Climate Change Impact on Tree Architectural Development and Leaf Area

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1. Introduction

1.1. Context

The response of forests to the forecasted increase in climate stress occurrence is considered a key issue in climate change scenarios [1]. Although forest productivity increased in most ecosystems during the 20th century [2,3], a review by Allen *et al*. [4] underlined an emerging trend of heat and drought induced forest decline and dieback at global scale. Several and generally combined physical and biological causes contribute to observed tree decline or die-off [4-7]. Apart extensive insect outbreaks [8], understanding the respective role of hydraulic failure and carbon starvation due to excessive or long lasting water stress is one of the major research goal in order to predict forest response to climate change [9].

The consequences of climatic events on forest health can be immediate but are often delayed up to 5 to 10 years [5,10], and may be significant for decades and sometimes irreversible on tree growth [11]. Recent studies on tree architectural development and primary growth suggested that the long lasting impact of repeated droughts on tree crown development could be one of the causes of these delayed effects [12-14].

Primary growth corresponds to the creation of new tissues outside existing organs, and includes bole, branch and root length growth, branching (birth of new branches or roots), creation and growth of leaves or needles and rootlets, flowering and fruiting [15,16]. It is therefore fully linked to plant architectural development patterns and processes. In contrast, secondary growth for trees corresponds to the radial growth of existing branches, bole and roots. In single trees and forests, although secondary growth usually exceeds primary growth and leaf production [17], the total amount of biomass allocated to primary growth may be very

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important [18]. As an example, leaf and fruit production measured through litter bags in French adult broadleaved stands (mainly beech and oak) reached 20 to 40% of wood production by stems [19]. The relative allocation to new shoots was not correctly assessed up to now but it can be inferred from leaf production and the leaf mass fraction (LMF), ratio between leaves and whole twig mass. In a recent study, twig wood/leaf biomass ratio was found to reach from 25 to 50% and from 50 to 75% during respectively dry and humid years for *Pinus halepensis* [20] which means low LMF values (25 to 75%). However, LMF was generally higher on dry sites in south eastern France: 40-70% for *Abies alba* [21], 70-80% for *Quercus ilex* [22]. It was found to vary between 80 and 90% for 107 Chinese species at various elevations [23]. As a whole, primary growth may represent between 25 and 70% of secondary growth. But except for tree height growth, scant literature exists on the relationship between tree primary growth processes and climate change or accidents, whatever the species, and plant architecture is commonly neglected in climate change impact studies.

The mediterranean climate is characterized by high temperatures associated with low rainfall in summer, drought being the main environmental constraint for vegetation growth [24]. For the 21st century, climatic models forecast that the Mediterranean basin will be prone to a faster warming than most other continental areas over the world, associated with a reduction of rainfall during the growth season [1,25]. Therefore, this area is a good place to detect and model any climate change impact on vegetation, all the more since a rapid decline in precipitation and higher temperatures were already noticeable in parts of this basin [26,27]. In Southeastern France, the period 1998-2007 was characterized by mean annual temperature and mean summer temperature 0.9°C and 1.3°C above the 30-year average (*figure 1*) Moreover, eight to ten of the twelve hottest years since 1850 were recorded during this time lapse [28] which give a foretaste of the climate forecasted for the next decades. In addition strong climatic events also recently occurred such as the 2003 heat

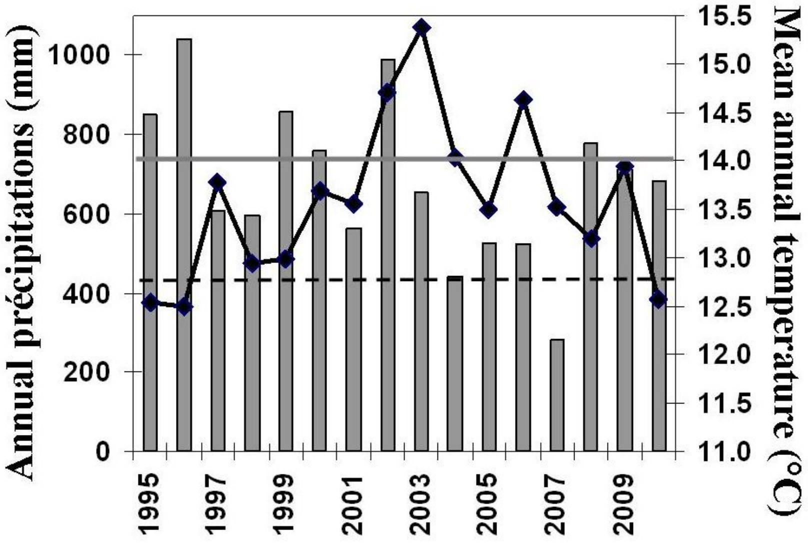

Figure 1. Average annual precipitations (grey bars) and temperatures (black line) in Font-Blanche since 1995. Horizontal lines are 1961–2010 average, grey line = mean rainfall, dotted black line = mean temperature.

wave which significantly impacted French Mediterranean forests as well as most of Europe [29]. Such extreme climatic events are likely to become frequent with global warming [1,30]. Scorching heat had direct and delayed negative effects on tree growth, especially on pine species [31]. The resulting increase in summer and spring water stress may reduce tree growth in Mediterranean areas [32-35]. Raising temperature may also lead to phenological lags [36], particularly in the beginning and end of the growth season, with direct consequences on some primary growth processes and architectural development such as polycyclisme and branching rates [37,38].

1.2. Goals

This study aimed at quantifying the influence of recent climatic trend and events, particularly intense heat and drought, on the primary growth and architectural development of six conifers and one broadleaved species growing in Mediterranean plains (*Pinus halepensis, P. pinea, P. pinaster, Quercus ilex*) and mountains (*P. nigra, P .silvestris, Abies alba*). The three last ones are at the lower limit of their distribution area in southern France. One of the final goals was to model the direct and delayed effects of climatic accidents on tree leaf area in order to help assessing the resulting risk in terms of decline and die-back.

2. Material and methods

2.1. Study area and species

The study area included 8 sites distributed between 80 and 1400 m of elevation, from the coast to hinterland mountains of Provence-Alpes-Côte d'Azur region in south-eastern France (*figure* 2).

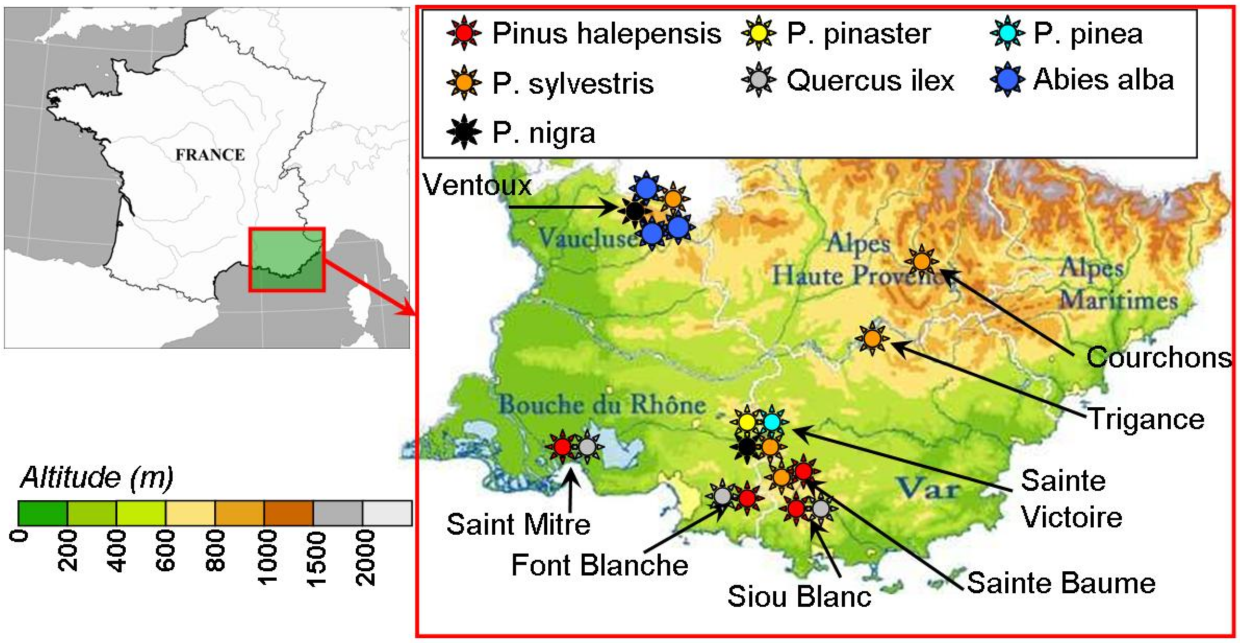

Figure 2. Study area and studied sites.

Nearly 5150 twigs from 1050 branches of 210 trees and 7 species were sampled between 2005 and 2011 (*Table 1*). Their architectural development was retrospectively measured from morphological markers (*figure 3*) over a period of 15 to 25 years. For each tree, the sampling design considered separately three thirds of the crown (top, middle and base), branch orientation (north and south), but also branch hierarchy (principal or secondary axis – *figure 4*) and branch vigor. Secondary axes were chosen according to their relative vigor (strong vs weak axes) within the branch they belong to (*figure 4*). Twig absolute vigor for each species was later split in three groups of equal number (vigorous, medium, frail) according to their total length growth in the last three years before sampling date.

Site name	Species (number of trees)	Altitude (m)	exposition	Dates of mesures
Saint Mitre	PH (11) QI (6)	80	Flat	2008-2009
Font-Blanche	PH (58) QI (34)	420	Flat	2005-2011
Siou Blanc	PH (11) QI (6)	650	Flat	2008-2009
Sainte Baume	PS (5+5+5), PM (5)	950	North	2005-2006
Sainte Victoire 1	PS (5); PN (5)	650	North	2009-2010
Sainte Victoire 2	PM (5); PP (5)	500	Flat	2010
Trigance	PS (5)	1000	Flat	2005-2006
Courchons	PS (5)	1350	North-east	2005-2006
Ventoux	PS (5), PN (10), AA (19)	1100 to 1400m	North	2009-2010

PH = Pinus halepensis Mill, PS = Pinus sylvestris L., PM = Pinus pinaster Aiton, PN = Pinus nigra ssp nigra Arn, PP = Pinus pinea L., AA = Abies alba Mill

Table 1. Study sites

2.2. Growth and architectural parameters

When present, 5 to 10 needles were randomly chosen from the base to the end of each twig and all around it to measure their length and width. Needle number per twig was counted on a subsample of twigs (1/3) with consideration of missing needles which were counted using their scars on the twig. As needles are lined up in three to five lines or spirals along the shoot, counting needles along one or two of these lines or spirals and then bulking up the count proved to be a very reliable assessment (error < 5%)

In order to bridge primary and secondary growth, ring width was measured for all studied trees. Two cores per tree were collected perpendicularly at 1.3 m height. Ring widths of each core were measured using a micrometer (±0.002 mm, Velmex Inc., Bloomfield, NY). Some trees were also logged for stem analysis and rings were counted along 4 perpendicular directions. Ring width series were firstly cross-dated and standardized with the classical methods of dendroecology, to remove age-related tendencies from the growth curve and to obtain a homogenised variance. Then elementary raw and detrended series were respectively averaged for each tree and master chronologies were constructed for each species and for each plot by averaging tree series.

For *Pinus halepensis* and *Quercus ilex,* a follow-up of phenology and architectural development was performed twice a month from 2008 to 2011 on one site (Font-Blanche) to understand their relationship with climate and their interrelations. Branches and twigs were chosen following the same protocols than for architectural studies.

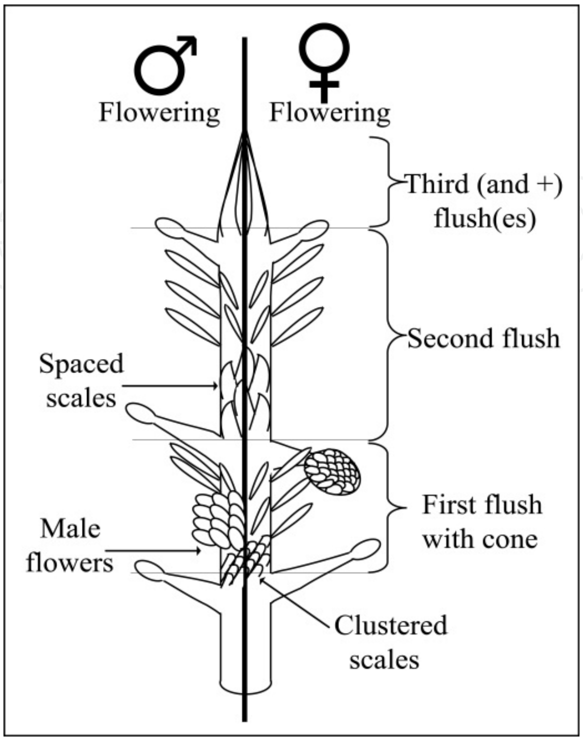

Figure 3. Morphological markers used for twig growth reconstruction in conifers. All growth units start by sterile scales, small and clustered on the first one, larger and spaced out on the following ones in case of polycyclisme (mainly Pinus halepensis and P. pinaster). Male flowering (left): male flowers appear at the base of the first annual growth unit over sterile scales for pines. The scars they left on the twig are generally different from needle scars. Female flowering (right): cones (with very few exceptions) appear at the top of the first annual growth unit. For pines, cones or their peduncles remain a long time on the branch or leave a specific scar. The presence of at least one branch or of a whorl indicates the limit of a growth unit for pines, but some growth units may be branchless. For firs and oaks, intermediate branches may appear, during all the branch life. A given pine twig never bears male and female flowers the same year. For Quercus ilex, a pseudo-whorl of branches indicates the limit between two annual shoots. The retrospective analysis of branch growth is far more difficult than for conifers.

2.3. Branch modeling

The observed variations of architectural parameters, needle number and needle size were integrated into a 2D-model of pine branch architectural development to simulate the impact of climate on pine total leaf area (*figure 5c*). We designed the model for the more complex of studied conifers: Aleppo pine (*Pinus halepensis)*. Aleppo pine gives potentially the higher number of growth units per year, so that the model can easily be simplified for other species. In a first attempt we considered medium vigor branches located in the middle part of the crown as representative of the average branch of a tree. Parameters for each twig category (principal and secondary axes, vigor, medium and frail axes) were implemented according to scenarios of successive years considered as "normal" or "bad" (defined afterwards; *figure 5 a -b, table* 2). As pine architectural development for a given year is partly to fully pre-determined by the climate of the previous year, the impact of bad years on polycyclism and the number of needles are delayed compared to the impact on leaf size.

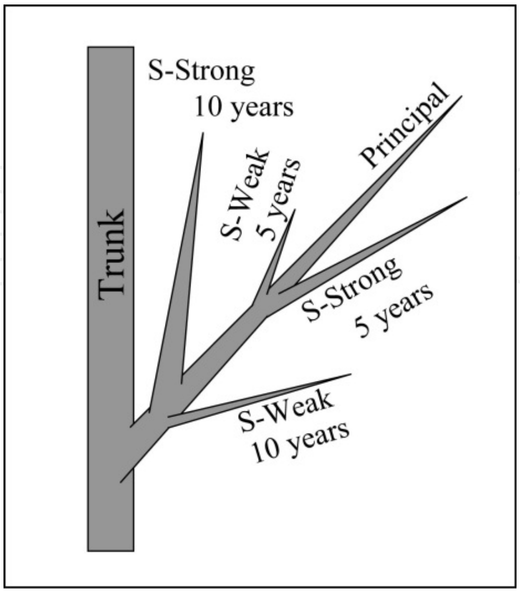

Figure 4. Twig sampling. Five axes are measured on each branch: the principal axis and two pairs of secondary axes one weak and one strong by pair five years-old and 10 years-old. The classes "weak" and "strong" are relative to each other in the concerned pair and their absolute vigour depends on branch vigour.

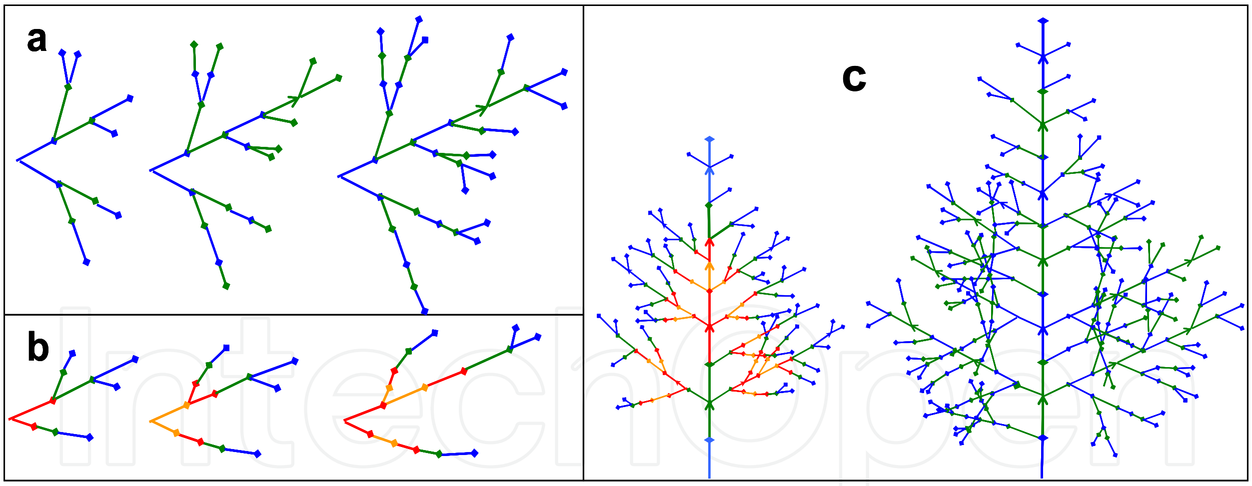

Figure 5. Example of the development of a medium vigor secondary axis of Pinus halepensis without (a) or with (b) 1 to 3 bad years. Example of a middle crown / medium vigor branch (principal and secondary axes) and development after 7 years with 4 successive bad years. The model includes strong and weak secondary axes and 3 classes of twig vigor. Color changes each year along each axis: blue and green for good years, orange and red for bad years.

At each step of branch development and at the end of each year, active twigs (with needles) could be counted and sorted by vigor. The number and size of needles per active twig was set according to *table 2*. Total needle surface (length*width*needle number) was calculated for each twig and bulked up for the whole branch.

This model was used to simulate branch growth for 10 years, as all parameters for secondary axes were obtained for this time span. For longer periods, the interaction and competition with neighboring branches, twig self pruning, branch aging and accidents may significantly change these parameters, so that a 3D model taking these interactions into account is necessary.

For *Abies alba*, some specific sampling and analyses were made to compare trunk, lateral axes and ring width responses to climate. Trees were sampled at 3 different elevations (1150, 1250 and 1350m) [26]. For 14 trees, annual shoot length was measured on the trunk. Laterals axis sampling and measurements followed the same protocol as other species.

2.4. Statistical analyses

As most architectural and growth parameters slowly evolve with branch aging, it was necessary to remove this natural trend. This was systematically done for each parameter using the difference measured at equal cambial age for branches of respectively top vs middle and middle vs base of the crown, for the period 1995-2000 considered as accident-free (*figure 8*, method in references [12,37]).

To quantify inter-annual variability between traits, an individual detrended coefficient of variation (dCV), for the period 1990-2010, was computed, for each trait of each tree, as follow: (i) individual trend was removed by taking the residuals of the linear or non-linear model with time as explanatory variable and (ii) the standard deviation of the detrended sequence was divided by the raw sequence mean (i.e. the mean trait value for each tree).

Thus, the detrended coefficient of variation of trait j for tree i can be written:

$$dCV_{j,i} = \frac{SD\left(X_{j,i} - \beta 0_{j,i} - \beta 1_{j,i} * Time\right)}{\overline{X_{j,i}}}$$

with $X_{j,i}$ the sequence of trait j values for tree i ; $\beta 0_{j,i}$ and $\beta 1_{j,i}$ the corresponding estimates of the model used for detrending and mean ($X_{j,i}$) the mean value of the trait j for tree i.

For a global assessment of the relationship between growth, architectural parameters and climate, a Principal Component Analysis (PCA) was performed considering years as observations and all detrended architectural and growth parameters as variables, species by species. PCA was also used to help sorting good years (favorable climate for tree growth) and bad years (*figure 7*). As some parameters were not common to all species (polycyclism, male flowering, needle number), each PCA was performed with and without these variables to check the stability of years and variables in PCA planes. Needle length was not always available for the same period than other factors. Thus each PCA was also performed with needle length for available years and without needle length on the whole studied period (1995-2010).

All growth and architectural variables were averaged per species for bad and normal years. Bad years were defined as the four worst years in the 2003-2008 period for each individual variable. All other years were merged to compute the data for "normal years": as exceptionally low values due to repeated severe drought were excluded, we considered other data as normally good, mean or bad, representative of the normal interannual variability.

Partial least square (PLS) regressions were used to investigate relationships between architectural or growth parameters and climate. This method was chosen because it handles many variables with relatively few observations [39] and deals with correlated variables [40]. The number of significant PLS components was chosen by a permutation test [41] with a 5% threshold for the explained variance. Variables were tested with a 1000-step cross-validation [42]: they were retained only when the confidence interval (p<5%) for their partial correlation coefficient excluded zero. According to the phenology of the species in South-eastern France, climatic monthly parameters tested in each PLS were rainfall (P), maximum temperature (MaxT), minimum temperatures (MinT) and mean temperatures (MT) from January of previous year (n-1) to November of current year (n) over the period 1995–2010 [43,44]. The low number of observations (16) and high inter-annual variability of climate made grouping monthly climatic parameters necessary to obtain significant variables. We grouped the successive months having same signs for their individual partial correlation coefficients (sum of precipitations, average temperature). To compare exposition, position, status and vigour classes for each growth variable, normality was checked using a standard Shapiro-Wilks test. When the distribution was normal, a variance analysis and a multiple comparison test were performed to look for significant differences globally and further compare the different classes two by two. When the distribution was non-normal, these comparisons were performed respectively by a Kruskall-Wallis test and a Nemenyi test [45].

3. Results

For all species, most growth and architectural variables showed decreasing values in the last 15 or 20 years, and also from the top to the base of the crown (*figure 6.a*). After detrending with the comparison between branch position in the 1995-2000 period (*figure 6.b*), their

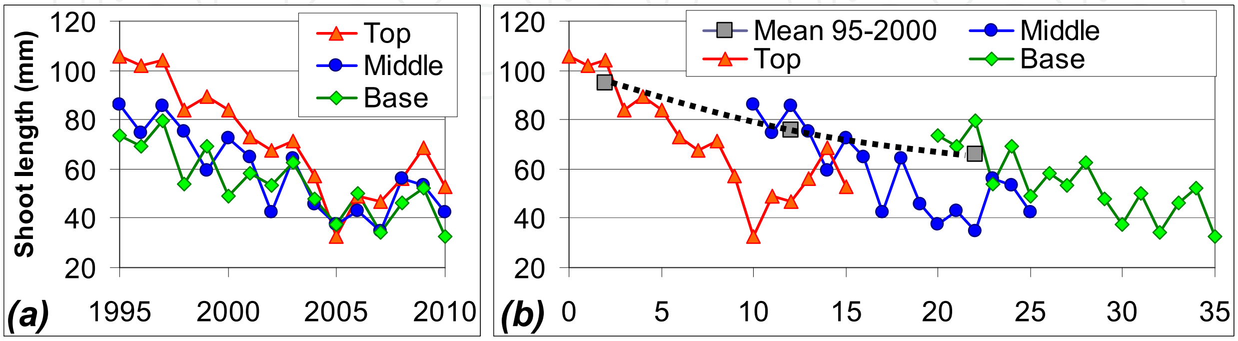

Figure 6. Pinus sylvestris annual branch length growth at Sainte Victoire for the top, middle and base of the crown (respective branch age 15, 25 and 35 years), for the same period (6.a) and with a 10-year shift (6.b) giving the natural trend of growth slowdown with age. Trees are approximately 60 year-old and measured branches are not competing with neighbouring trees.

decreasing rate from 2000 was always faster than the natural trend and showed a deep trough lasting 2 to 5 years after 2003 or 2004 (*figures 8-12 and 14*).

Whatever the species and variables used, PCA axis 1 and 2 were dominant with respectively 50-70% and 17-32% of explained variance, far over Axis 3 (4-12%). PCA results were highly coherent between species for the distribution of years in 3 groups (*figure 7*): bad years (2004 to 2007) and good years (1995 to 1998) were stable across all analyses, other years being more variable, generally in intermediate situation but sometimes good or bad (2003 and 2008). Some variables were stable for most species: shoot length, polycyclism and needle number were correlated with Axis 1 and between each other. Fruiting rate and needle length were better correlated to axis 2. Male flowering was available for *Pinus halepensis* and *P. sylvestris* only and was linked to the occurrence of bad years. Ring width occupied a variable position between axis 1 and 2 according to species. No noticeable difference was observed in year ranking or inter-variable correlations for a given species when PCA was performed with a variable number of years to include needle length.

The period 2004-2007 was characterized by a reduction of all growth and architectural parameters: shoot length, ring widths, needle length and number, and branching rate (*figures 6 and 8 to14*). Production of female reproductive organs was also disfavored during this period while male flowering twigs were more numerous, particularly in the middle and top crown. This PCA approach indicated that most growth and architectural parameters were inter-correlated, but *figure 8* shows time lags in the response to bad years and recovery. For example, the original position of 2007 in the PCA plane for *Abies alba* is due to the high

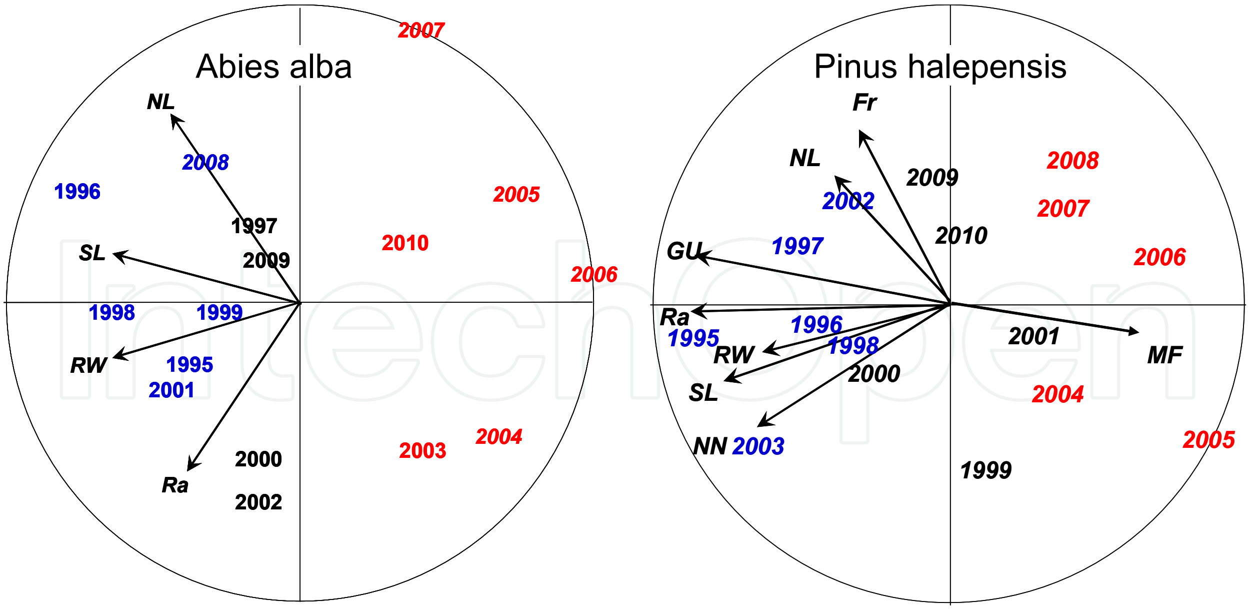

Figure 7. PCA plane for Abies alba (left) and Pinus halepensis (right) with years and variables: SL = shoot length, NL = needle length, Ra = ramification (branching rate), Rw = ring width, GU = number of growth units (polycyclism), NN = needle number, Fr = fructification, MF = male flowers. In red: bad years, in blue, good years.

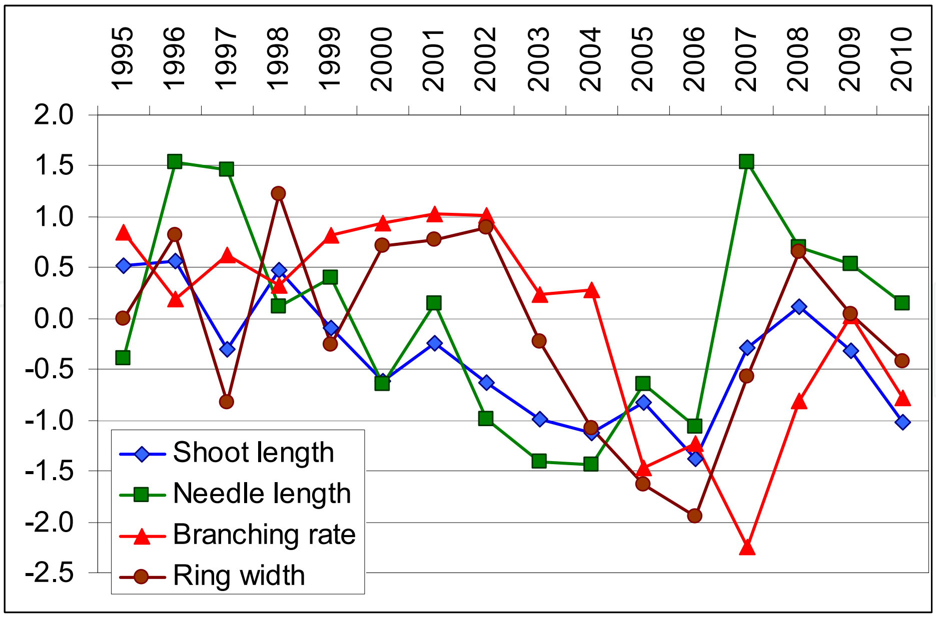

Figure 8. Evolution of detrended and standardized growth traits of Abies alba showing the consistent fall in the heart of the 2003-2007 climatic accident but time lags in their response to climatic variations and recovery after 2006.

value of needle length in 2007 (*figure 8*) while all other variables did not recover so fast, particularly branching rate.

Branching rate, one of the important architectural development indicator, is a good example of the common pattern between all species (*figure 9*). Differences were observed in the response to individual years and in the speed of recovery after the lower values, but the global trend was similar.

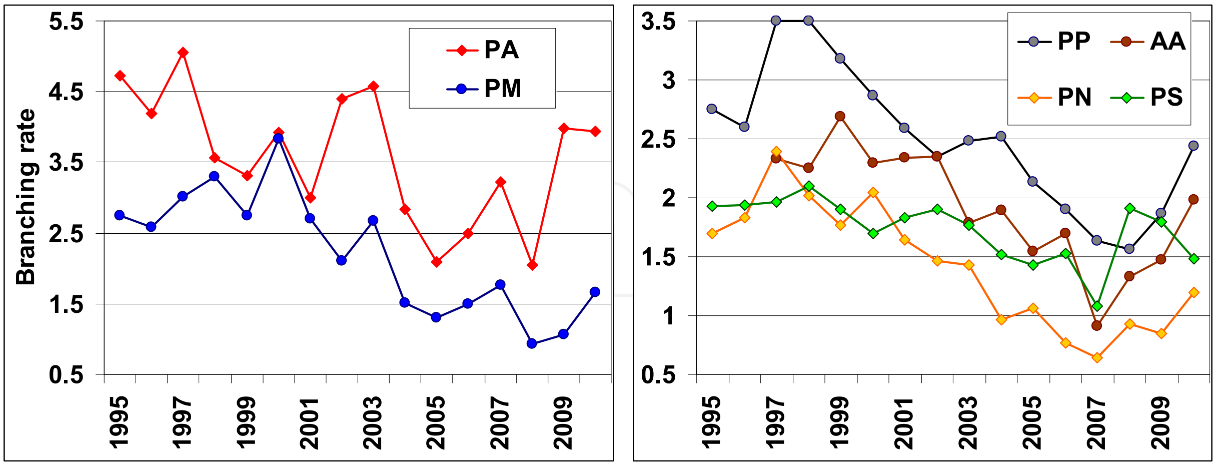

Figure 9. Branching rate (undetrended) on principal axes of the 6 studied conifers. PA = Pinus halepensis, PM = P. pinaster, PP = P. pinea, PN = P. nigra, PS = P. sylvestris, AA = Abies alba

Polycyclism, a fundamental growth trait for some pines species, confirmed this pattern (*figure 10*). It influences branching rate as each growth unit may give birth to new branches. This is why these two parameters are highly correlated (*figures 9 and 10*).

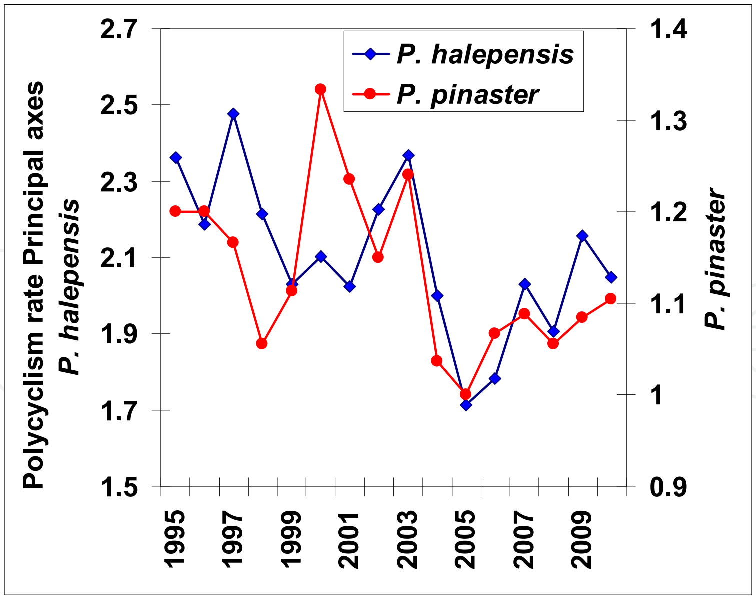

Figure 10. Polycyclism rate of branch principal axes for the two polycyclic pines, P. halepensis (left scale) and P. pinaster (right scale)

All architectural variables were positively correlated to branch vigour. *Figure 11* shows the example of needle number for *P. halepensis* according to branch vigour. The difference between the 3 classes of vigour was always significant all years in the aggregate, and also for most individual years.

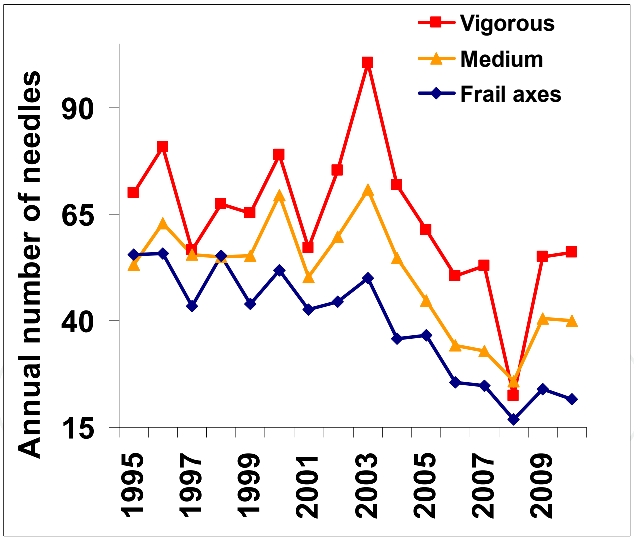

Figure 11. Number of needles per annual shoot for Pinus halepensis according to twig vigour.

The relative fall of growth and architectural variables after 2003 was generally more severe for vigorous and principal axes and at the top of the crown than on weaker and secondary axes and in the middle and bottom of the crown (*figures 6, 11 and 12*). Between 2004 and 2007, during 1 to 4 years according to species and variables, there were no longer significant differences according to branch vigour and hierarchy, and sometimes between positions in the crown. This higher relative sensitivity was also visible in a faster or better recovery: for most variables and all species, low and weak axes started recovering one or two years after top and vigorous ones and sometimes showed no significant increase up to 2010 (*figure 11*). However, the detrended coefficient of variation was not always significantly different between trunk and branch principal or secondary axes length growth, e.g. for *Abies alba* (*figure 12*). Ring width proved to be less variable than shoot length in *Abies alba*, but not in Pines, particularly because of their sharp decrease after 2003 and their high sensitivity to some accidents due to heavy snow falls.

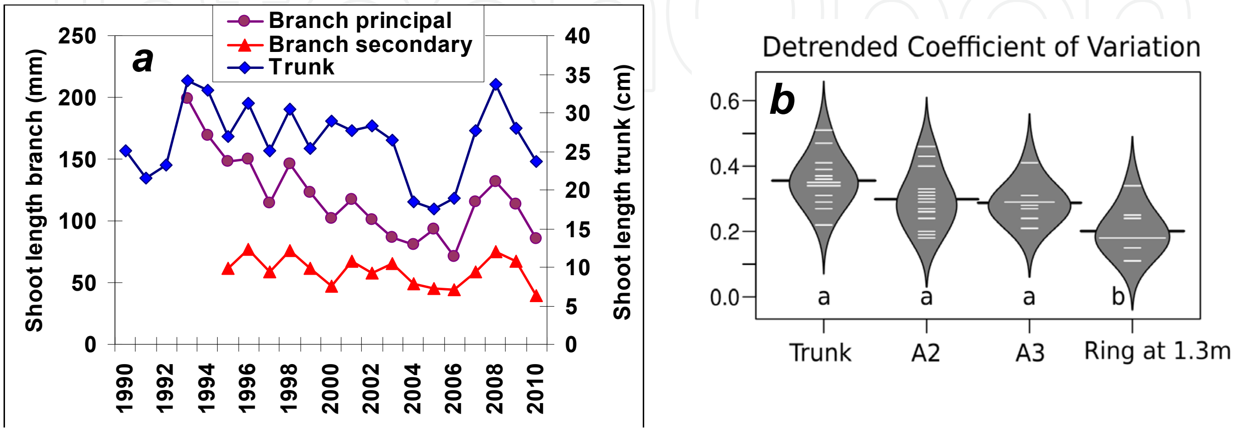

Figure 12. a - Abies alba trunk and branch detrended length growth (LG). Each series starts with its first real value. b - Detrended coefficient of variation (dCV) "beanplot" of the mean value (black lines), the kernel density function (in grey) and the raw values (white lines with size proportional to the number of measurements stacked. Letters summarize the results of a pairwise comparisons using Wilcoxon rank sum tests (P=0.05).

Although branch vigour was correlated to branch hierarchy and position within the crown, each of these factors significantly influenced branch architectural development (*figure 13*). For the same vigour (same mean length growth during the last 3 years), a branch had higher values on branch principal axes than on secondary axes and on axes of following orders, and decreasing values from the top to the base of the crown. Vigour, hierarchy and position were always highly significant (P<0.01%). South-exposed branches had sometimes higher values than north-exposed ones, but the difference was rarely significant (P<5%) and always at the very limit.

Needle length was highly variable from one year to the other (*figures 7 and 14*). It was severely affected by 2003 heat wave for all species, loosing from 25 to 45% on previous years average and recovered only slowly. According to species and sites, 4 to 8 years were necessary to regain normal values (mean of 1995-2002 values when available, or values from literature and herbariums: see reference [12]).

For *Pinus nigra* and *Abies alba*, 2006 and 2007 respectively were the first years after 2003 to reach normal values, but needle length further decreased again to significantly lower values. *Pinus halepensis* and *Pinus sylvestris* needles remained under normal values up to 2010.

Although we only have short series of data for *Quercus ilex*, it seems to follow the same trends as conifers (*figure 15*). Individual leaf area remained very low in 2009 compared to normal values for the French Mediterranean area, but inter-individual variability is very high and prevents assessing the normal values without older references on the same trees.

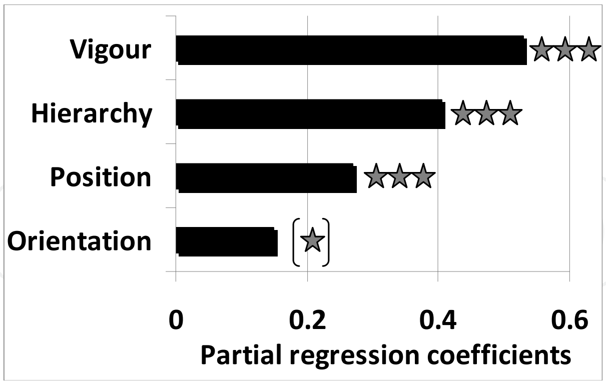

Figure 13. Mean relative weight of branch vigour, hierarchy (principal vs secondary), position (low, middle, top of the crown) and orientation (north vs south) in the determination of branching rate, polycyclism when relevant and needle number and length for the 6 studied conifers. The bars corresponds to the mean partial correlation coefficient of PLS regressions for each growth and architecture parameter and each species. Stars indicate the level of confidence: *** P<0.01%, * P<0.5%.

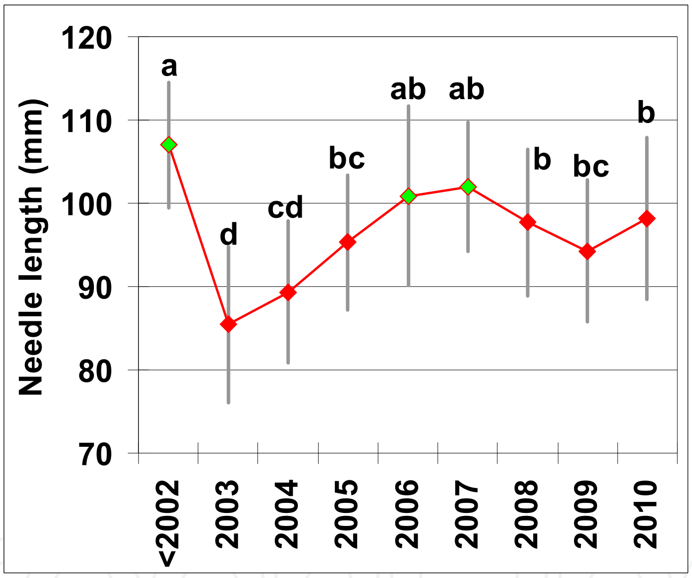

Figure 14. P. nigra needle length for branch principal axis in Mount Ventoux. Vertical bars indicate 2 standard deviation. Letters summarize the results of a Nemenyi test (P=0.05). Years sharing one letter are not significantly different. <2002 = mean values from all previous years (few samples) and from literature and herbariums for the study area.

Table 2 presents *Pinus halepensis* needle mean size and number according to axis vigour for good and bad years, and the resulting leaf area per twig. Leaf area for a given twig decreases with time due to accidents, parasites and aging. Survival rates measured in our plots (at the bottom of the table) varied according to twig vigour: needles remained longer on frail twigs than on vigorous ones.

These values were used to compute the total leaf area of a branch during 10 years with and without a 4-year accident, corresponding to the four worst years observed for many variables in this study (*figure 6*). According to the branch model, the deficit of active twigs (carrying needles) and of leaf area amounted respectively to 59 % and 78 % for *Pinus halepensis* compared to the values simulated with only normal years and average parameters (*figure 16*). This deficit was only slowly absorbed: it remained close to 30% and 40 % respectively two years after the end of the accident and disappeared only after 5 years.

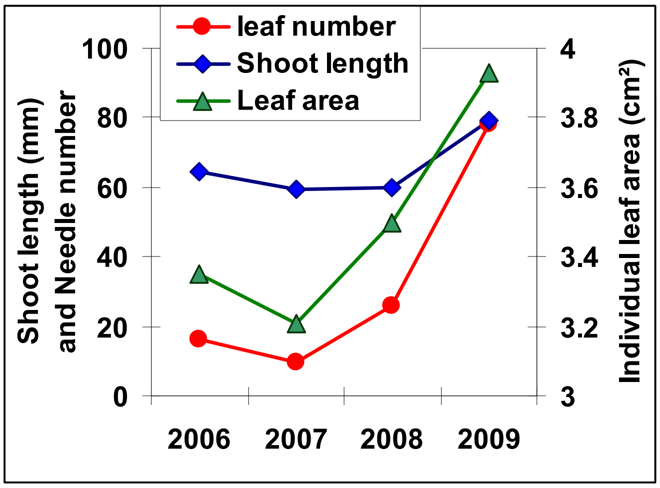

Figure 15. Quercus ilex growth at Font-Blanche.

Axis vigor	vigorous	medium	frail
needles number per twig			
normal year	69	59	49
bad year	52	38	28
needles length (mm)			
normal year	81	71	65
bad year	67	54	42
Needle width (mm)			
normal year	0.9	0.8	0.6
bad year	0.75	0.65	0.55
Needle surface (mm^2)			
normal year	72.9	56.8	39
bad year	50.25	35.1	23.1
Leaf area per twig (mm^2)			
normal year	4995	3357	1919
bad year	2601	1351	645

Needle survival rates: year 1 = 100%, year 2 = 85%, year 3 = 5%, 15% and 40% respectively on vigorous, medium and frail twigs.

Table 2. Needle number and size and leaf area according to twig vigor and climate for Pinus halepensis.

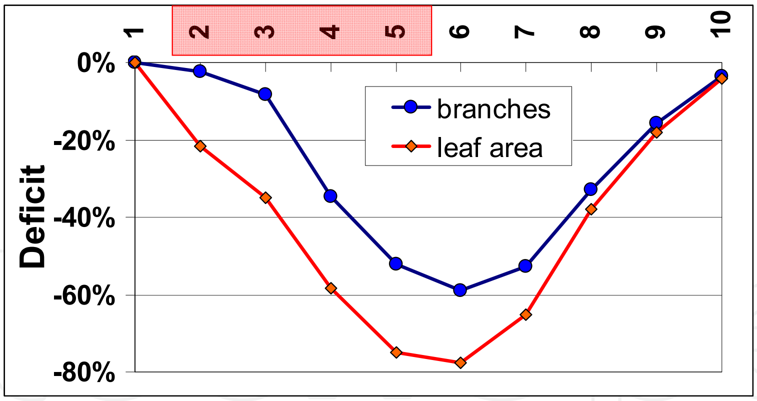

Figure 16. Evolution of the relative deficit of active twigs and total leaf area for a branch of Pinus halepensis submitted to a 4-year long climatic accident (2nd to 5th year), compared to a branch developing with mean climate parameters.

4. Discussion

4.1. Endogenous and climatic effects on crown architecture components

Ontogeny and axis morphogenetical gradients

Most of the studied morphological traits present a progressive decreasing trend along time (*figures 6, 9, 10, 11 and 12*). This decrease corresponds to a morphogenetical gradient named axis drift [15,46,47]. Morphological traits values are also driven by axis vigor, hierarchy and position within the crown (*figure 13*).

Theses endogenous constraints can be viewed as a variational module sensu Wagner *et al.* [48] that constraints any independent trait variations and thus partly explain the strong covariations found between morphological traits (*figures 7 and 8*).

Pre-induction of the primary growth characteristics (and when relevant of several flushes) in buds induces a strong dependence of primary growth on the global health status of trees and branch vigour at the time of bud formation, i.e. in previous year. Except in case of successive intense stress or extreme events, tree vigour and health rarely sharply changes between two years as trees can use non-structural carbohydrates stored in the stem and branches for growth and respiration. Such an autocorrelation between growth units is well known in ring width series [5,49,50] and was logically found for primary growth in this study.

Climatic effect on primary and secondary growth

Climatic effect on tree growth are generally analyzed using classical dendroclimatic analyses based on tree-ring data [51]. They usually conclude that tree radial growth is affected by continuous changes in climatic conditions (trends) and by strong climatic events [3,26,52]. Height growth was more occasionally used as indicator due to time-consuming measurements in the field, but gave reliable results [53]. This study revealed that a temporal survey of branch elongation and architectural parameters is of interest to this aim.

The occurrence of successive drought years between 2003 and 2007 led to a clear fall in all growth and architectural parameters: branch length and tree height growth, branching rate and polycyclism, needle number and needle length reached very low values during two to five years. These reductions could be clearly attributed to climate as the natural trends induced by branch or tree aging were slower, and all parameters finally recovered, at least partly, with more favorable climatic conditions.

As an extreme event with deleterious effects on forest health and productivity throughout Europe [54] and on studied species in Southeastern France [13], the 2003 summer heat-wave was supposed to have deeply impacted tree architectural development and growth. The direct impact of 2003 was mainly visible on needle length and individual leaf area (*figures 8 and 14*), on ring width and to a lesser extent on some parameters of *Abies alba* (*figure 8*). Leaf development and ring width were stopped very early at the end of spring due to extreme water stress. But for most other parameters and species (*figures 8 to 12*), 2003 was a normal or even a good year. The predetermination of most architectural parameters in the buds during 2002 which was a rainy year, and for polycyclic species the ability to add a new growth unit at the end of the year explain that 2003 impact is mainly visible from 2004. But our study cannot accurately assess this impact as 2003 was followed by several very dry years. However, the fact that some of the traits (*Pinus halepensis* and *Pinus pinaster* polycyclism and branch length growth, needle length for many species) started or completed their recovery in 2006 or 2007 (*figures 8 to 10, 12 and 14*) although they were extremely dry years, could be interpreted as the end of the delayed effects of 2003. This is consistent with the time necessary for all studied pine species to built up a full set of normal needles again after the loss of a large amount of old needles in summer 2003 [31], and to get read of the short needles of 2003. This time could have been also necessary to overcome the disorders caused by hydraulic failure in tree sapwood in summer 2003 [9,55,56].

Intra-specific variability in traits response to climate

All the traits did not respond similarly to climate variability and accidents (*figures 8, 12, 15*) for a species on a given site. Each of them is driven by many factors, related to climate or to functional relations between organs within a tree.

Needle length is mainly determined by the climate of the year of their development. For polycyclic species, needles of the later cycle can be very short when they lack time to complete their lengthening before the end of the growth season. Conversely, needle width and thickness mainly depend on twig diameter and vigour [57] and therefore, at tree level, on the climate of previous years and more generally on branch and tree health status. Although they are slightly sensitive to climate conditions of their growing year, they do not follow the rapid changes of needle length. Consequently, needle area is a compromise between its length and width which do not vary synchronously. Needle number and branching rate on a given twig are predetermined in the terminal bud of the twig. For monocyclic species, they are fully controlled by the climate of the previous year and by twig vigour. For polycyclic species, several growth units can be predetermined by previous year conditions but additional cycles may be formed later in the growing year according to climate and other constraints [15]. These new growth units can give birth to both needles and new branches, or only needles or branches. Branches are, however, also controlled by the climate of their first growth season: some of the preformed buds remain dormant and young shoots abort in case of unfavourable conditions. The total leaf area at branch level is thus complex to model due to the many factors at stake.

The variable response of traits in time and intensity may also be linked with phenology: secondary growth occurs longer than shoot extension in monocyclic species [58], but the opposite is observed in some polycyclic species when shoot growth occurs late in autumn and even in winter without cambial activity [20]. Early or late climate-related stresses may not have the same impact.

Ring width seemed to present a reduced plasticity compared with annual shoot lengths for *Abies alba* (*figure 12b*). This result, poorly investigated in the literature, highlight the critical need of multi-traits approaches to assess the effect of climate change on trees and open questions about tree carbon allocation under stress conditions. Although ring width is known to present autocorrelated series, it was generally mainly driven by the climate of its growth season and the previous winter for studied sites and species [13,21,59].

Recently, Girard *et al*. [12] found a significant expanded influence of the previous year for *Pinus halepensis* ring width: rainfall from February to June and temperature from April to September. Moreover, Sarris et al. [60] showed the significant influence of cumulated rainfalls expanding from one to five previous years from the more humid to the driest area of this species distribution range. Thus, climate change should increase the autocorrelation in tree response to climate and make it far more complex in integrating medium term climate variations in each annual growth pattern. The slow response of many growth variables after the 2003-2007 droughts may be a normal adaptation to this arid period and globally to an exceptionally hot and dry climate during one decade in the study area [61].

The inertia of branching patterns, driving leaf number and total leaf area, may explain the increasing length of the integration period with climate aridity.

Inter-specific response variability

Although some differences can be observed in the response of species to inter-annual climate variability, this study showed globally consistent trends in time for all traits and all species (*figures 7, 9 and 10*). Discrepancies consist mainly in time lags of one or two years for the lower values in the 2003-2007 periods, and in the speed of recovery after 2007. In some cases, a significant decreasing trend was observed from 1998 or 2000 for some species, while in the same sites the other species showed no fall before 2003. Inter-specific differences seamed relatively higher before 2003 than during and after the crisis. This proves that species and traits varied resistance to drought or other stresses, which allowed these initial differences, was smoothed by the intensity of the crisis. This conclusion should be tempered as we only present measures for living trees: *P. sylvestris* and *Abies alba* mainly, *P. nigra* to a lesser extent, experienced high rates of die-back in the hinterland. Dead trees could have shown different response patterns.

As already stated, within the six studied conifers, only two (*P. halepensis and P. pinaster*) present frequent polycyclism that should contribute to a different response pattern to climate change. As illustrated by *figure 10,* the number of growth cycles within a year present huge inter-annual variations that are directly linked with climatic conditions [37]. Polycyclism can be viewed as a fast way to improve foraging abilities when growth conditions are favourable. On the other hand, late cycles induced by hot autumns and recently observed even in winter in the study area are detrimental to tree health and growth due to frost damages [38,62].

4.2. Effect of crown architecture components on tree health

Leaf area deficit vs branching rate

Tree leaf area is the product of numerous architectural components. It is the result of the number and size of leaves per growth unit and the number of growth units per annual shoot and the branching rate. At tree level, it also depends on competition between branches and between trees, and on crown shape related to age and tree history. At all scales, it depends on twig, branch and tree vigour and health status, not to mention external factors as defoliators and diseases. Up to now, leaf area deficit and tree growth (radial, height, or volume) were the main factors used to quote tree health [63,64]. If leaf area deficit can initially occur as an avoidance mechanism to maintain a favorable water balance by reducing transpiration, it also induces a reduction in carbon assimilation [65]. Consequently leaf area deficit may be the early warning of a sequence leading to tree death [63,66], and could be used to predict tree mortality [67]. But this deficit was always assessed globally without desentangling its distinct causes. In this study, we quantified with our branch model an extreme leaf area real deficit, reaching nearly 80% after 4 very bad years (*figure 16*). This is far over the "leaf deficit" usually quoted by crown transparency, reaching such an extreme only for dying trees which is far from being the case in our plots. This discrepancy can be partly explained by the reduction of branch length growth and of the distance between leaves or needles along the twigs, which concentrates them in a smaller crown volume.

According to the branch model, during the two first bad years, branch deficit remained under 10% and could not explain the leaf area reduction which reached 35%. Thus, leaf number and size were the main factors at stake. With the lengthening of the drought period, the deficit in branch number became dominant, explaining most of the gap in total leaf area. Finally, during the recovery period after the end of bad years, branching shortage entirely matched leaf area deficit. This is consistent with *figures 8 and 9* showing that branching rate reached its minimum in 2007 or 2008, after the other variables, and particularly after needle length. Its recovery rate was slower than needle number (*figure 11*), which also showed a minimum in 2008 for *Pinus halepensis.* Finally, branching deficit during bad years is probably one of the key issues in leaf area long lasting deficit leading to forest decline.

Functional equilibrium

According to the concept of functional equilibrium [68,69] plants allocate biomass in priority to organs concerned by the most limiting factors [70]: roots if case of nutrients or water shortage, shoots and leaves when their environment is deficient in CO_2 or light. Accordingly, plants show remarkable resilience when part of their leaves, branches or roots are destroyed or artificially removed. They generally recover a normal leaf area or root length and biomass in a few years [71]. This may be true when repeated or long lasting climatic stresses reduce first their aerial growth (shoot and needle length) (*figures 8 and 16*), in order to maintain and develop the root system while limiting evapotranspiration. After the release of the stress, tree favors leaf production to reach the balanced level (*figures 8 and 14*) as well as shoot length. This priority in resource allocation to primary growth seams to the expense of secondary growth as indicated by a slower recovery in ring width, as already described by Girard et al. [12] for *Pinus halepensis*.

5. Conclusion and prospects

Modeling tree responses to climate change and particularly dieback hazard is a key issue since strong changes in tree productivity, survival and recruitment were observed recently [4,63]. A main concern is the assessment of tree vulnerability to increasing drought periods. Empirical models based on statistical relationships are not reliable as they cannot accurately take thresholds and extreme events into account. In contrast, mechanistic models explicitly represent the processes by splitting them into different blocks, which describe the response of the process to some input variables. However the variability of architectural components is poorly represented up to now in process-based models of individual tree growth. Most of them ignore their spatial variations and differentiated temporal response according to axis position in the crown, hierarchy in the branch and vigour. Their improvement with these new findings is urgently needed.

Our analysis made on many sites and species in Southeastern France revealed common patterns of response of tree architectural development to climate change and accidents. The role of long lasting delayed consequences of climate accidents on branching rate, holding back the potential leaf area for years, is one of the key issues to be tackled. Low leaf area, through carbon shortage, may contribute to forest decline and die-back.

This study highlights the necessity of more thorough investigations, in terms of field work and modeling. Our preliminary results must be confirmed for new species and climates and with longer data series to disentangle the multiple and contradictory effects of climate change on tree architectural development.

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