order polynomial functions (Dufour and Piégay, 2008) were fitted to the mean values of annual ring widths of all the individuals of each species and stratified by saturation class. The growth curve r^2 values ranged 0.76–0.88 among the three classes for *Alnus*, and 0.91–0.95 for *Salix*. Repeated measures ANOVA in SPSS 16.0 was used to test the null hypothesis of no differences in mean growth over time among classes. For analyzing the influence of environmental factors on recent growth we averaged the last five rings (representing 1999–2003) for each stem, excluding older rings because of uncertainty as to the historical environmental conditions, and stems <15 years old to minimize age effects on growth (mean age of sampled trees \pm SD; 25.4 ± 10.1 years). For individuals in which the cores did not reach pith, age was estimated using the diameter, the average annual growth ring width in the first years of life for each species (obtained from the species predicted growth curves described above) and the average bark width for each species. This method resulted in an age estimation error rate of 1.3 ± 1.2 years for *Alnus* and 2.4 ± 2.3 years for *Salix* (mean \pm SD); these estimates were obtained using the samples for which pith age was known.

We calculated annual basal area increment (BAI) for cored individuals, and over the whole plot as a robust estimate of individual and stand-level aboveground productivity and health (Mitsch et al., 1991; Anderson and Mitsch, 2008). Calculating BAI at the plot level is the most relevant measure of whole-stand productivity because it accounts for co-occurring trends in tree composition, density and growth rate, all of which may vary across wetness categories. Sampling limitations precluded taking increment cores from each stem of each tree. To estimate individual BAI (cm² tree⁻¹) we applied the radial growth rates for cored stems to all stems of the tree. Measured increment growth rates were applied to non-cored stems by

subtracting radially from the current diameter measurement. As a proxy for a full stand-level aboveground biomass measurement of all stems, we estimated annual stand BAI ($\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$) using the plot-averaged 5-year growth of all cored trees and the full census of stems in the plot. Plot-average growth rates were stratified by species for the whole-plot BAI estimates. Differences in annual stand BAI among saturation classes were tested using ANOVA.

2.4. Modelling environmental indicators of stand density, tree growth and health

In order to test the effects of all environmental variables on stand structure and tree growth and health, we consolidated the soil variables using a Principal Components Analysis (PCA) using CANOCO 4.5 (ter Braak and Šmilauer, 2002). All environmental variables shown in Table 1 were used in the PCA except redox potential (because of several missing values), organic phosphorus (which was highly correlated with extractable P) and nitrogen and carbon contents (which were substituted by C:N ratio). We used the first three principal components of the PCA as explanatory factors to model four vegetative indicators of aboveground productivity and tree health: (1) tree density, in trees/ha; (2) shrubbiness growth form, measured as the plot-based average of live stems per tree; (3) stem mortality, measured as the proportion of dead basal area per tree; and (4) recent average residual growth rate (1999–2003). Each of the two species was modelled separately. Linear mixed-effects

models were implemented in R 2.5.1. (*lme* function, R Development Core Team, 2007; Pinheiro and Bates, 2000) using forest stand as a random effect to account for the nesting of plots within stands.

For model selection, we took an information-theoretic approach, using Akaike information criterion (AIC) to compare a suite of competing models (Burnham and Anderson, 2002). The best models were selected using the lowest AICc values in a candidate set, and alternate models were assessed using differences from the minimum AIC (Δ_i) and associated Akaike weights (w_i). The best model in each candidate set has the lowest Δ_i and highest weight. For each response factor tested (tree density, shrubbiness, growth rate and mortality), we constructed a set of candidate models that included all additive combinations of the first three principal components of the PCA (eight models total).

3. Results

3.1. Plot environmental conditions

Table 1 shows the main hydrologic and edaphic gradients across the three wetness classes. The first two factors listed, percent surface saturation and depth to water table were used to stratify the classes initially, and as a result have large differences between classes. Aside from these, the variable showing the widest range of variation between wetness classes was redox potential (–291 to 307 mV); this range is consistent with findings in Northwest

Table 1
Environmental and vegetation characteristics of studied plots ($n = 49$) by soil saturation class. Soil chemistry parameters are averages from 0 to 60 cm depth. All measurements were done in summer. Ca, Mg, Na and K are exchangeable forms. *Alnus* and *Salix* growth rates correspond to the last 5 years of measurements (1999–2003).

Variable description	All plots ($n = 49$)			Wetness class 1 ($n = 7$)	Wetness class 2 ($n = 21$)	Wetness class 3 ($n = 21$)
	Mean \pm sd	Min	Max	Mean \pm sd	Mean \pm sd	Mean \pm sd
Water						
% waterlogged area	46.70 \pm 36.00	0	100	0 \pm 0	35.00 \pm 23.29	83.50 \pm 10.73
Depth to water table (cm)	27.15 \pm 30.67	–10	150	87.29 \pm 37.16	22.18 \pm 11.40	8.43 \pm 7.95
pH	6.05 \pm 0.58	4.53	7.29	6.35 \pm 0.77	6.07 \pm 0.62	5.89 \pm 0.45
Redox potential (mV)	–91.74 \pm 196.20	–291	307	248.5 \pm 82.73	–81.00 \pm 203.37	–167.25 \pm 125.22
Soil						
% organic matter	9.51 \pm 7.79	1.67	33.03	6.99 \pm 4.87	10.57 \pm 8.63	8.93 \pm 7.50
Organic C (mg/g)	55.15 \pm 45.20	9.67	191.60	40.59 \pm 28.25	61.35 \pm 50.07	51.81 \pm 43.54
Total N (mg/g)	3.17 \pm 2.48	0.06	9.64	2.54 \pm 2.27	3.48 \pm 2.70	3.00 \pm 2.27
C:N	16.31 \pm 8.25	8.08	66.93	12.24 \pm 3.11	15.55 \pm 3.65	19.28 \pm 13.04
Organic P ($\mu\text{g/g}$)	217.00 \pm 163.00	56.57	743.63	212.97 \pm 236.41	242.39 \pm 166.20	178.95 \pm 118.56
Extractable P ($\mu\text{g/g}$)	27.61 \pm 32.30	0.09	176.81	34.22 \pm 63.49	32.92 \pm 28.11	16.36 \pm 13.82
Ca (cmol/kg)	6.00 \pm 7.48	0.19	32.93	7.82 \pm 10.88	7.46 \pm 8.06	2.88 \pm 2.92
Mg (cmol/kg)	3.41 \pm 3.00	0.19	10.10	3.33 \pm 3.63	4.10 \pm 3.12	2.35 \pm 2.21
Na (cmol/kg)	0.72 \pm 0.49	0.09	1.99	0.63 \pm 0.33	0.83 \pm 0.55	0.58 \pm 0.40
K (cmol/kg)	0.22 \pm 0.23	0.01	1.09	0.26 \pm 0.37	0.26 \pm 0.23	0.12 \pm 0.09
% clay	22.27 \pm 16.44	4.32	63.20	23.92 \pm 4.75	28.36 \pm 21.31	15.08 \pm 8.81
% silt	21.70 \pm 12.46	2.16	47.08	30.93 \pm 10.39	23.63 \pm 10.41	16.81 \pm 13.87
% fine sand	21.16 \pm 9.28	4.67	32.35	25.60 \pm 8.76	18.94 \pm 10.14	22.26 \pm 8.64
% coarse sand	34.86 \pm 25.19	0.2	79.48	19.54 \pm 16.82	29.06 \pm 23.57	45.85 \pm 26.24
Vegetation						
Maximum stem age (years)	31.31 \pm 14.16	9	72	26.00 \pm 12.42	35.44 \pm 16.38	27.19 \pm 9.52
Tree density (trees/ha)	1314.76 \pm 734.79	346.15	4166.67	1049.13 \pm 634.27	1213.09 \pm 532.71	1618.75 \pm 974.57
Stem density (stem/ha)	4601.04 \pm 3156.99	1230.77	19100	3434.74 \pm 991.33	3844.72 \pm 1943.86	6388.85 \pm 4421.47
Stems per tree <i>Alnus</i>	3.20 \pm 3.40	1	19	2.27 \pm 1.75	3.22 \pm 3.99	5.21 \pm 3.71
Stems per tree <i>Salix</i>	4.10 \pm 5.35	1	48	4.50 \pm 3.32	3.57 \pm 4.88	4.52 \pm 6.01
<i>Alnus</i> growth rate (mm/year)	3.73 \pm 2.43	0.13	12.03	5.49 \pm 3.00	2.97 \pm 2.37	3.70 \pm 1.03
<i>Salix</i> growth rate (mm/year)	4.20 \pm 2.71	0.61	12.74	7.81 \pm 1.73	4.11 \pm 2.47	3.03 \pm 2.24
DBH largest stem (cm)	33.23 \pm 12.09	13.8	71	34.90 \pm 15.08	34.58 \pm 10.22	29.55 \pm 13.34
Weighted average DBH (cm)	11.36 \pm 4.50	4.06	26.41	12.35 \pm 3.88	12.50 \pm 3.64	8.92 \pm 5.27
Tree height (m)	15.12 \pm 4.38	8	23	16.14 \pm 4.63	15.64 \pm 4.27	13.46 \pm 4.13
Weighted average <i>H</i> (m)	9.84 \pm 2.48	5.205	14.75	11.20 \pm 2.08	10.11 \pm 2.28	8.83 \pm 2.75
<i>Alnus</i> relative BA over plot	0.30 \pm 0.39	0	0.99	0.43 \pm 0.41	0.30 \pm 0.40	0.21 \pm 0.34
<i>Salix</i> relative BA over plot	0.64 \pm 0.39	0	1	0.54 \pm 0.41	0.61 \pm 0.41	0.76 \pm 0.33
<i>Salix</i> regeneration cover (%)	0.00 \pm 0.00	0	0	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
<i>Alnus</i> regeneration cover (%)	0.01 \pm 0.07	0	0.5	0.00 \pm 0.00	0.02 \pm 0.10	0.00 \pm 0.00
% dead stems	24.85 \pm 14.61	1.23	58.73	27.88 \pm 16.41	21.85 \pm 14.55	28.83 \pm 13.92
% dead BA per tree	14.62 \pm 29.09	0	100	21.84 \pm 35.11	12.95 \pm 27.88	14.21 \pm 28.30

Iberian floodplain forest soils (Gallardo, 2003). Class 3 sites, the most saturated, were characterized by the most negative redox potentials and the lowest levels of soil nutrients (phosphorous and cations). These sites also have the highest C:N values, indicating lower rates of organic matter mineralization, and the coarsest texture. The factor correlation matrix indicated that fine-textured soils (high percentage clay) were positively associated with high nutrient concentrations. Soil pH was negatively correlated with C:N ratio, indicating that soils with high organic matter accumulation were the most acidic (Appendix C).

The first three principle components (PCs) of the PCA model accounted for 86.1% of the variance in the environmental data set (Appendix B-2) and allowed us to collapse the factors along three axes corresponding generally to hydrology (PC1), soil nutrients (PC2), and soil texture (PC3). PC1 accounted for 45.9% of the variance and was highly correlated with plot saturation and water table depth (Appendix B-2). It was thus interpreted as representing wetland hydrology, with more negative values signifying wetter plots (Appendix B-2). PC2, with 27.8% of the variance explained, was most highly correlated with soil nutrients and water table depth. Positive values for PC2 indicated more fertile and somewhat moister sites. The driest (i.e., least saturated) sites had the highest PC1 values and the lowest PC2 values (Appendix B-2). PC3 (12.4% of the variance explained) represents a gradient of soil texture, with positive values signifying coarser substrates.

3.2. Tree and stem size distributions

Across the gradient of wetness classes, high site saturation was correlated with high total stem density, and decreased tree height, diameter, and growth rate (Table 1). The least saturated plots (Class 1) were characterized by similar proportions of *Alnus* (0.43 ± 0.41 relative basal area) and *Salix* (0.54 ± 0.41), whereas the most saturated plots were dominated by *Salix* (0.76 ± 0.33 , Table 1).

Stem diameter and tree height distributions varied by saturation class (Fig. 2). *Salix* displayed higher stem and tree densities than *Alnus* for all wetness and girth classes (Fig. 2 and Table 1).

The stem size distribution in saturated sites (Class 3) for *Salix* is highly skewed compared to drier sites, with substantially higher stem densities (750 to 2500 stems/ha) in the three smallest girth classes (DBH < 15 cm), very low densities of stems > 15 cm DBH. *Alnus* trees show an opposite trend; saturated sites supported the lowest stem densities and a more even size distribution relative to the drier plots. Tree height distributions for both species were skewed toward taller trees, with virtually no small saplings (Fig. 2). For *Alnus*, drier sites supported higher tree densities, and mean tree height decreased with wetness class. For *Salix*, a smaller proportion of the tallest trees (> 15 m) were found in the most saturated plots relative to drier ones (Fig. 2). Seedling regeneration was absent from 98% of the wetland forest sites surveyed (Table 1).

3.3. Tree density, basal area, and growth rate

The two species displayed opposite trends in tree density across the hydrologic gradient (Fig. 3a and b), with *Alnus* density significantly decreasing with increased site wetness (ANOVA $F_{2,17} = 6.92$, $P < 0.01$) and *Salix* increasing moderately (though not significantly, $F_{2,45} = 1.57$, $P = 0.22$). Shrubiness, or number of stems per tree (Fig. 3c and d), was positively correlated with site wetness for *Alnus* ($F_{2,180} = 9.20$, $P < 0.001$), and was significantly different between the two drier and the saturated site classes. *Salix* trees maintained equal numbers of stems per tree across the three classes ($F_{2,508} = 1.01$, $P = 0.36$). There were no statistical differences in overall stem density (data not shown) for either species ($F_{2,17} = 1.64$, $P = 0.22$ for *Alnus*; $F_{2,45} = 0.76$, $P = 0.48$ for *Salix*); however, as with tree density there is a modest monotonically increasing trend with soil saturation for *Salix*. Probably because of the compensating trends in tree density and shrubiness, the overall stem density for *Alnus* was not significantly different comparable among groups.

For the 451 increment core samples to analyze growth, annual ring increment averaged 0.49 cm (range 0.01–2.39 cm) for *Alnus* and 0.45 cm (range 0.02–2.46 cm) for *Salix*. Similar to tree density, *Alnus* and *Salix* had opposite patterns of live basal area and

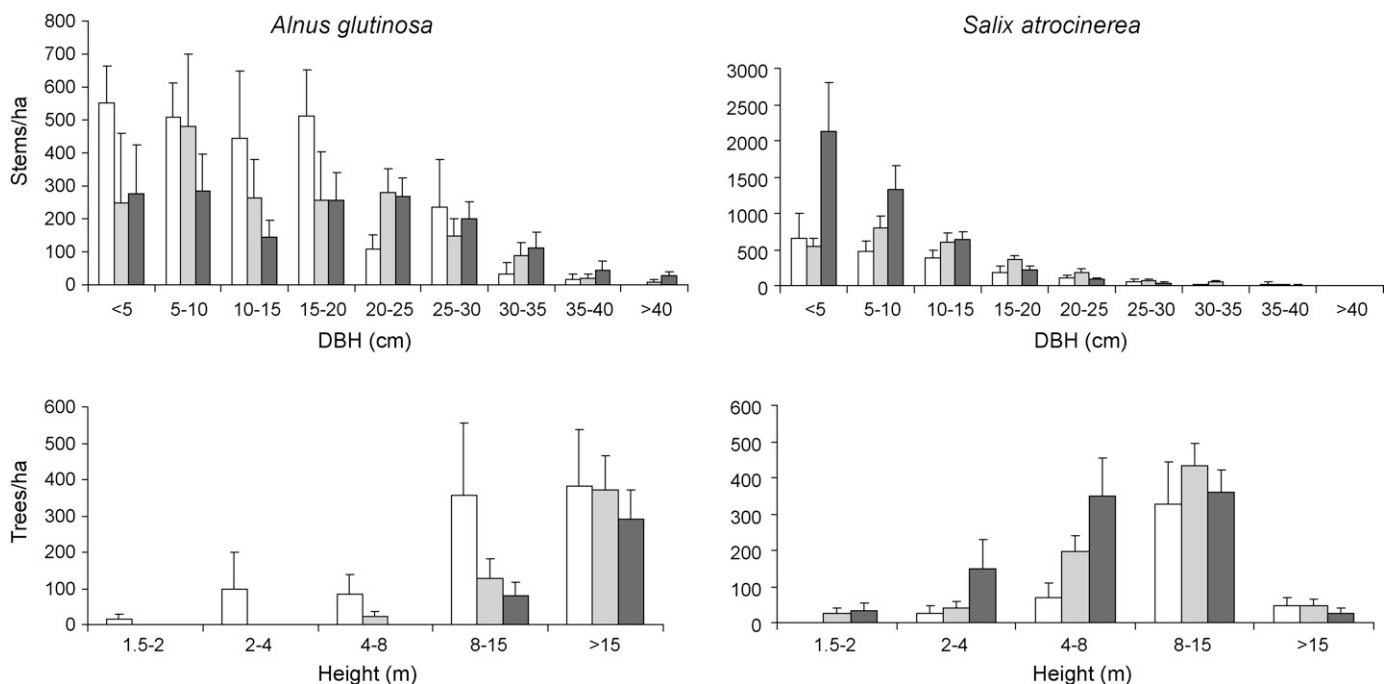


Fig. 2. Size distribution of stem diameters and tree heights, by size class. Bars indicate plot-based values averaged by soil saturation class (open bars, unsaturated; light grey, semi-saturated; dark grey, saturated). Whiskers indicate standard error.

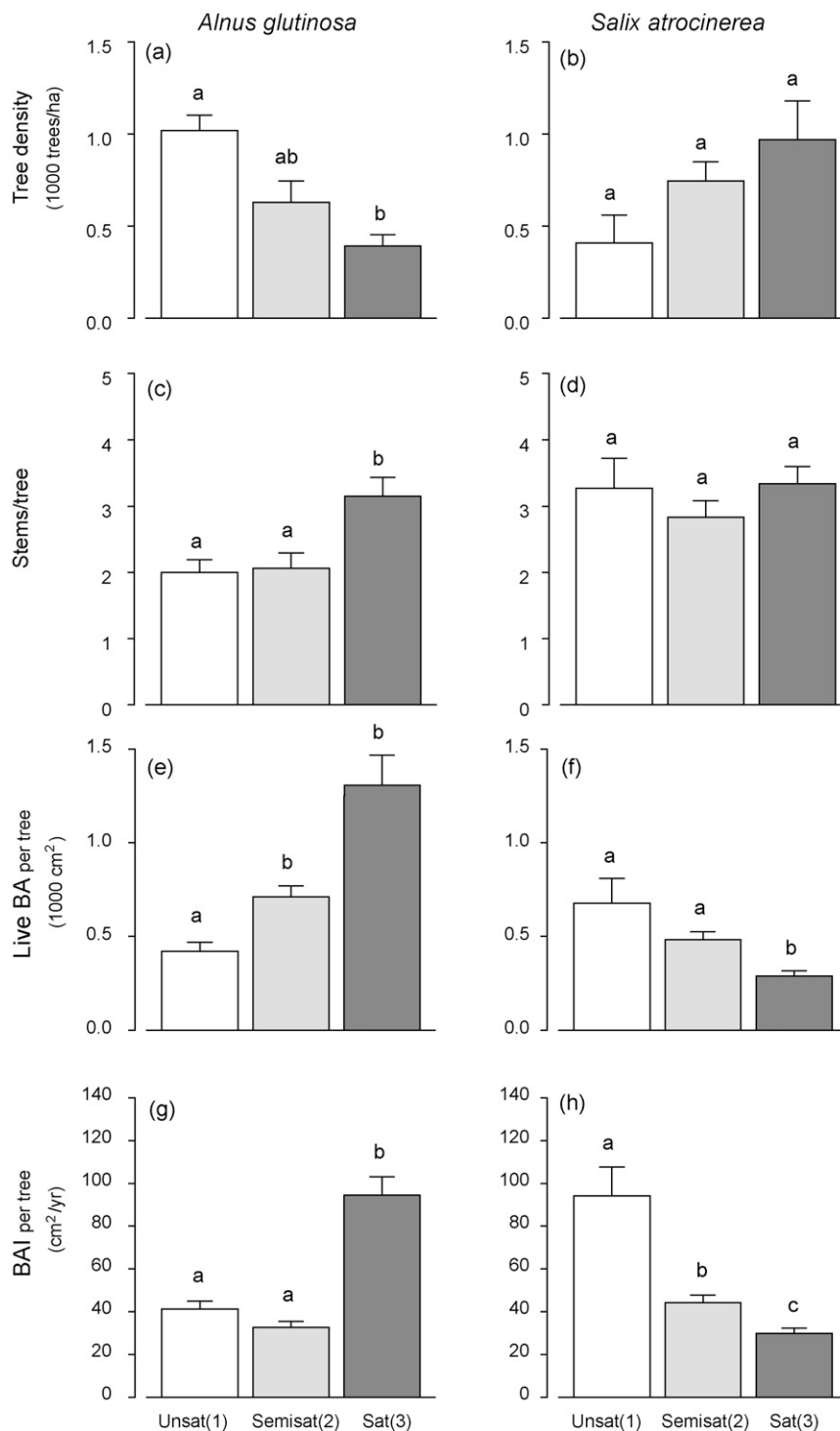


Fig. 3. Plot averages of tree density (a and b); stems per tree, or shrubiness (c and d); and averages on a per-tree basis of live basal area (e and f); annual basal area increment (g and h) by plot saturation class. Open bars, unsaturated; light grey, semi-saturated; dark grey, saturated. Whiskers indicate standard error. Letters indicate significant ($P < 0.05$) differences between saturation classes by Tukey's honest significant difference test. Data used in ANOVA's were log-transformed to satisfy residual assumptions.

basal area increment across the saturation gradient. Live basal area per tree increased significantly across the wetness classes for *Alnus* ($F_{2,185} = 17.76$, $P < 0.001$; Fig. 3e), but decreased for *Salix* in the wettest plot class ($F_{2,515} = 27.20$, $P < 0.001$; Fig. 3f). Estimates of the annual basal area increment per tree, which was based on class-average growth rates applied to the full census of live stem diameters, also indicated opposite patterns for the two species. For *Alnus* there was significantly higher BAI among trees only at the wettest sites ($F_{2,180} = 16.64$, $P < 0.001$; Fig. 3g), whereas for *Salix*,

BAI decreased significantly across each wetness class ($F_{2,508} = 45.84$, $P < 0.001$; Fig. 3h). The proportion of dead basal area per tree (data not shown) was not significantly different among wetness classes for *Salix* ($F_{2,570} = 1.71$, $P = 0.18$) but was highest for *Alnus* in Class 1 ($F_{2,192} = 7.68$, $P < 0.001$). Net stand aboveground productivity, as represented by the 5-year average annual basal area increment, is significantly higher ($F_{2,46} = 4.62$, $P = 0.01$) in unsaturated plots (Class 1, >50 cm water table depth) than in the plots in the other two classes with a shallower water table (Fig. 4).

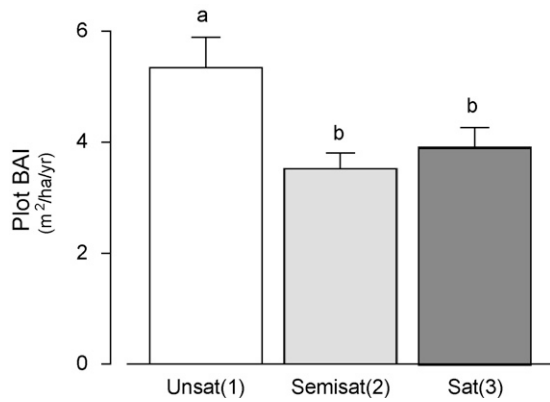


Fig. 4. Whole-plot basal area increment ($\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$) estimates with species-specific growth rates applied to relative stem densities (see text). Open bars, unsaturated; light grey, semi-saturated; dark grey, saturated. Whiskers indicate standard error. Letters indicate significant ($P < 0.05$) differences between wetness classes by Tukey's honest significant difference test.

For both *Alnus* and *Salix*, trends in annual increment growth during the first 20 years of life are significantly different for trees growing in sites with different wetness classes (repeat-measures ANOVA (*Alnus*, $F_{2,38} = 6.27$, $P = 0.004$; *Salix* $F_{2,38} = 23.69$, $P < 0.000$). Both species grow fastest (i.e., have the largest annual increments) at unsaturated sites and slowest (smallest increments) at saturated sites (Fig. 5). The greatest absolute range in growth between drier and wetter sites is for young (approx. 3–6-year-old) *Salix* trees (Fig. 5b), but in *Alnus*, large differences are maintained throughout the entire first 20 years of life (Fig. 5a). For both species, the differences in growth rate decrease with age, but are still apparent at age 20.

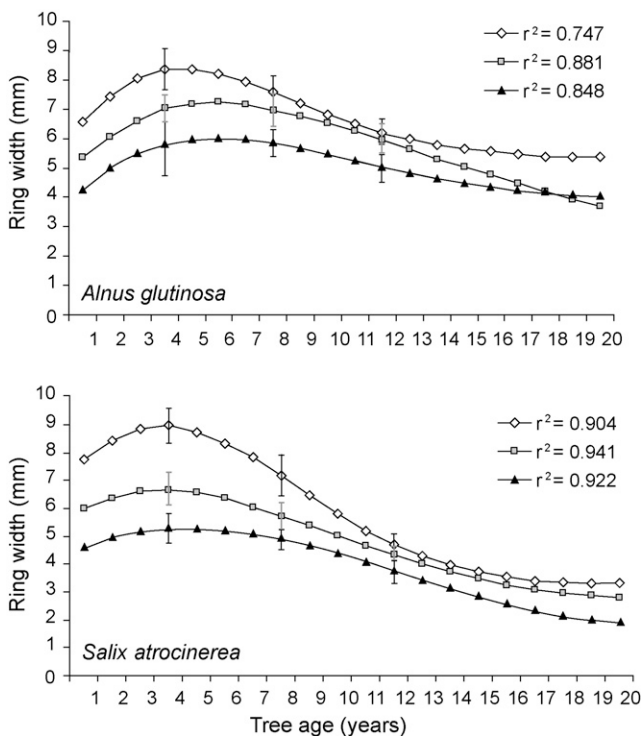


Fig. 5. Fourth order polynomial fitted growth curves for each species by saturation class (open diamonds, unsaturated, grey squares, semi-saturated, black triangles, saturated). Sample standard error bars are plotted; remaining bars are omitted for clarity.

3.4. Models of environmental factor influences on tree demography

Among the linear mixed models for density, shrubbiness, growth and mortality considered (Table 2), models that included hydrologic and edaphic predictor variables were stronger than the null model (no predictors) in the analyses of *Alnus* density and of shrubbiness and growth for both species. Mortality models that included predictor variables were no stronger than the null model for either species. *Alnus* density is best predicted by PC3 (soil texture), and to a lesser extent PC2 (nutrients) and PC1 (hydrology). The sign of the model parameters ($\text{PC3} > 0$, $\text{PC2} < 0$, $\text{PC1} > 0$) show that higher *Alnus* densities are associated with larger proportions of coarse textures, lower soil nutrients and saturation.

The most important predictors of shrubbiness were hydrology for *Alnus* and soil texture for *Salix*. Models including hydrology account for 68.1% of the collective Akaike weight of the *Alnus* shrubbiness analysis and the best model (PC1) is 38.3% likely given the candidate set of models. The sign of the parameters ($\text{PC1} < 0$, $\text{PC3} < 0$) indicate that increasing waterlogging and, to a lesser extent, a fine soil texture (high clay and low sand), support higher shrubbiness. For *Salix*, in contrast, shrubbiness is best predicted by soil texture. The best model (PC3 alone) is 44.5% likely given the candidate set of models and the top three models, which all contain PC3 account for 85.5% of the model weights. The sign of the parameters ($\text{PC3} > 0$, $\text{PC1} < 0$) indicate that coarse soil texture (high sand and low clay) and, to a lesser extent, high degree of site saturation are associated with shrubbiness in *Salix*.

Models for the last 5 years of current radial growth showed a negative influence of soil saturation ($\text{PC1} > 0$) on growth for both species. Soil texture (PC3) strongly influenced *Alnus* and nutrients (PC2) were important for *Salix* growth. The top three *Alnus* models, which have $\Delta \text{AIC} < 2$, accounted for 65.3% of the candidate set weights and included mainly PC3 (> 0), indicating a preference for well-drained soils with higher sand content. The top model included PC1 (> 0), indicating a negative influence of saturation. The best *Salix* models ($\Delta \text{AIC} < 2$) accounted for 65.3% of the candidate set weights and included mainly PC1 and PC2, which suggest that wetness and soil nutrients are the main drivers of *Salix* growth. The positive signs of both parameters show that radial growth in *Salix* is lower when waterlogging increases and the nutrient content decreases.

4. Discussion

4.1. Hydrological influences on forest stand characteristics

Site saturation and associated soil properties (e.g., redox potential, clay and soil cation concentrations) exerted a strong influence on stand density, composition, structure and growth (Figs. 2–3 and Table 1). Though the number of sites and the geographic scale of sampling precluded taking detailed time series hydrological records at each location, annual precipitation across the sites were representative of long-term conditions (Appendix A), and multiple factors measured at the sites were well correlated (e.g., dry season water table depth, degree of soil saturation, and soil redox potential), allowing us to coarsely characterize site hydrology. The wettest sites, those with the shallowest water table, highest level of surface waterlogging during the dry season (Appendix B), and lowest soil redox potential, had high relative densities of *S. atrocinerea* as measured by number of trees, total number of stems, and relative basal area. *A. glutinosa* stem density remained constant across the wetness gradient, but this resulted from a simultaneous decrease in tree (genet) density with a compensating increase in shrubbiness

Table 2
Top five candidate models for plot density, shrubbiness, mortality and growth. All responses were modelled for each species individually as mixed-effects models with forest stand as a random variable. Data for each response variable are plot averages except for growth, which considers the average radial growth of individual trees. Delta AIC values ≤ 2 represent minimal differences in parsimony among models. Principle components 1, 2, and 3 are weighted heavily for site hydrology, soil nutrients, and soil texture respectively (see text and Appendix B).

Variable	Species (model N)	Model rankings	K^a	AIC ^b	Δ_i^b	w_i^b	Parameters ^c
Density	<i>Alnus glutinosa</i> (20)	1	3	281.55	0.000	0.376	PC3 + PC2
		2	3	282.65	1.098	0.217	PC3 + PC1
		3	4	283.49	1.940	0.142	PC3 + PC2 + PC1
		4	2	283.55	2.003	0.138	PC2
		5	2	284.93	3.378	0.069	PC1
	<i>Salix atrocinerea</i> (48)	1	1	596.72	0.000	0.378	–
		2	2	598.24	1.515	0.177	PC2
		3	2	598.87	2.153	0.129	PC1
		4	2	598.95	2.225	0.124	PC3
		5	3	600.24	3.521	0.065	PC2 + PC3
Shrubiness	<i>Alnus glutinosa</i> (20)	1	2	97.79	0.000	0.383	PC1
		2	3	99.28	1.489	0.182	PC1 + PC3
		3	3	100.17	2.384	0.116	PC1 + PC2
		4	1	100.22	2.430	0.114	–
		5	2	101.02	3.226	0.076	PC2
	<i>Salix atrocinerea</i> (48)	1	2	159.81	0.000	0.445	PC3
		2	3	161.42	1.620	0.198	PC3 + PC1
		3	3	161.97	2.164	0.151	PC3 + PC2
		4	1	163.36	3.562	0.075	–
		5	4	163.80	3.999	0.060	PC3 + PC1 + PC2
Mortality	<i>Alnus glutinosa</i> (20)	1	1	51.76	0.000	0.433	–
		2	2	–49.89	1.874	0.170	PC3
		3	2	–49.45	2.317	0.136	PC2
		4	2	–49.33	2.431	0.128	PC1
		5	3	–47.29	4.479	0.046	PC3 + PC2
	<i>Salix atrocinerea</i> (48)	1	1	–85.04	0.000	0.312	–
		2	2	–84.37	0.931	0.196	PC2
		3	2	–83.28	1.755	0.130	PC1
		4	2	–83.27	1.771	0.128	PC3
		5	3	–82.28	2.761	0.078	PC2 + PC1
Radial growth	<i>Alnus glutinosa</i> (63)	1	3	243.80	0.000	0.310	PC1 + PC3
		2	2	244.40	0.607	0.229	PC3
		3	3	245.79	1.995	0.114	PC2 + PC3
		4	4	246.02	2.228	0.102	PC1 + PC2 + PC3
		5	1	246.13	2.331	0.097	–
	<i>Salix atrocinerea</i> (104)	1	3	421.26	0.000	0.445	PC1 + PC2
		2	4	422.78	1.522	0.208	PC1 + PC2 + PC3
		3	2	424.00	2.740	0.113	PC2
		4	2	424.17	2.909	0.104	PC1
		5	3	425.84	4.579	0.045	PC2 + PC3

^a K , number of model parameters, including intercept.

^b AIC, Akaike Information Criteria; see text for explanation of AIC difference values (Δ_i) and AIC weights (w_i).

^c Parameters represent the first three principle components of the environmental factor PCA (see text). Each component is heavily weighted respectively toward hydrology (PC1), soil nutrient status (PC2) and soil texture (PC3).

(multiple ramets). For *Alnus*, the lower tree density in saturated sites may result from a combination of lower germination rates as well as physiological stress from flooding on seedlings (Kozłowski, 2002; van Eck et al., 2005; Battaglia and Collins, 2006). The absence of small trees and seedling regeneration in the wettest sites (Fig. 2 and Table 1) may be the result of both stressful hydrology and competition for light with mature trees (Jones and Sharitz, 1998) due to their low shade tolerance (Johnson, 2000; Battaglia and Sharitz, 2006). Low rates of sexual reproduction (e.g., seeds with low longevity and dispersal) and seedling establishment have been

documented in a variety of wooded riparian and wetland ecosystems (Niiyama, 1990; Jones and Sharitz, 1998; Johnson, 2000; Middleton, 2000; Dixon et al., 2002; Lord and Westoby, 2006; Dufour and Piégay, 2008; Breen and Richards, 2008; Turnbull et al., 2008). Linear models developed for *A. glutinosa* showed a strongly negative influence of clay content and related soil factors on tree density (Table 2). Consistent with this finding, other studies in Southern and Northern Europe have shown that heavy clay soils are less suitable for alder forests than better drained soils (Johansson, 1999; Yalçın et al., 2004).

4.2. Influences on sprouting and shrubbiness

Though poor seedling regeneration was observed in our study, both *Salix* and *Alnus* species demonstrated a multi-stemmed clonal growth form which was correlated with various hydrologic and edaphic factors. An increase in sprouting has been observed for woody plants in other chronically stressful environments such as coastal dunes (Nzunda et al., 2007) and erosive slopes with shallow soils (Sakai et al., 1995). At our sites, sprouting in *Alnus* was positively associated with shallow water tables. For *Salix*, sprouting was associated primarily with coarser soils and secondarily with wet sites. The *Alnus* sprouting behaviour in these wetland forests can be interpreted both as a response to flooding stress (Odum, 1985) and a key strategy for persisting at sites with poor seedling recruitment (Bond and Midgley, 2001; Eriksson, 1996). It is common for wetland vegetation to be dominated by long-lived species (Battaglia and Collins, 2006) that use vegetative reproduction and cloning to persist under permanently flooded conditions (Ernst and Brooks, 2003). A higher stem density serves to reduce the transport distance of oxygen to roots (Kozłowski and Pallardy, 2002; Lugo, 1990). A greater stem area also would presumably increase the surface area available for gas exchange in *A. glutinosa*, which as young trees can elevate O₂ concentrations in the secondary cortex via stem photosynthesis and thereby increase root aeration (Armstrong and Armstrong, 2005).

In contrast to *Alnus*, shrubbiness in *S. atrocinerea* was found to be strongly associated with coarse-textured soil and secondarily with site wetness (Table 2). Regeneration and colonization success were correlated with both soil texture and water level in six Japanese *Salix* species (Niiyama, 1990) and texture was the dominant correlate with *Salix nigra* seedling survival (Schaff et al., 2003). The ability to regenerate from both shoots and roots is well-known for the genus *Salix* (Krasny et al., 1988; Karrenberg et al., 2002; Li et al., 2005; Day et al., 2006; Johnston et al., 2007). Clonal reproduction in some *Salix* species is associated with more extreme conditions (both dry and wet) while sexual reproduction is more important in mesic sites (Krasny et al., 1988), where short-lived seeds have a better chance of encountering favourable conditions for germination and establishment (Johnson, 2000; Stella et al., 2006).

4.3. Growth rate and net aboveground wood production

Radial growth suppression, which occurred with higher soil saturation particularly in the first decades of life, is often a consequence of the physiological dysfunctions induced by soil anaerobiosis (Kozłowski, 2002). Waterlogging-related reductions in growth have been documented in a variety of bottomland tree species (Pezeshki and Anderson, 1997; Nakai and Kisanuki, 2007).

Stem mortality was not higher on wetter sites (Table 1) and though the proportion of dead biomass at our sites—approximately 5–25%—is typical of unmanaged forests (Kirby, 1998), trees that were completely dead constituted only 5% of the total. This is a lower proportion of dead trees than reported for Irish wetland forests (Iremonger, 1990). However, dead standing biomass may not be the best measure of mortality, because branch dieback and abscission rates are high for riparian and wetland species (Rood et al., 2000).

Our models showed that the highest *Alnus* growth was associated with well-drained soils with higher sand content, but no relationship with nutrient status was found. *Alnus* species can fix their own nitrogen (Huss-Dannell, 1997) and are consequently less dependent on soil nitrogen. *Salix* displayed the lowest growth rate and annual basal area increment in the wettest sites (Figs. 3 and 4). Both hydrology (PC1) and soil nutrient status (PC2) were good predictors of residual growth in the regression models (Table 2). Therefore, nutrient availability may interact with hydroperiod and

disturbance frequency to affect *Salix* growth given that flooding is correlated with low nutrients and coarse texture (Table 2). In an experimental study, phosphorous and potassium, the most highly loaded variables in the PCA nutrient axis (PC2, Appendix B-2), strongly influenced *Salix nigra* growth through a significant hydroperiod–nutrient interaction (Day et al., 2006).

The tree-ring analysis established that there is a clear reduction in growth on saturated sites for individual stems (Fig. 5). However, the effect on net aboveground annual wood production is less clear given that for alder the basal area per tree was higher in the most saturated classes (Fig. 3e) because of the higher number of stems per tree (Fig. 3c). The extensive geographical scale of sampling in this study required us to use annual growth and diameter increment as a proxy of productivity. More complex measurements of litterfall quantity and quality, and aboveground versus belowground biomass would presumably provide a more accurate estimation of overall stand productivity, as well as determine priority shifts in carbon allocation with flooding and drought (Magonigal et al., 1997). Nevertheless, our results imply that although annual wood production is generally lower in wetter plots, increased sprouting may compensate for reduced growth of individual stems in these wetland habitats.

5. Conclusions

Our results indicate that hydrology is the dominant driver of stand composition structure and growth, as well as tree architecture in wetland forests of Southern Europe. While *Alnus* appears to be a good competitor in well-aerated soils, *Salix* can tolerate a greater degree of flooding, albeit with reduced growth and increased sensitivity to nutrient limitation. Increased site waterlogging results in more densely distributed (primarily *Salix*), shorter (both *Salix* and *Alnus*), shrubbier (primarily *Alnus*) and slower growing (both *Salix* and *Alnus*) trees. These effects, as well as the stand-level decreases in aboveground productivity at the wettest sites (Fig. 4), strongly suggest that flooding in these arid-climate wetlands is primarily a stressor, rather than a stimulus for increased growth (Odum et al., 1979). However, these morphological characteristics can also be interpreted as an effective strategy to persist under stressful conditions (Bond and Midgley, 2001; Grime, 2002), because they effectively hold the growing space and preserve the community in the absence of seedling regeneration. The dominance of the community by *Alnus* and *Salix*, particularly *Salix* in the wettest sites, supports this interpretation.

The almost complete absence of recruitment (Table 1) and the older-skewed age structure (Fig. 2) in the most saturated sites raises the question of whether these patches represent senescing remnant populations on a trajectory to replacement by other community types. However, the low incidence of dead trees and stems, together with the high total basal area across the site gradient suggest that concomitant adjustments in tree density, shrub architecture, and reduced growth rates mitigate to some level the negative effects of soil saturation. The low incidence of recruitment may be also related with the current fragmentation of these forests, and thus, these patches may be senescing populations at the site scale, but not at the river corridor scale, provided new regeneration habitat was created.

The diversity of community types and hydrology within wetland forests may have large-scale implications for the conservation and management of these ecosystems. The dominant trees in this community display common patterns of increased shrubbiness and decreased growth with increasing soil moisture and associated soil factors. The interaction of texture and nutrients with hydrology may determine site preferences and shifts in dominance among tree species favouring *Alnus* in poorer but well-aerated sites and

Salix in the most waterlogged ones. The ability of wetlands forests to persist over thousands of years has been reported by palaeoecological studies and current patches may well be the fragmented remnants of larger, riparian-related woods. The preservation of the whole community dynamics, including the natural shifts in species composition, structure and growth and their associated strategies is directly dependent on the existence of a sufficiently developed mosaic of hydrologic conditions maintaining the wetland condition. This requires the limitation of water overextraction and the protection of remnant patches promoting their expansion to larger areas that allow their persistence through time. Forests lacking this diversity and patchiness in hydrological conditions may experience decreased integrity and increased fragility in the face of uncertain climate variability and anthropogenic pressures (e.g., water diversions, timber cutting, conversion to agriculture) to which they are currently subjected.

More research is still needed to fully understand the processes underlying the community dynamics of Southern European wetland forests. We suggest that further study focuses on the role of sprouting in within-tree stem ages distribution, genetic structure and the maintenance of better adapted genotypes and the implications of sex ratios (in dioecious species: *Salix*) for their conservation on a large temporal and spatial scale.

Acknowledgements

This work was supported by the Portuguese Foundation for Science and Technology (BD/6030/2001 and POCTI/AGG/46842/2002), by the European Commission (ECODOCA) and by Fundación Pedro Barrié de la Maza. We would like to thank Alex Fremier, John Battles, Pedro Segurado, Sara Scanga and Simon Dufour, and four anonymous reviewers for comments on earlier manuscript drafts and Dalila Espirito Santo and Cristina Nabais for logistic support.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.foreco.2010.02.012](https://doi.org/10.1016/j.foreco.2010.02.012).

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