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Influence du réchauffement climatique sur la croissance des ligneux bas dans les Alpes françaises : analyse dendroécologique de *Rhododendron ferrugineum* L. en contextes topoclimatiques contrastés

Loïc Francon

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**Influence du réchauffement climatique sur la croissance des
ligneux bas dans les Alpes françaises : analyse
dendroécologique de *Rhododendron ferrugineum* L. en
contextes topoclimatiques contrastés**

**Influence of global warming on the growth of dwarf shrubs in the French Alps:
dendroecological analysis of *Rhododendron ferrugineum* L. in contrasting
topoclimatic contexts**

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Géographie
sous la direction d'Irène Till-Bottraud et de Christophe CORONA

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Résumé

Les écosystèmes alpins, comme la toundra arctique, subissent un réchauffement accentué par rapport au reste du globe. En Arctique, une approche dendroécologique basée sur l'analyse des relations entre la croissance annuelle radiale et le climat a permis de mettre en évidence les paramètres climatiques qui contrôlent l'expansion des arbustes nains (ligneux bas). Ces changements au sein de la toundra ont de vastes répercussions sur l'albédo, le manteau neigeux, le sol, le microclimat au niveau du sol ainsi que sur le cycle du carbone et le climat à l'échelle planétaire. Les Alpes européennes se sont considérablement réchauffées ces dernières décennies, et ce de manière non-linéaire, avec un point d'inflexion situé à la fin des années 80. Par analogie avec l'Arctique, nous émettons l'hypothèse qu'à haute altitude la diminution des contraintes climatiques (hausse des températures estivales, diminution de l'enneigement) favorise une augmentation de la croissance radiale des ligneux bas. Afin de valider cette hypothèse, huit populations de *Rhododendron ferrugineum* L. (Ericaceae) ont été prélevées dans des sites, le long de gradients topoclimatiques et dans des massifs caractérisés par des niveaux de continentalité représentatifs des Alpes françaises. Afin de caractériser finement la réponse de *R. ferrugineum* au changement, les chronologies de largeur de cernes établies pour chaque population ont été comparées aux séries météorologiques en utilisant les approches statistiques courantes en dendrochronologie (fonctions de corrélation) mais également sur la base de modèles empruntés à l'écologie (modèles linéaires mixtes, modèles d'équations structurelles).

Le premier chapitre de la thèse met en évidence le potentiel dendroécologique de *R. ferrugineum*. Sur la base de fonctions de corrélation, il a permis de démontrer que les températures estivales étaient le principal facteur limitant de la croissance radiale d'une population de *R. ferrugineum* échantillonnée dans le massif du Taillefer (Alpes françaises, 2000 m d'altitude) mais également une très forte sensibilité de cette population aux précipitations hivernales, phénomène non observé sur une population d'arbre (*Picea abies*) située à proximité. Dans le deuxième chapitre, l'échantillonnage initial a été complété par des prélèvements réalisés sur deux placettes étagées le long d'un gradient altitudinal (1800-2400 m). La comparaison de la croissance radiale de *R. ferrugineum* et des séries nivo-météorologiques locales issues de la base de données SAFRAN-crocus au moyen de modèles d'équations structurelles démontre une forte hétérogénéité spatiale et temporelle de la réponse des ligneux bas aux fluctuations du climat. La population en limite altitudinale supérieure (2400 m) est très sensible à la durée de saison végétative et à la température estivale. Cette sensibilité décroît fortement à plus basse altitude (1800, 2000 m) en relation avec l'augmentation du stress lié aux gels printaniers depuis la fin des années 1980. De la même manière, l'affaiblissement des relations cernes-climat au cours des deux dernières décennies est attribué à un phénomène de divergence similaire à celui observé dans les populations d'arbres en Arctique. Le troisième chapitre est consacré à l'analyse de populations prélevées dans le massif du Queyras (Alpes françaises du sud) où l'aridité estivale liée à la continentalité est plus marquée que dans le Taillefer. Les résultats obtenus sur deux populations localisées sur des versants ouest et nord montrent le rôle déterminant de la situation topoclimatique sur la réponse de *R. ferrugineum* au climat et l'impact négatif de l'augmentation de la sévérité des vagues de chaleur et de la sécheresse estivale sur la population exposée à un rayonnement solaire important. Le quatrième chapitre intègre les huit populations échantillonnées dans les Alpes. Il démontre une forte non-linéarité de la réponse de *R. ferrugineum* au changement climatique à l'échelle des Alpes françaises. Cette non-linéarité est modulée par le topo-climat. La croissance radiale des ligneux bas, régie par la température avant les années 1980 semble ainsi dorénavant contrainte par l'accessibilité à l'eau et par les événements de gel printanier. Le chapitre de conclusion synthétise les résultats de ce travail mais met également en évidence ses limites et propose des perspectives de recherche. Malgré des avancées importantes pour la compréhension du rôle du réchauffement climatique sur la croissance des ligneux bas en montagne, il souligne que les résultats obtenus reposent sur des corrélations statistiques et insiste sur la nécessité d'approfondir les connaissances sur l'écophysiologie des ligneux bas en montagne. En ce sens, il plaide pour une approche multi-échelle regroupant télédétection (productivité des landes arbustives), approche dendroécologique (réponse au climat et profondeur temporelle) et suivi microclimatique et dendrométrique des ligneux bas (mécanismes physiologiques) qui permettrait une analyse approfondie du verdissement alpin.

Abstract

Alpine ecosystems, such as the Arctic tundra, are experiencing a pronounced warming compared to the rest of the world. In the Arctic, dendroecological studies have documented the climatic drivers of the expansion of dwarf shrubs. These changes in the Arctic tundra have far-reaching implications for albedo, snow cover, soil, ground-level microclimate, global carbon cycle and climate. The European Alps have warmed considerably in recent decades, and this has occurred in a non-linear way, with an inflection point the end of the 1980s. Since then, summer temperature has sharply increased and snow cover durability in spring has declined. By analogy with the Arctic, we hypothesize that at high elevation, the decrease in climatic constraints (increase in summer temperatures, decrease in snow cover duration) favors an increase in shrubs radial growth. In order to validate this hypothesis, eight populations of *Rhododendron ferrugineum* L. (Ericaceae) were collected in the French Alps, throughout a network designed to be representative of the contrasts in continentality, elevation and slope aspect across the French Alps. Classical statistical procedures used in dendroecology (Correlation functions) and models traditionally used in ecology (Structural Equation Models, Linear Mixed Models, SEMs, LMMs) have been coupled to finely assess the relationships between the radial growth of *R. Ferrugineum* and nivo-meteorological variables.

The first chapter shows the dendroecological potential of *R. Ferrugineum* in a population (2000 m asl) from the Taillefer massif. Correlation function analyses reveal that winter precipitation and summer temperature act as main co-limiting factors for shrub growth while comparable sensitivity to snowfall was not observed in a population of adjacent trees (*P. abies*). In chapter 2, two additional *R. ferrugineum* plots were sampled in the Taillefer massif at 1800 and 2400 m asl. The radial growth of *R. ferrugineum* along the elevation gradient was compared to local re-analyses from the SAFRAN-crocus nivo-meteorological network. Comparison of the radial growth of *R. ferrugineum* and local snow and weather series from the SAFRAN-crocus database using structural equation models shows a high spatial and temporal heterogeneity in the response of dwarf shrubs to climate fluctuations. The population sampled at the upper shrubline (2400 m) is very sensitive to the length of the growing season and summer temperature. This sensitivity decreases sharply at lower elevations (1800, 2000 m) in relation to the increase in stress associated with early frosts since the late 1980s. Similarly, the weakening of climate-growth relationships over the past two decades is attributed to a divergence phenomenon similar to that observed in tree populations in the Arctic. Chapter 3 focuses on the analysis of populations taken from the Queyras massif (southern French Alps) where summer aridity linked to continentality is more pronounced than in the Taillefer. The results obtained in two populations located on western and northern slopes show the decisive role of the topoclimate on the response of *R. ferrugineum* to climate and the negative impact of the increase in the severity of heat waves and summer drought on populations exposed to higher solar radiation. In Chapter 4, all the populations sampled over the French Alps were analyzed simultaneously. Our results show a strong non-linearity of *R. ferrugineum* response to climate change exacerbated in specific topoclimatic situations. Shrubs, whose radial growth was clearly controlled by temperature before the 1980s, now seem to be constrained by water availability and spring frost events. Finally, the last chapter synthesizes the main results of this study and proposes perspectives for future research. More particularly, and albeit the major outcomes of this PhD thesis, it highlights the limitations of correlation analyses to understand climate-growth relationships and stresses the need to improve knowledge on the ecophysiology of dwarf shrubs in mountain areas. In this sense, it pleads for a multi-scale approach combining remote sensing (spatial dynamics and productivity of shrublands), dendroecological approach (response to climate and temporal depth) and microclimatic and dendrometric monitoring of alpine shrubs (physiological mechanisms) that would allow for in-depth analysis of alpine greening.

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Introduction



Photographie de page précédente : Paysage en contrebas du site d'étude de Loriaz. Vue sur le massif du Mont-Blanc. Au premier plan : landes à rhododendrons et à genévriers au niveau de la limite de l'arbre.

Les écosystèmes alpins et arctiques (arctico-alpins) connaissent un réchauffement accentué par rapport au reste du globe, l'Arctique plus de deux fois et les montagnes environ une fois et demi plus vite que la moyenne globale (IPCC, 2019; Mountain Research Initiative EDW Working Group, 2015). Ce réchauffement devrait se poursuivre dans les décennies à venir, selon toutes les projections climatiques, en réponse au forçage anthropique du climat (IPCC, 2019). Cette hausse des températures est exacerbée dans les régions septentrionales et en montagne par un ensemble de rétroactions entre la température, la couverture neigeuse, la banquise, l'albédo et la concentration en vapeur d'eau de l'atmosphère (IPCC, 2019; Ohmura, 2012; Scherrer et al., 2012).

Les régions de haute-montagne supraforestière (que j'appellerai dans ce manuscrit « écosystèmes alpins », ou simplement « l'alpin » ; en référence à la notion d'« étage alpin », ce dernier terme sera utilisé dans son intégralité) et arctiques sont caractérisées par une végétation basse, de type toundra, dont la croissance est limitée par les températures qui conditionnent la persistance nivale et donc la durée de la période végétative. Ces écosystèmes sont donc particulièrement sensibles à la hausse des températures (Elmendorf et al., 2012 ; Post et al., 2009). Ainsi, un des changements les plus spectaculaires observé en toundra arctique, l'expansion des arbustes (ou ligneux bas) à travers le paysage et leur productivité accrue, ont été attribués au réchauffement du climat (Myers-Smith et al., 2011; Tape et al., 2006; Wilson and Nilsson, 2009). Afin de mieux cerner cette augmentation de la productivité et ses relations avec les variables climatiques, de nombreuses études dendroécologiques ont été réalisées, depuis le milieu des années 1990, sur plusieurs espèces arbustives arctiques (voir par exemple, Myers-Smith et al., 2011; Woodcock and Bradley, 1994). Ces études ont permis de reconstituer la productivité sur plusieurs décennies avec une résolution annuelle. En ce sens, elles ont fortement contribué à améliorer la compréhension des facteurs de contrôle de la dynamique des ligneux bas arctiques (voir par exemple Bär *et al.*, 2008; Forbes *et al.*, 2010; Hallinger *et al.*, 2010; Weijers *et al.*, 2018; Myers-Smith et al., 2015a). Par comparaison avec l'Arctique, les zones de haute montagne n'ont été que paradoxalement peu étudiées. La plupart des analyses dendroécologiques portant sur des ligneux bas ont été réalisées en Himalaya (voir par exemple Li *et al.*, 2013; Liang *et al.*, 2015; Liang et Eckstein, 2009). En contexte tempéré, seules deux autres études ont été recensées dans les Alpes (Pellizzari et al., 2014; Rixen et al., 2010), et une unique en Sierra Nevada californienne (Franklin, 2013). Ces travaux ponctuels sont limités à l'analyse des relations cernes de croissance / climat mais ne prennent pas en compte l'hétérogénéité liée aux forts gradients topoclimatiques qui caractérisent les montagnes.

Ce chapitre introductif synthétise les connaissances relatives (1) à l'impact du réchauffement climatique sur la végétation arctico-alpine puis (2) les études consacrées à l'utilisation de la dendroécologie sur des ligneux bas en insistant sur les différences entre hautes latitudes et hautes altitudes. Cet état de l'art nous a ensuite permis (3) d'identifier plusieurs verrous scientifiques et (4) de définir précisément les objectifs de ce travail de thèse.

1 La végétation arctique-alpine face au changement climatique

1.1 Les tendances régionales : expansion arbustive, thermophilisation et verdissement des écosystèmes arctico-alpins

En Arctique, les impacts du réchauffement climatique sur la végétation ont été mis en évidence par de très nombreuses études au cours des 30 dernières années. La majorité des études convergent vers une expansion des arbustes et une augmentation de la biomasse (Callaghan et al., 2011). Ces résultats, basés sur des observations diachroniques, confirment les résultats des études expérimentales coordonnées dans les années 1980 et 1990 dans le cadre du programme de recherche ITEX (*International Tundra Experiment*) (Arft et al., 1999). Ils mettent en évidence :

- (1) une expansion de la strate arbustive (*shrubification*, en anglais) qui se traduit par l'expansion des patches d'individus ligneux bas conduisant à une fermeture progressive du paysage (Figure 1a), à l'augmentation de la taille des individus (Figure 1b) et à la colonisation d'espaces septentrionaux et à plus haute altitude (Figure 1c ; Myers-Smith et al., 2011). Cette dynamique est avérée par de très nombreuses études (voir Figure 2 et, par exemple, Elmendorf et al., 2012b; Epstein et al., 2013; Fraser et al., 2014; Myers-Smith et al., 2011; Pearson et al., 2013; Tape et al., 2012). Par comparaison, très peu d'études évoquent une stabilité ou un recul de la végétation arbustive (Myers-Smith et al., 2011).

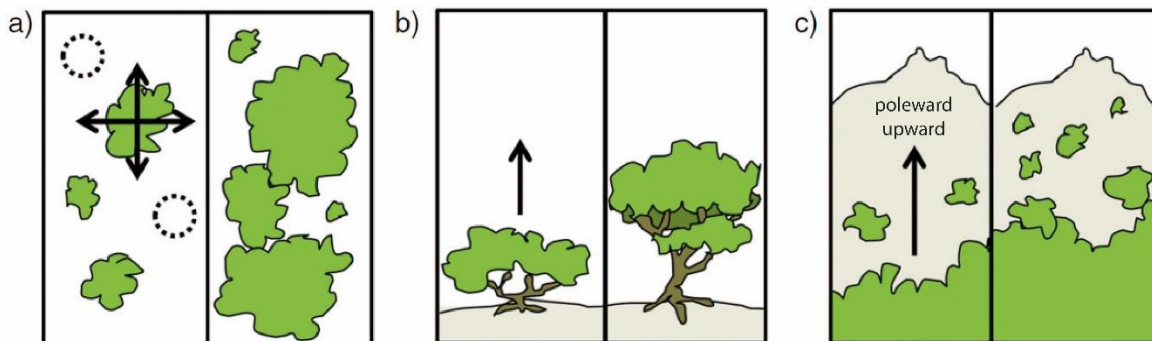


Figure 1 : Types d'expansion de la strate arbustive (*shrubification*) observés en Arctique : (a) fermeture du paysage par expansion des patches de ligneux bas ; (b) augmentation de la croissance en hauteur ; (c) extension de la limite altitudinale ou septentrionale. Extrait de Myers-Smith et al. (2011), modifié.

- (2) un remplacement des espèces les plus adaptées aux conditions froides par des espèces meso/thermophiles (*thermophilisation*). La *thermophilisation* caractérise l'expansion, dans les communautés d'espèces végétales qui tirent parti de la diminution des contraintes climatiques. Ces dernières remplacent les espèces adaptées à un climat froid, moins compétitives lorsque les conditions s'adoucissent (Elmendorf et al., 2012a, 2015) ;

- (1) un verdissement (*greening*) des écosystèmes (Figure 2) lié à une augmentation de la productivité végétale et de la biomasse (voir Forbes et al., 2010; Macias-Fauria et al., 2012; Stow et al.,

2004). Le verdissement est souvent lié à la colonisation arbustive et à la thermophilisation des communautés (Epstein et al., 2012; Tape et al., 2006).

Dans les écosystèmes alpins, des phénomènes comparables ont été identifiés (IPCC, 2019). A large échelle, on assiste ainsi à une *thermophilisation* des communautés (Gottfried et al., 2012; Lamprecht et al., 2018) concomitante de la remontée de certaines espèces en altitude (Morueta-Holme et al., 2015; Rumpf et al., 2019). Les études qui mettent en évidence une expansion arbustive sont cependant rares (Carlson, 2016). L'évolution du climat (augmentation de la température et de la saison végétative par la fonte avancée du manteau neigeux) suggère qu'un phénomène de *shrubification* analogue à celui observé en Arctique soit possible. Localement, certaines études ont mis en évidence une expansion des arbustes en altitude en lien avec le réchauffement du climat (voir Figure 2c; Cannone et al., 2007; Formica et al., 2014). Les études régionales réalisées par télédétection démontrent un verdissement (voir Figure 2d ; Carlson et al., 2017; Filippa et al., 2019) attribué à l'augmentation de la productivité des arbustes et à l'expansion de la strate arbustive. Les causes de cette expansion des arbustes en milieu alpin sont d'origine anthropique et climatique, et la part respective de chaque facteur varie localement (Carlson et al., 2017; Dullinger et al., 2003; Filippa et al., 2019). Ces tendances au verdissement des montagnes confirment les études locales ou expérimentales démontrant que la productivité végétale a généralement augmenté en lien avec la fonte précoce du manteau neigeux (Choler, 2015; IPCC, 2019; Jonas et al., 2008). Toutefois, l'ensemble de ces résultats ne sont valables que localement. En effet, l'hétérogénéité paysagère, les diversités bioclimatiques et topoclimatiques le long de forts gradients environnementaux (Körner, 2003) et l'anthropisation importante dans les Alpes compliquent la mise en évidence de tendances générales comparables à celles observées en Arctique.

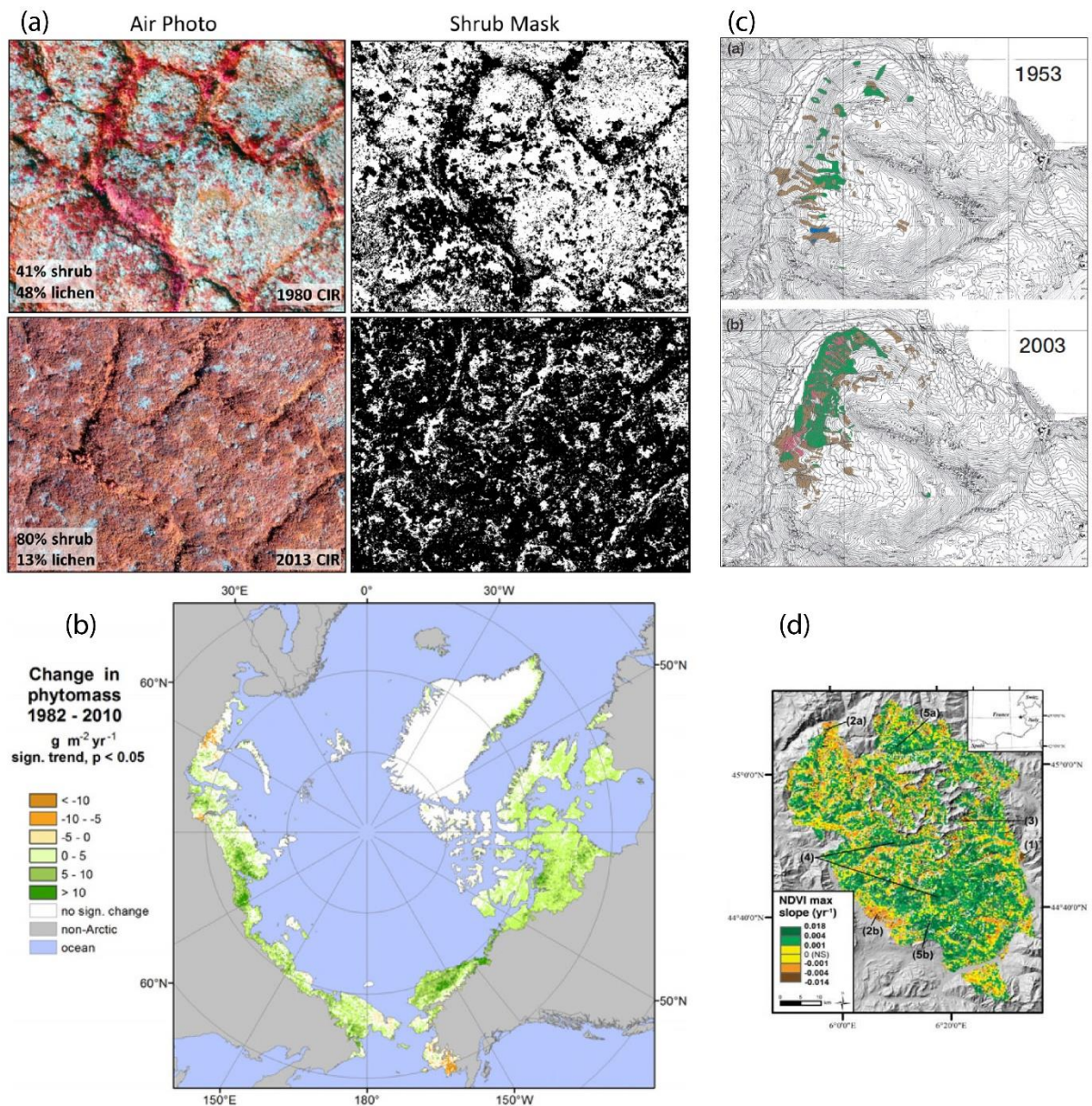


Figure 2 : Analyses diachroniques de photographies aériennes (a), de cartes phyto-sociologiques (c) et de valeurs de biomasse végétale extraites par télédétection (ici, en utilisant le NDVI : normalized difference vegetation index (b, d)) qui mettent en évidence l'expansion des arbustes et le verdissement de la toundra arctique (a, b) et des Alpes (c, d). Adapté de Cannone et al., (2007); Carlson et al., (2017); Epstein et al., (2012); Fraser et al., (2014)

1.2 Les nuances locales liées à la topographie et le rôle des évènements climatiques extrêmes

Plusieurs facteurs - le feu, la présence d'herbivores ou la limitation en nutriments - ont été démontrés comme étant limitants pour l'expansion des arbustes et la tendance au verdissement de l'Arctique (Myers-Smith et al., 2015a). Plus localement, des facteurs microtopographiques (Ackerman et al., 2017; Elmendorf et al., 2012a; Frost et al., 2013; Lara et al., 2018; Ropars and Boudreau, 2012)

ou des interactions inter/intra spécifiques (Angers-Blondin et al., 2018) modulent la tendance générale. Ces modulations sont confirmées, sur plusieurs décennies, par les études dendroécologiques qui démontrent, par exemple, que la sensibilité climatique des arbustes aux températures estivales est très hétérogène dans l'ensemble de la toundra (Myers-Smith et al., 2015a). Elles montrent également que, dans certaines positions topographiques défavorables, où l'aridité de la toundra est accentuée, les impacts positifs de la hausse des températures sur la croissance des arbustes peuvent être contrebalancés par la limitation des ressources en eau du sol. L'allongement de la période végétative et l'intensification du stress hydrique sont ainsi à l'origine de non-linéarités dans le processus de verdissement des écosystèmes alpins et arctiques (Buermann et al., 2018; Ernakovich et al., 2014).

Enfin, très récemment, des preuves de brunissement de la végétation arctique ont été apportées en lien avec des événements de gels extrêmes favorisés par l'avancement des dates de déneigement au printemps (Phoenix and Bjerke, 2016; Treharne et al., 2019). Dans les écosystèmes alpins, les déneigements expérimentaux confirment que la fonte précoce du manteau neigeux peut avoir un effet négatif sur la croissance des arbustes du fait de leur exposition et de leur plus forte vulnérabilité aux gels tardifs potentiels (Rixen et al., 2012; Wipf et al., 2009; Wipf and Rixen, 2010).

1.3 Multiplicité des rétroactions liées au changement du couvert végétal

L'expansion des espèces arbustives a des répercussions très importantes sur l'albédo et le climat régional et global (Chapin, 2005; Pearson et al., 2013), sur le manteau neigeux, la température du sol et son activité microbienne (Hagedorn et al., 2019; Sturm et al., 2001). Elle pourrait notamment induire des rétroactions positives dans le fonctionnement écosystèmes. En effet, le couvert arbustif favorise l'accumulation locale de neige, réduit les amplitudes thermiques dans le sol ce qui favorise le fonctionnement microbien sous couvert ligneux. Ces conditions sont plus favorables à la croissance en hauteur et à la densification du couvert arbustif (Domine et al., 2016). Ainsi, ces processus couplés neige-végétation pourraient accélérer la recolonisation par les ligneux bas, en particulier au niveau de l'écotone subarctique-arctique où le manteau neigeux est moins épais qu'en montagne (Sturm et al., 2005b). La Figure 3 regroupe la majorité des rétroactions identifiées et résumées par Myers-Smith et al. (2011) en lien avec l'expansion arbustive.

Enfin, l'expansion arbustive induit des changements paysagers importants ayant un effet négatif sur la biodiversité et l'hétérogénéité des communautés végétales subalpines et alpines (Anthelme et al., 2007; Boscutti et al., 2018; Koch et al., 2015; Pajunen et al., 2011). Ces changements bousculent notre imaginaire des « confins du monde », des « *high places* », qui ressemblent de moins en moins aux déserts froids de nos représentations (Cosgrove and Della Dora, 2009).

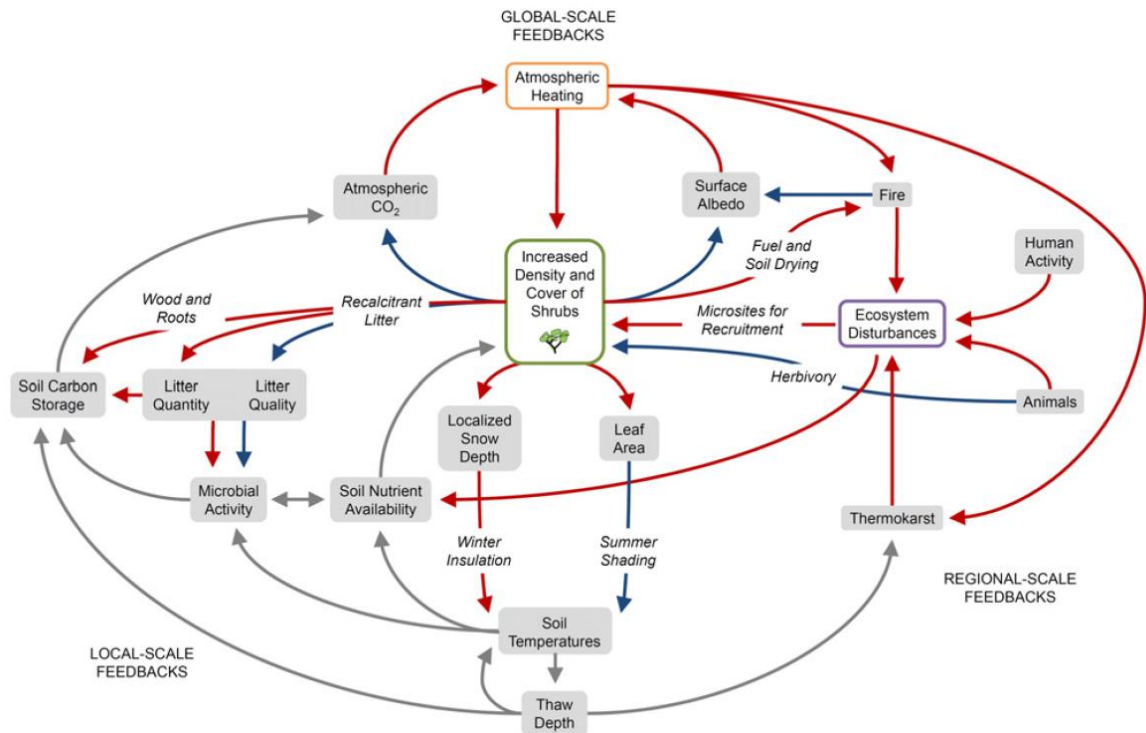


Figure 3 : Boucles de rétroaction potentiellement liées à la densification de la couverture arbustive. Les flèches rouges indiquent des relations positives et les flèches bleues indiquent des relations négatives entre les compartiments connectés ; les flèches grises indiquent des influences encore indéterminées. Extrait de Myers-Smith et al. (2011).

Ainsi, en réaction au changement climatique, même si de grandes tendances sont identifiées à travers les régions froides, il semblerait que la topographie et le manteau neigeux tamponnent localement les effets bénéfiques de la hausse des températures sur la productivité des écosystèmes, en modulant l'accès à la ressource en eau, aux nutriments et en agissant sur l'exposition des plantes aux gels de printemps. De plus, la réponse de la végétation semble différente entre l'alpin et l'Arctique, du fait, notamment des particularités physiques intrinsèques à ces deux milieux.

1.4 Les différences du milieu physique entre l'alpin et l'Arctique : importance écologique pour la végétation

Le terme de « tundra » est utilisé indifféremment pour caractériser les écosystèmes alpins et arctiques (tundra arctique et tundra alpine, Billings, 1973). Ces derniers partagent, en effet, des points communs, tels que des températures basses, une saison végétative réduite limitant la productivité et la décomposition de la matière organique (Ernakovich et al., 2014). Dans les deux cas, les paysages sont dominés par des plantes de petite taille, protégées par le manteau neigeux pendant l'hiver. De plus, les deux écosystèmes ont près de 50% d'espèces communes (Billings, 1973). Pourtant, le biotope très différent (Figure 4) a conduit plusieurs auteurs à s'interroger sur la pertinence d'un terme commun aux deux milieux (Chapin and Körner, 1995; Virtanen et al., 2016). Les différences concernent la topographie (plus hétérogène en montagne qu'en tundra arctique), la saisonnalité et le climat (journées plus courtes en été mais radiations solaires incidentes supérieures en milieu alpin) ainsi que l'interaction

entre ces deux facteurs (topoclimat). En termes de saisonnalité et de climat, les toundras arctique et alpine se distinguent ainsi par :

- (1) *les dates de début et la durée de saison végétative* (Figure 4c) : le début de saison végétative est généralement plus précoce et la saison végétative plus longue dans les Alpes qu'en Arctique.
- (2) *la radiation solaire moyenne* (Figure 4a) : au cours de la période végétative, les moyennes journalières sont comparables mais les amplitudes nyctémérales sont supérieures en milieu alpin alors que le refroidissement « nocturne » est très faible en Arctique. La radiation solaire est également inversement corrélée à la latitude (Figure 4b).
- (3) *le manteau neigeux et son action sur la température du sol* (Figure 4de) : les hivers sont, en moyenne, plus doux et plus neigeux dans les Alpes qu'en Arctique. La température du sol est maintenue proche de 0°C en hiver en raison du manteau neigeux, plus épais, qui agit comme un isolant thermique. De plus, les propriétés de la neige diffèrent grandement entre les deux milieux, avec une couche de givre plus réduite en montagne, en moyenne. Ces facteurs induisent une conductivité thermique du manteau neigeux plus faible dans les Alpes qu'en milieu subpolaire (Brun et al., 2012; Domine et al., 2016).

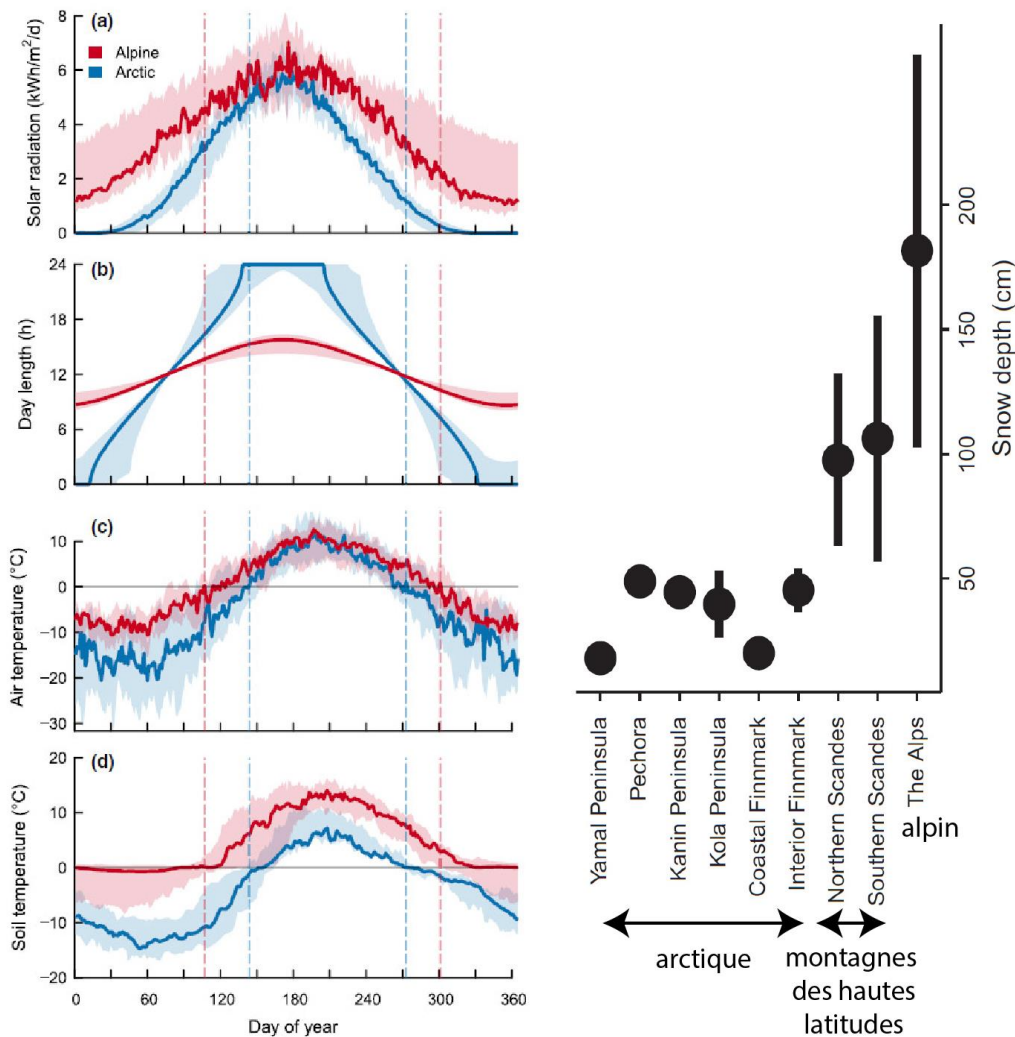


Figure 4 : Comparaison des climats alpins et arctique. (a) Rayonnement solaire moyen journalier ; (b) durée du jour ; température moyenne journalière (c) de l'air et (d) du sol (-10cm) moyenne journalière. (e) Épaisseur moyenne du manteau neigeux dans 9 sites situés en toundra arctique, en montagne alpine des hautes latitudes (transition) et en haute montagne tempérée (alpin). Adapté de Ernakovich et al., (2014) et de Virtanen et al., (2016).

De plus, en raison de gradients environnementaux plus marqués, le climat alpin est plus fortement conditionné par la méso (versants/altitude) et la microtopographie (Dobrowski, 2011; Scherrer and Körner, 2011) qu'en arctique. Cette hétérogénéité topoclimatique est un facteur de complexité supplémentaire pour les relations végétation/climat en milieu alpin car les espèces végétales sont plus sensibles au microclimat qu'au climat régional (Körner, 2003). Elle induit également une variabilité importante de la durée et de l'épaisseur de la couverture nivale (Carlson, 2016) qui conditionne la composition des communautés, la phénologie et la productivité des espèces alpines (Baptist and Choler, 2008; Carlson et al., 2015; Choler, 2015; Evans et al., 1989; Jonas et al., 2008). Le manteau neigeux influe ainsi sur :

- (1) la durée de la période végétative et notamment sur l'énergie totale reçue par la végétation pendant cette période,

- (2) l'exposition au gel, notamment au printemps au moment où des journées douces peuvent être suivies par des épisodes de gels nocturnes intenses,
- (3) la protection contre le vent,
- (4) la disponibilité en eau et en nutriments pendant la période végétative.

Ces différences (saisonnalité, climat, topographie) entre les régions arctiques et alpines expliquent très probablement les réponses contrastées de la végétation au réchauffement climatique observées en milieu alpin. Ces différences laissent également présager des réponses divergentes entre les deux écosystèmes (Ernakovich et al., 2014) et limitent la portée des raisonnements par analogie. La complexité topographique et climatique de l'alpin, notamment en ce qui concerne les effets du manteau neigeux et des rétroactions neige/végétation le long de gradients topographiques sont des points cruciaux à prendre en compte dans toute étude visant à caractériser la réponse des écosystèmes alpins au changement climatique (Choler, 2015; Wipf and Rixen, 2010).

2 Etat de l'art de la dendroécologie arbustive dans les écosystèmes arctico-alpins

La dendroécologie est une sous-discipline de la dendrochronologie permettant d'extraire des cernes annuels de croissance des végétaux ligneux, des informations sur les fluctuations du climat ou sur les changements environnementaux (Fritts, 1976). Elle consiste, par l'observation, la mesure et la datation des fluctuations annuelles (voire intra-annuelles ou décennales) de la croissance radiale (ou d'autres traits anatomiques du xylème), à étudier les relations entre les plantes ligneuses et leur environnement, et en particulier les relations cernes/climat. Cependant, les études dendroécologiques se sont longtemps cantonnées aux régions où le climat permet la croissance de la strate arborée (Filion and Payette, 2013).

La première étude dendroécologique spécifiquement dédiée aux ligneux bas remonte à 1994. Conduite sur l'île d'Ellesmere, au Canada, sur des sections transversales de saule arctique (*Salix arctica*), Woodcock et Bradley (1994) ont mis en évidence que cet arbuste prostré formait des cernes de croissances permettant de dater l'année d'établissement des individus. Ils ont été les pionniers de la dendroécologie arbustive appliquée aux dynamiques de populations en Arctique. Cependant, malgré ces résultats encourageants, le potentiel dendroécologique des arbustes en toundra arctique et en montagne n'a été réellement formulé que par Schweingruber et Dietz (2001).

2.1 Les arbustes des régions arctiques et alpines

Dans les milieux alpins et arctiques, la strate arbustive domine les communautés végétales situées sur une large zone/bande altitudinale au-dessus des limites septentrionale ou supérieure de la forêt (Billings, 1973). Les arbustes sont les uniques plantes ligneuses encore présentes (Ozenda, 2002). Cependant, leurs formes de croissance sont très diverses. Leur taille, notamment, varie au sein et entre les différentes espèces du fait de différences génétiques ou de réponse plastique aux conditions du milieu (Bliss, 1956; Kaplan, 2003; Myers-Smith et al., 2011). De plus, on les retrouve se développant sous

forme de fourrés, de landes (couverture quasi-continue) ou, aux limites septentrionale ou altitudinale de leur aire de répartition, isolés les uns des autres.

Les arbustes sont définis comme des plantes ligneuses de taille inférieure à quatre mètres, se développant sur plusieurs tiges. Kaplan (2003) et Myers-Smith et al. (2015b) proposent une classification en fonction de la taille et du port (Tableau 1). Rydsaa et al. (2017) estiment que cette délimitation en différentes classes s'explique en partie par la température moyenne estivale qui caractérise les étages et zones bioclimatiques. Le tableau 1, inspiré de cette classification, adaptée au milieu alpin, distingue ainsi : les petits arbustes (<0.7m) ou « ligneux bas » (*dwarf shrubs* dans la littérature anglophone) des arbustes de plus grande taille (*tall shrubs* ; 0.7-4m). Cette différence de taille est cruciale car elle détermine la capacité des espèces arbustives à coloniser les espaces les plus froids, afin de bénéficier de la protection du manteau neigeux pendant l'hiver. Les ligneux bas sont ainsi capables de survivre à l'étage alpin en raison de leur taille comparable à celle des espèces herbacées. Au sein des ligneux bas, les auteurs distinguent souvent les ligneux bas érigés (*erect dwarf shrubs* ; 0.1-0.7m) des ligneux bas prostrés (*prostrate dwarf shrubs* ; <0.1m).

Tableau 1 : Classification de quelques espèces de ligneux bas, communes en milieu alpin, en fonction de la taille. Adapté de Kaplan (2003), Myers-Smith et al. (2015b) et de Rydsaa et al. (2017)

Type	Terminologie	Exemples d'espèces arbustives	Etage maximal
	Grand arbuste (0.7-4m) (<i>shrub</i>)	<i>Alnus</i> sp., <i>Juniperus communis</i> , <i>Salix hastata</i>	Subalpin
Arbuste	Ligneux bas érigé (0.1-0.7m) (<i>erect dwarf shrub</i>)	<i>Juniperus cummunis nana</i> , <i>Rhododendron ferugineum</i> , <i>Salix retusa</i> , <i>Vaccinium</i> sp.	Alpin inférieur et moyen
	Ligneux bas prostré (0-0.1m) (<i>prostrate dwarf shrub</i>)	<i>Salix retusa</i> , <i>Salix herbacea</i>	Alpin moyen et supérieur

2.2 Potentiel des arbustes pour l'étude dendrochronologique

2.2.1 Des spécificités à prendre en compte

Sous un climat à alternance saisonnière, les végétaux ligneux, arbres et arbustes, produisent par division cambiale un cerne de croissance annuel durant la période d'activité végétative. La structure anatomique du bois des ligneux bas diffère peu de celle des arbres ce qui permet des analyses dendrochronologiques comparables (Schweingruber and Dietz, 2001). De plus, la longévité des plantes pérennes au niveau de la limite altitudinale supérieure de l'arbre est élevée : c'est par exemple au niveau de la limite supraforestière (entre 2200 et 2500 mètres) que les végétaux sont les plus longévifs (Figure 5). Toutefois, l'influence du gradient altitudinal sur la longévité est spécifique (Schweingruber and Poschold, 2005). La durée de vie d'*Erica carnea* est fortement corrélée à l'altitude alors que *Calluna vulgaris* y semble peu sensible, par exemple.

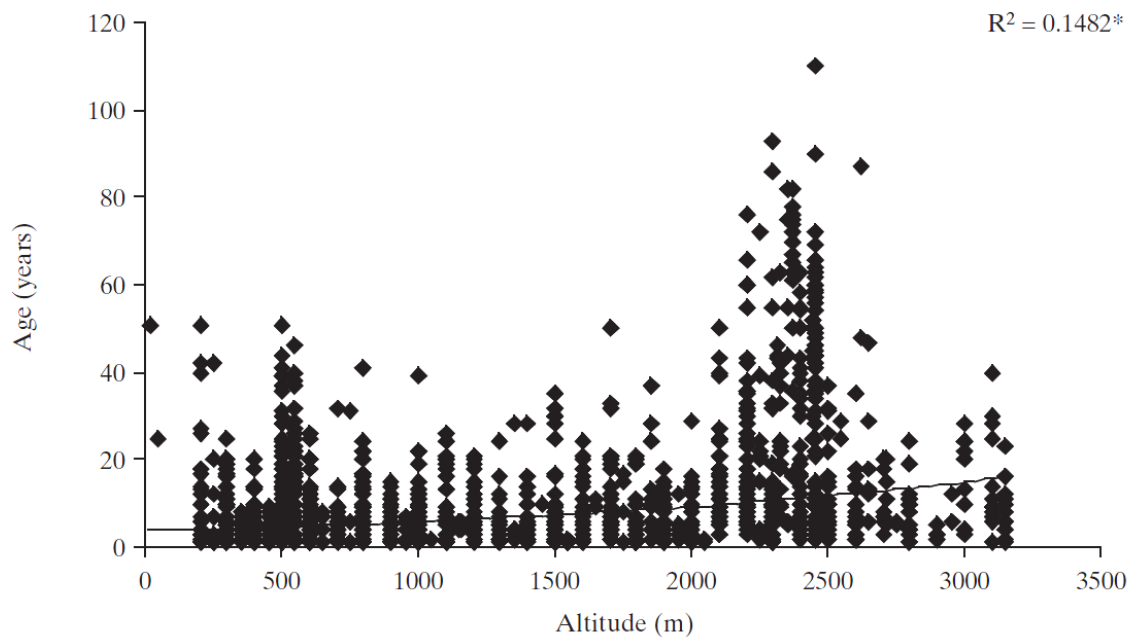


Figure 5 : Corrélation entre l'âge de plantes herbacées et de ligneux bas et l'altitude. * = $p < 0.05$. Extrait de Schweingruber et Porschold (2005).

Les conditions extrêmes des hautes altitudes et des hautes latitudes (froid intense, stress hydrique, gel, enneigement, mouvement du sol, herbivorie...) sont des facteurs limitants pour la croissance radiale des arbustes. Les cernes, souvent étroits, sont constitués d'un nombre de cellules limité, ce qui rend leur détection complexe. Les cernes absents, liés notamment à des années extrêmes d'un point de vue climatique, sont fréquents (Schweingruber, 1996). L'anatomie du bois des arbustes diffère également selon les espèces et l'atlas de Schweingruber *et al.*, (2011, 2013) qui recense l'anatomie de la majorité des arbustes et des plantes herbacées facilite la sélection d'espèces aux cernes clairement délimités.

Des facteurs morphologiques compliquent également l'étude dendrochronologique. La forme prostrée et tortueuse des arbustes, notamment des plus petits, la multiplicité des tiges ou la multiplication en colonies clonales par rhizomes (Myers-Smith, 2014) doivent être prises en compte. Les relations de compétition inter- et intra-spécifiques, ainsi que la compétition entre différentes tiges d'un même individu peuvent avoir une influence importante sur la croissance radiale (Myers-Smith *et al.*, 2015b). Les facteurs microtopographiques et microclimatiques rendent également la comparaison des séries dendrochronologiques plus complexe pour les ligneux bas que pour les arbres, qui du fait de leur grande taille, ont le plus souvent un facteur limitant commun (Schweingruber and Porschold, 2005).

2.2.2 Des adaptations méthodologiques

Myers-Smith *et al.* (2015) ont synthétisé les méthodes utilisées en dendroécologie arbustive, et détaillé les étapes du protocole permettant l'édification de chronologies de largeur de cernes. Cette méthodologie adaptée aux petites sections intègre deux avancées majeures : le *serial sectionning* développé par Kolishchuk (1990) (Figure 6a) et le protocole de réalisation de lames minces proposé par

Schweingruber et Poschold (2005). Le *serial sectionning* consiste à échantillonner plusieurs sections d'un même individu, de la base jusqu'à l'apex d'un rameau, de manière à détecter tous les cernes potentiellement manquants à la base mais visibles au niveau de la partie apicale. Le protocole détaillé et reproductible proposé par Schweingruber et Poschold (2005) est basé sur la réalisation en laboratoire de micro-sections. Ces dernières permettent l'observation microscopique de l'anatomie du bois et facilite l'identification des cernes annuels (Figure 6b). Ce travail particulièrement fastidieux, nécessite beaucoup de rigueur et la qualité de réalisation est cruciale car elle conditionne la précision des mesures de largeur de cernes et l'interdatation. Le reste du protocole, directement emprunté à la dendrochronologie classique, est brièvement décrit ci-dessous.

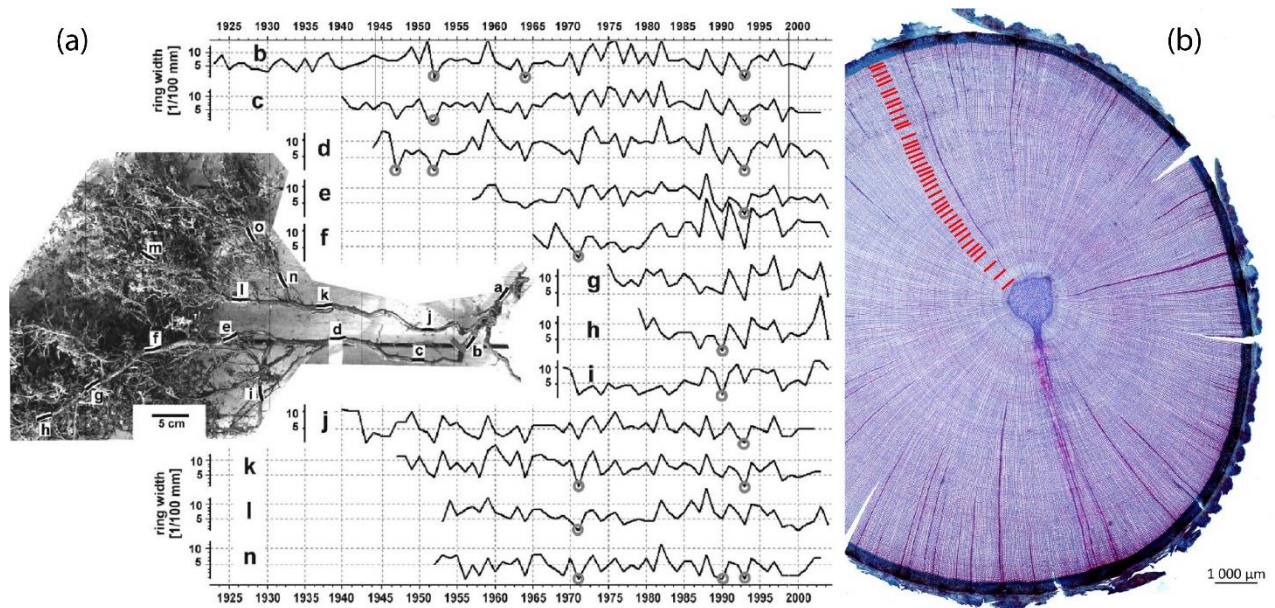


Figure 6 : Solutions méthodologiques pour le traitement de petites sections de ligneux bas en dendrochronologie : (a) serial sectionning le long de différentes tiges d'un individu de *Empetrum hermaphroditum* (figure extraite de Bär et al., 2006) et (b) réalisation d'une micro-section de *R. ferrugineum* permettant de visualiser les délimitations entre chaque cerne de croissance (traits rouges) (photographie de l'auteur).

En dendrochronologie, le protocole de développement de chronologies de largeurs de cerne, ainsi que la méthode statistique permettant d'en extraire le signal climatique ont été détaillés par Fritts (1976) ou Lebourgeois et Mérian (2012). Schématiquement, il se décompose en trois phases : (1) l'interdatation, (2) la standardisation des séries chronologiques puis leur agrégation en chronologies de référence. Ces dernières sont ensuite (3) comparées aux co-variables météorologiques.

- (1) L'interdatation consiste à attribuer à chaque cerne l'année exacte de sa formation, le dernier cerne formé étant théoriquement daté à l'année de la dernière saison végétative (en cours ou achevée) au moment du prélèvement. La datation est vérifiée par la comparaison visuelle et statistique des séries de largeurs de cernes. Elle n'est possible que si un ou plusieurs facteurs limitants communs agissent sur la croissance des individus échantillonnés. Sous cette condition, le cerne de croissance formé est comparablement et relativement grand ou petit entre les individus et les séries de largeur de cernes sont comparables les unes aux autres

(Fritts, 1976). Dans le cas des arbustes, les largeurs de cerne sont généralement mesurées le long de plusieurs rayons sur une même section (Buras and Wilmking, 2014; Myers-Smith et al., 2015b). Ces séries élémentaires sont interdatées puis agrégées au moyen d'une moyenne arithmétique. Cette agrégation par section permet de corriger les anomalies géométriques (cernes non concentriques) et de détecter des cernes partiels. Les séries moyennes obtenues pour chaque section sont ensuite interdatées et agrégées entre sections en séries individuelles afin de détecter notamment des cernes absents au niveau de certains rameaux. Enfin, l'agrégation des séries individuelles en chronologies de référence à l'échelle d'un site ou d'une population permet de détecter des cernes absents et d'éliminer les individus dont la croissance, trop atypique, n'est que partiellement limitée par le climat.

- (2) La standardisation consiste à transformer les séries de largeurs de cernes en indices de valeurs uniformes et sans unité, comparables d'un individu à l'autre. Elle permet surtout d'éliminer les signaux non-climatiques telles que la réduction de la croissance radiale liée à l'âge (tendance d'âge) ou à des modifications écologiques du microsite autour de l'individu (Filion and Payette, 2013; Lebourgeois and Mérian, 2012). Dans le cas des arbustes (voir Tableau 3 :), la standardisation est réalisée au stade des séries moyennes pour chaque section (Myers-Smith et al., 2015b). Généralement une courbe exponentielle négative est utilisée pour éliminer la tendance d'âge car c'est la fonction mathématique qui correspond le mieux à la réduction géométrique des largeurs de cerne au cours des années. Une courbe de type spline est utilisée pour retirer les fluctuations résiduelles d'origine non-climatiques, telles que les fluctuations des conditions stationnelles spécifiques à chaque individu (Blok et al., 2011; Hallinger et al., 2010; Myers-Smith et al., 2015b). Cependant certaines études n'utilisent aucune standardisation (Ackerman et al., 2018; Myers-Smith et al., 2015b) afin de ne pas éliminer les différences inter-individuelles qui peuvent avoir un grand sens écologique, par exemple pour comparer les dynamiques de croissance en situations topographiques contrastées (Tape et al., 2012).
- (3) La majorité des études dendrochronologiques réalisées sur des arbustes visent à établir des relations entre la croissance radiale et le climat, le plus souvent caractérisé par des températures moyennes et des totaux pluviométriques mensuels (Lebourgeois and Mérian, 2012). Pour cela, la majeure partie des études utilisent des fonctions de corrélation et/ou des fonctions de réponse (Blasing et al., 1984; Fritts, 1976) souvent couplées à une procédure *bootstrap* (Guiot, 1991). Ces méthodes font l'hypothèse d'une relation linéaire entre la largeur du cerne et le climat (Lebourgeois and Mérian, 2012). La fonction de corrélation est une simple analyse bivariée dans laquelle des corrélations simples sont calculées entre chaque variable climatique mensuelle et les chronologies de référence (Blasing et al., 1984). Son interprétation peut être fortement biaisée par les colinéarités entre les variables climatiques. Les fonctions de réponse permettent de pallier ces biais en intégrant une analyse en composantes principales (ACP). Les variables climatiques sont ainsi transposées en vecteurs propres avant le calcul des fonctions de corrélation ce qui permet de découpler des variables potentiellement colinéaires (Blasing et al., 1984; Meko et al., 2011). En contrepartie, les fonctions de réponse se révèlent très sensibles au choix des variables climatiques incluses dans l'analyse. Ainsi, les fonctions de corrélations sont souvent

préférées malgré les problèmes cités plus haut car plus simples à interpréter et à répliquer (Blasing et al., 1984). Une autre alternative pour pallier à la colinéarité consiste également à utiliser des fonctions de corrélations partielles (Meko et al., 2011; Zang and Biondi, 2015).

Toutes ces méthodes sont toutefois suffisamment robustes pour détecter le rôle respectif des températures et des précipitations mensuelles sur la croissance des arbres. Dans le cas des arbustes, pour lesquels la variabilité microclimatique joue un rôle important (cf. §1.3) et où des variables nivométéorologiques fortement corrélées peuvent moduler la croissance (par exemple cumul de précipitation hivernal, durée du manteau neigeux, date de déneigement, durée de la période végétative), ces modèles se révèlent imparfaits. De plus, l'hypothèse de linéarité sous-jacente à l'utilisation des fonctions de corrélation et de réponse a été récemment remise en question dans les régions froides où une divergence entre les séries dendrochronologiques et climatiques a été observée depuis le début des années 2000 (voir p.ex. D'Arrigo *et al.*, 2008; Liang et Camarero, 2018; Wilson *et al.*, 2007).

Des modèles statistiques multivariés empruntés à l'écologie (les modèles linéaires mixtes, par exemple) ont été récemment utilisés pour analyser ces relations non-linéaires et quantifier le poids respectif des différentes co-variables climatiques sur la croissance des ligneux bas (Ackerman et al., 2018; Carrer et al., 2019; Myers-Smith et al., 2015a; Schmidt et al., 2006; Weijers et al., 2018b). L'utilisation de ces modèles statistiques permet également de quantifier (1) le poids de la variabilité individuelle ou (2) le rôle de la variabilité (micro) topographique sur les relations cerne/climat.

2.3 La dendroécologie arbustive dans les régions froides : synthèse des résultats obtenus en Arctique

Après les recherches pionnières et les mises au point méthodologiques des années 1990 et début 2000, de nombreuses études dendroécologiques ont été conduites sur les arbustes des hautes latitudes (Au and Tardif, 2007; Bär et al., 2006a; Schmidt et al., 2006; Zalatan and Gajewski, 2006). Les cernes de croissance des arbustes ont ainsi été utilisés pour reconstruire les températures (Rayback and Henry, 2006; Weijers et al., 2010), la durée de la saison végétative (Schmidt et al., 2006) ou le retrait glaciaire en Scandinavie ou au Groenland (Buras et al., 2012, 2017). De plus, les facteurs de contrôle de l'expansion arbustive en Arctique ont pu être mis en évidence en comparant les chronologies de largeurs de cernes avec les variations de productivité des communautés végétales obtenues par télédétection (au moyen du NDVI, indice de végétation par différence normalisée, fréquemment utilisé pour quantifier l'évolution de la biomasse et de l'activité photosynthétique des végétaux) ou avec les phases d'expansion des ligneux bas dans le paysage (Blok et al., 2011; Forbes et al., 2010; Macias-Fauria et al., 2012; Tape et al., 2012; Weijers et al., 2018b).

L'état de l'art exhaustif, présenté dans la Figure 7 et les Tableau 2 et Tableau 3, recense ainsi 41 analyses dendroécologiques visant à étudier l'effet du (micro)climat sur la croissance radiale des arbustes. La majorité a été réalisée en toundra arctique (e.g. Blok *et al.*, 2011; Buchwal *et al.*, 2013; Forbes *et al.*, 2010; Schmidt *et al.*, 2006; Zalatan et Gajewski, 2006). Dans les massifs montagneux norvégiens, suédois ou canadiens (Bär *et al.*, 2006, 2008; Hallinger *et al.*, 2010; Weijers *et al.*, 2018), les caractéristiques topoclimatiques se rapprochent de celles de l'Arctique (climat assez sec, altitude et limitée, topographie) et sont très différentes de celles rencontrées dans les montagnes de moyenne latitude. La synthèse des relations cerne-climat montre que la croissance radiale des arbustes est, dans

la majorité des sites, positivement et significativement corrélée à la température moyenne estivale (Tableau 3 ; Myers-Smith et al., 2015a). L'enneigement, plus rarement évoqué, semble également favoriser la croissance des arbustes (Jørgensen et al., 2015; Ropars et al., 2015; Wheeler et al., 2016; Zalatan and Gajewski, 2006). Il conditionne notamment la disponibilité en eau et en nutriment pendant la saison végétative et a un effet protecteur contre le gel. Seuls Schmidt et al., (2006, 2010), dans le nord-est du Groenland, mettent en évidence un effet négatif de la date de déneigement sur la croissance radiale de *Salix arctica*.

Le rôle de la topographie, susceptible de moduler les effets de la température et l'accès à l'eau a également été analysé en comparant la réponse de populations localisées (1) en situations d'interfluves et dans des dépressions ou (2) sur des versants d'expositions différentes (Bär et al., 2008; Ropars et al., 2015). Toutefois, ces différences topographiques ne semblent avoir qu'un impact limité sur la sensibilité climatique des arbustes (Bär et al., 2008). De la même manière, la réponse de différentes espèces arbustives au climat n'est que modérément affectée par la position des individus le long d'un vaste gradient écologique en Alaska (Ackerman et al., 2018). Cependant, à l'échelle circumarctique, le degré de sensibilité des arbustes, considérés individuellement, semble dépendre de la distance au pôle et de la microtopographie (accès à l'eau) (Myers-Smith et al., 2015a). Les plus grands arbustes, localisés à égale distance entre la taïga et les zones polaires, et en situation où l'eau est disponible pendant la saison végétative sont donc les plus sensibles à la hausse des températures (Myers-Smith et al., 2015a).

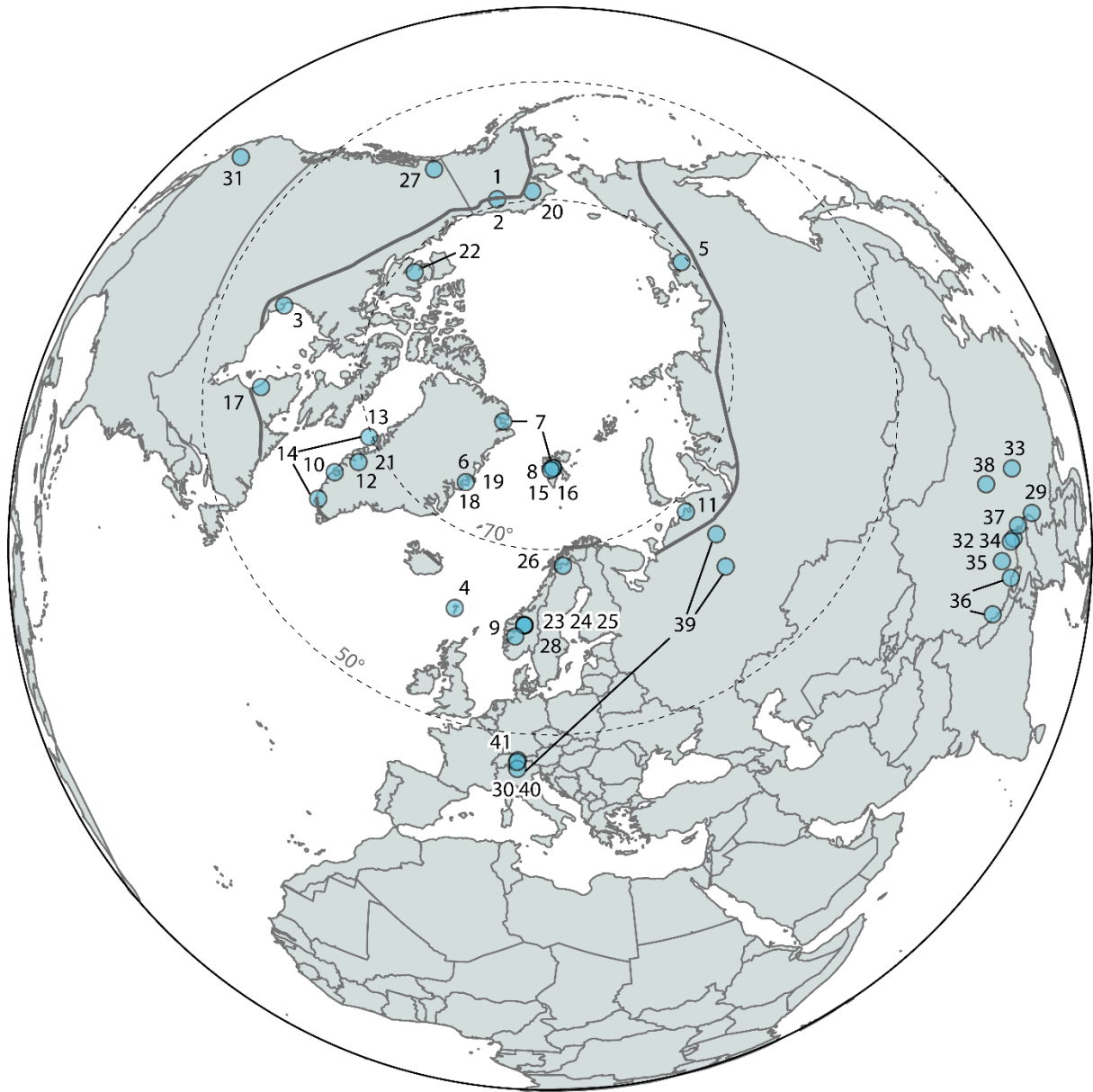


Figure 7 : Synthèse des analyses dendroécologiques visant à étudier l'effet du (micro) climat sur la croissance radiale des arbustes. Les nombres font référence aux études détaillées dans les tableaux 2 et 3.

Tableau 2 : Synthèse des analyses dendroécologiques présentées en Fig. 7. Chaque ligne correspond à une publication. La colonne Ref. fait référence aux numéros des études figurant sur la fig. 7. Les colonnes suivantes présentent les auteurs, l'année de publication, le type de milieu concerné (A : arctique, MH : montagne des hautes latitudes, HM : haute montagne), la latitude ou l'altitude du site étudié (en fonction du type de milieu), le cumul annuel moyen de précipitations, la (les) espèce(s) arbustive(s) étudiée(s) et le type d'arbuste (grand arbuste, +++, ligneux bas érigé, ++, ligneux bas prostré, +).

Ref.	Auteur	Année	Env	Lat./Alt.	Prec Moy	Espèce	Type
1	Ackerman et al.	2018	A	68.67	312	<i>Salix pulchra</i>	+++
2	Ackerman et al.	2017	A	68.67	312	<i>Salix pulchra</i>	+++
3	Au and Tardif	2007	A	58.73	432	<i>Dryas integrifolia</i>	+
4	Beil et al.	2015	A	62	1330	<i>Calluna vulgaris</i>	++
5	Blok et al.	2011	A	70.8	203	<i>Betula nana</i> <i>S. pulchra</i>	++
6	Boulanger-L et al.	2016	A	74	150	<i>Salix arctica</i>	+
7	Buchwal et al.	2019	A	78.7	184	<i>S. arctica</i> + <i>polaris</i>	+
8	Buchwal et al.	2013	A	78.7	184	<i>Salix polaris</i>	+
9	Buras et al.	2012	A	60.58	-	<i>S. lapponum</i> + <i>glauca</i>	+++
10	Buras et al.	2017	A	64.26	-	<i>Juniperus nana</i>	++
11	Forbes et al.	2010	A	68.66	300	<i>Salix lanata</i>	+++
12	Gamm et al.	2017	A	67.11	250	<i>S. glauca</i> <i>B. nana</i>	+++
13	Hollesen et al.	2015	A	69.25	273	<i>Betula nana</i>	+++
14	Jørgensen et al.	2014	A		444-1324	<i>A. viridis</i> <i>S. glauca</i>	+++
15	Le Moullec et al.	2018	A	78.5	192	<i>Salix polaris</i>	+
16	Opala-Owczarek et al.	2018	A		443	<i>Saxifraga oppositifolia</i> , <i>S. polaris</i>	+
17	Ropars et al.	2015	A	57.75	460	<i>Betula glandulosa</i>	+++
18	Schmidt et al.	2010	A	74.5	180	<i>Salix arctica</i>	+
19	Schmidt et al.	2006	A	74.5	180	<i>Salix arctica</i>	+
20	Tape et al.	2012	A	68.4	312	<i>Alnus viridis</i>	+++
21	Young et al.	2015	A	67.02	131-338	<i>S. glauca</i> <i>B. nana</i>	+++
22	Zalatan and Gajewski	2006	A	71.28	162	<i>Salix alaxensis</i>	+++
23	Bär et al.	2006	MH	1100-1400	300-400	<i>Empetrum</i> <i>hermaphroditum</i>	++
24	Bär et al.	2008	MH	1400	300-400	<i>E. hermaphroditum</i>	++
25	Bär et al.	2007	MH	1400	300-400	<i>E. hermaphroditum</i>	++
26	Hallinger et al.	2010	MH	700-1100	310	<i>J. nana</i>	++
27	Weijers et al.	2018	MH	1900	502	<i>S. pulchra</i>	++
28	Weijers et al.	2018	MH	1100	450	<i>B. nana</i> <i>E.</i> <i>hermaphroditum</i>	++
29	Bi et al.	2017	HM	3300-4400	1000	<i>Rhododendron</i> spp.	+++
30	Carrer et al.	2019	HM	1800-2000	700-2000	<i>Juniperus nana</i>	++
31	Franklin	2013	HM	3100	1500	<i>Linanthus pungans</i>	++
32	Kong et al	2012	HM	4400	900	<i>Rhododendron</i> <i>aganniphum</i>	+++
33	Li et al.	2013	HM	4050	600-1000	<i>Rhododendron</i> <i>przewalskii</i>	+++
34	Liang and Eckstein	2009	HM	4500	836	<i>Rhododendron nivale</i>	++
35	Liang et al.	2012	HM	4800	312	<i>Juniperus pingii</i>	++
36	Liang et al.	2015	HM	4100-4500	300-900	<i>Cassiope fastigiata</i>	++
37	Lu et al.	2015	HM	4000-4400	957	<i>R. aganniphum</i>	+++
38	Lu et al.	2019	HM	3200-3800	150-300	<i>Salix oritrepha</i>	+++
39	Pellizzari et al.	2016	HM	2000-2400	-	<i>Juniperus nana</i>	++
40	Pellizzari et al.	2014	HM	2100-2400	600-12000	<i>Juniperus nana</i>	++
41	Rixen et al.	2010	HM	2200	1150	<i>Vaccinium myrtillus</i>	++

Tableau 3 : Facteurs climatiques identifiés comme les plus limitants de la croissance radiale. Pour chaque étude, sont détaillés successivement : la variable climatique la plus fortement corrélée à la croissance radiale et le signe de la corrélation, le type standardisation utilisée (negex : exponentielle négative ; spline ; horizontale : ligne droite de valeur égale à la moyenne ; RCS : Regional Curve Standardization (Melvin and Briffa, 2014) et le type modèle utilisé pour l'analyse des relations cerne/climat (Corr. F : fonction de corrélation, Resp. F. : fonction de réponse, Reg. Multiple : régression multiple, LMM : modèle linéaire mixte)

Ind.	Meilleure variable climatique corrélée	Type de standardisation	Statistiques relations cernes/climat	Observations
1	T. juin (+)	aucune	Corr F. + LMM	
2	T. juin (+)	spline	Reg. multiple	Relation de 2 nd ordre
3	Tmin. oct (+), Tmin. mai (-)	spline	Corr F.	
4	T. juillet + août (+)	spline	Corr F.	
5	T. juin + juillet (+)	negex + spline	Corr F.	Corrélation + avec NDVI
6	-	-	-	Productivité corrélée + avec neige
7	T. juillet + août (+)	RCS	Corr F.	Corrélation + avec NAO
8	T. été (+)	aucune	Corr F.	
9	-	spline	-	Fluctuations glaciaires
10	-	RCS	-	Fluctuations glaciaires
11	T. juillet (+)	RCS ou spline	Resp. F.	Corrélation + avec NDVI
12	Pas de facteur limitant détecté	RCS	Corr F.	Effet négatif des températures après 1990
13	Degrés jours croissance	spline	Corr. F.	
14	T. juin + juillet (+)	horizontale ou negex	Corr. F.	
15	T. été (+)	RCS ou spline	Corr F. + LMM	
16	Températures (-), précip. (+)	horizontale	Corr. F. + Resp. F. + Reg. multiples	Sensibilité à la sécheresse
17	T. été (+), P. hiver (+)	horizontale	Resp. F.	Corrélation + avec NDVI
18	Neige (-)	aucune	LMM	
19	Neige (-)	aucune	LMM	
20	T. été (+)	negex ou RCS	Corr. F.	Effet site
21	T. mars + avril (-)	negex ou droite	Corr F. + LMM	Effet espèce/site
22	Neige (+)	droite	Corr. F.	
23	-	BAI	-	
24	T. été (+)	spline	Corr. F.	Effet topographie
25	T. été (+)	spline	Corr. F.	Pas d'effet topographie
26	T. été (+)	negex ou droite	Corr. F.	
27	T. juin + juillet (+)	horizontale	Corr F. + LMM	
28	P. été (-)	RCS	Corr F. + LMM	Corrélation - avec T. printemps
29	Tmin. hiver (-)	negex ou droite	Corr. F.	
30	Neige (-)	spline	Corr F. + LMM	Pas d'effet site
31	T. juillet (+), neige (-)	spline	Corr. F. + Resp. F.	
32	T. juin (+)	droite	Corr. F.	Corrélation + avec NPP
33	T. hiver + printemps (+)	negex ou droite	Corr. F.	
34	Tmin. novembre (+), Tmin. juillet (+), neige (+)	negex ou droite	Corr. F.	Sensibilité au gel
35	Sécheresse (-), P. juin (+), Tjuin (-)	negex ou droite	Corr. F.	Sensibilité à la sécheresse
36	T. hiver + printemps (+)	aucune	Corr. F.	
37	T. juin + juillet (+)	spline	Corr. F.	
38	T. juillet (+)	negex + spline	Corr. F.	
39	T. été (+), neige (-)	spline	Corr F. + LMM	T. été (+) en Oural, et neige dans les Alpes (-) Utilisation GAMM pour étudier évolution productivité
40	Neige (-)	spline	Corr. F.	
41	T. été (+)	aucune ou RCS	Corr. F. + Reg. multiples	Effet des températures modulé par manteau neigeux

2.4 Synthèse des études réalisées en montagne

En montagne tempérée, les recherches sont beaucoup plus rares qu'en Arctique. Elles ont majoritairement été conduites en Himalaya (Kong et al., 2012; Li et al., 2013; Liang et al., 2012, 2015; Liang and Eckstein, 2009). Dans les Alpes, les études sur placettes expérimentales visent surtout à mettre en évidence la réponse des ligneux bas à un réchauffement artificiel (Anadon-Rosell et al., 2014) et à la fonte des neiges (Rixen et al., 2010). Les seules analyses dendroécologiques *sensu stricto* ont été réalisées dans les Alpes italiennes sur le genévrier nain (Carrer et al., 2019; Pellizzari et al., 2014). L'étude de Franklin (2013) est pour l'instant la seule recensée dans les rocheuses américaines.

Ces études ne permettent pas, à la différence de l'Arctique, de faire ressortir un facteur limitant commun à la croissance radiale des ligneux bas. Certaines mettent en évidence le rôle des températures estivales (Tableaux 2 et 3 ; Kong et al., 2012; Lu et al., 2015, 2019; Rixen et al., 2010) ; d'autres démontrent le rôle négatif des précipitations hivernales qui conditionnent la durée de saison végétative et donc la croissance radiale (Carrer et al., 2019; Franklin, 2013; Pellizzari et al., 2014). Rixen et al. (2010) soulignent cependant l'effet bénéfique de l'enneigement qui peut protéger des gels tardifs. Enfin, certaines études n'attribuent la variabilité de largeur de cernes à aucune variable climatique (Li et al., 2013; Liang et al., 2012, 2015). Les sécheresses hivernales ou estivales, le gel ou l'enneigement sont fréquemment avancés comme facteurs limitants mais les données utilisées (moyennes mensuelles de température et de précipitations) sont le plus souvent de qualité ou de résolution insuffisantes pour détecter leurs impacts. Enfin, aucune étude n'intègre les gradients environnementaux. Cette lacune est d'autant plus préjudiciable que ces derniers ont une influence déterminante sur la croissance, la distribution des espèces et la composition des communautés végétales en montagne (von Humboldt, 2010; Körner, 2003).

3 Les verrous scientifiques identifiés

Cet état de l'art a permis d'identifier quatre verrous scientifiques et méthodologiques majeurs qui limite l'identification des facteurs de contrôle de la croissance des ligneux bas en montagne.

- (1) Il souligne en premier lieu la rareté des analyses dendroécologiques sur ligneux bas en montagne tempérée comparée à la toundra arctique (voir teamshrub.com et Myers-Smith, Elmendorf, *et al.*, 2015). Les connaissances concernant les impacts du réchauffement climatique sur la croissance radiale des ligneux bas sont, par conséquent, très limitées malgré une hausse importante des températures, la migration en altitude des espèces, et la thermophilisation avérées des communautés. La répartition des études est également très hétérogène : dans les Alpes, seul le genévrier nain a fait l'objet d'analyses dendroécologiques (Carrer et al., 2019; Pellizzari et al., 2014) ce qui ne permet pas de prendre en compte la variabilité des réponses au (réchauffement du) climat.
- (2) Les relations entre croissance radiale et climat semblent plus complexes et moins uniformes en montagne qu'en Arctique. Les études recensées montrent que les ligneux bas alpins ne répondent pas à une variable climatique commune (les températures durant la période végétative). Elles suggèrent également un rôle crucial du manteau neigeux sur la croissance radiale mais ce dernier a été appréhendé indirectement via les cumuls de précipitation

hivernaux. Aucune étude n'a utilisé de séries météorologiques à haute résolution spatio-temporelle, suffisamment longues pour permettre des comparaisons pluri-décennales avec les chronologies de largeur de cernes et disponibles pour des paramètres susceptibles de conditionner la croissance des ligneux bas (neige, température, humidité du sol).

- (3) De plus, les massifs montagneux de moyenne latitude se caractérisent par des gradients topoclimatiques importants et emboîtés, de l'échelle stationnelle à l'échelle régionale. Pourtant, seuls Carrer *et al.* (2019) et Pellizzari *et al.* (2016) pour *Juniperus nana* ont cherché à mettre en évidence l'impact des gradients sur la croissance, et ce, seulement à l'échelle régionale et pas du tout à l'échelle méso/micro. Paradoxalement, c'est en Arctique, où les contrastes topographiques sont beaucoup moins marqués que leurs effets sur la croissance des ligneux bas ont été démontrés. Compte-tenu des impacts de la topographie sur la disponibilité en eau, la radiation solaire et le manteau neigeux ainsi que de l'analogie faite entre mètre de dénivellation et kilomètre en latitude, nous pouvons faire l'hypothèse que l'influence du relief sur la croissance radiale des ligneux bas reste fortement sous-estimée dans les Alpes.
- (4) Enfin, la prise en compte de paramètres topographiques via notamment l'utilisation de séries nivo-météorologiques à haute résolution spatio-temporelle qui intègrent des paramètres très fortement corrélés nécessitent l'utilisation d'outils statistiques adaptés. Dans le contexte de réchauffement actuel, l'analyse dendroécologique traditionnelle, basée sur des fonctions de corrélations simples ou sur des fonctions de réponse est insuffisante pour dissocier l'impact des différents paramètres et détecter d'éventuels non-stationnarités liées au franchissement de seuils.

4 Objectifs et plan du manuscrit

Sur la base de cet état de l'art et compte tenu des verrous scientifiques identifiés, cette thèse vise à (1) explorer le potentiel dendroécologique, d'une espèce arbustive dominante dans les étages subalpin et alpin des montagnes tempérées ; (2) identifier les paramètres (micro)climatiques limitant sa croissance radiale, dans des situations géographiques et topographiques contrastées et (3) mettre en évidence les effets du changement climatique sur la croissance radiale ; (4) proposer des alternatives aux méthodes traditionnellement utilisées en dendrochronologie afin de mieux prendre en compte les spécificités des ligneux bas.

Afin d'atteindre ces objectifs, des populations de *Rhododendron ferrugineum* L. (Ericacée), un ligneux bas communément retrouvé aux étages subalpin et alpins des Alpes européennes, ont été échantillonnées le long de gradients topographiques (altitudes et orientation) dans quatre massifs des Alpes françaises se distinguant par des niveaux de continentalité représentatifs de l'arc alpin. Afin de caractériser finement le (micro)climat et notamment l'évolution du manteau neigeux, nous avons utilisé des réanalyses météorologiques issues du modèle SAFRAN-crocus de météo-France spécialement élaboré pour le contexte alpin. Ces séries sont fournies avec une résolution horaire par classe d'altitude (300 m), d'orientation et de pente pour chaque massif alpin.

Ce travail de thèse s'articule en quatre chapitres suivis d'un chapitre de conclusion. Ils correspondent aux analyses menées pour répondre aux objectifs exposés et ont été écrits sous forme de publications scientifiques conformes aux standards exigés par les journaux internationaux à comité de lecture. Le chapitre 1, publié dans *Science of the Total Environment*, cherche à cerner le potentiel dendroécologique de *Rhododendron ferrugineum*. Sur la base de fonctions de corrélation, il démontre que les températures estivales sont le principal facteur limitant de la croissance radiale d'une population échantillonnée dans le massif du Taillefer (Alpes françaises, 2000 m d'altitude, voir Figure 9). Il met également en évidence une très forte sensibilité de cette population aux précipitations hivernales, non observé sur les populations d'arbres (*Picea abies*) situées à proximité. Dans le chapitre 2, soumis à la revue *Ecological indicators*, l'échantillonnage initial a été complété par des prélèvements réalisés sur deux placettes situées à 1800 et 2400 m d'altitude (voir Figure 9). L'objectif est d'étudier l'effet de la dynamique du manteau neigeux sur la croissance radiale de *R. ferrugineum* en lien avec le changement climatique, le long du gradient altitudinal. La comparaison de la croissance radiale de *R. ferrugineum* et des séries nivo-météorologiques extraites de la base de données SAFRAN-crocus pour chaque placette au moyen de modèles d'équations structurelles démontre une forte hétérogénéité spatiale et temporelle de la réponse des ligneux bas aux fluctuations du climat. Les populations situées à la limite supérieure du gradient (2400 m) sont très sensibles à la durée de saison végétative et à la température estivale. Cette sensibilité décroît fortement à plus basse altitude (1800, 2000 m) en raison notamment de l'augmentation du stress lié aux gels printaniers depuis la fin des années 1980. De la même manière, l'affaiblissement des relations cernes-climat au cours des deux dernières décennies est attribué à un phénomène de divergence comparable à celui observé dans les populations d'arbres en Arctique. Le chapitre 3, accepté pour publication dans la revue *The American journal of Botany*, est consacré à l'analyse de populations prélevées dans le massif du Queyras (Alpes françaises du sud, voir Figure 9) où l'aridité estivale liée à la continentalité est plus marquée que dans le Taillefer. Ce chapitre cherche à quantifier l'effet des sécheresses et des canicules, plus fréquentes depuis la fin des années 1980, sur la croissance de *R. ferrugineum*. Les résultats obtenus sur deux populations localisées sur des versants ouest et nord montrent le rôle déterminant de l'exposition sur la réponse de *R. ferrugineum* au climat. Ils mettent également en évidence l'impact négatif des vagues de chaleur et de la sécheresse estivale sur les populations exposées à un rayonnement solaire important. Le quatrième chapitre intègre les huit populations échantillonnées dans les Alpes (Figure 9). L'objectif est ici de cerner l'évolution de la sensibilité au climat de *R. ferrugineum* dans différents contextes topoclimatiques représentatifs des Alpes françaises. Prochainement soumis, il démontre que la réponse de *R. ferrugineum* au changement climatique à l'échelle des Alpes françaises est fortement non-linéaire et que la divergence observée depuis la fin des années 1980 est modulée par le topoclimat. La productivité des ligneux bas, fortement corrélée aux températures de la saison végétative avant les années 1980 semble depuis contrainte par l'accessibilité à l'eau et par les événements de gel printanier. Le chapitre de conclusion synthétise les résultats de ce travail mais met également en évidence ses limites et propose des perspectives de recherche. Malgré des avancées importantes pour la compréhension du rôle du réchauffement climatique sur la croissance des ligneux bas en montagne, il souligne que les résultats obtenus reposent sur des corrélations statistiques et insiste sur la nécessité d'approfondir les connaissances sur l'écophysiologie des ligneux bas en montagne. En ce sens, il plaide pour une approche multi-échelle regroupant télédétection (dynamique spatiale et productivité des landes arbustives à l'échelle régionale), approche dendroécologique (réponse au climat sur plusieurs décennies pour un réseau de placettes représentatives)

et suivi microclimatique et dendrométrique des ligneux bas (mécanismes physiologiques dans quelques sites témoin) qui permettrait une analyse approfondie du verdissement dans les Alpes.

5 Contexte biogéographique de l'étude et choix de *Rhododendron ferrugineum* L.

Les étages subalpin et alpin des Alpes françaises forment le cadre géographique de cette étude. Les limites inférieure et supérieure de l'étage alpin correspondent respectivement à la limite écologique potentielle du développement de l'arbre et à la base de l'étage nival essentiellement minéral et englacé. L'étage subalpin est un étage de transition - ou *treeline ecotone* (Körner, 2007) - plus ou moins large, entre la forêt dense et les pelouses de l'étage alpin. La végétation y est un composé d'espèces arborées qui parfois restent prostrées (*Krummholz*), d'arbustes plus ou moins grands et d'herbacées. Le long de cet écotone, Körner (2007) décrit trois seuils écologiques : la limite supérieure de la forêt (*timberline*), la limite écologique de l'arbre (*treeline*) et à la limite supérieure écologique potentielle du développement de l'arbre (*tree species line*), jusqu'à laquelle on peut trouver des *Krummholz*. Ces transitions sont souvent diffuses avec une réduction progressive de la taille des individus avec l'altitude (Harsch and Bader, 2011). Les perturbations géomorphologiques peuvent également modifier fortement ces limites écologiques. Enfin, dans beaucoup de chaînes de montagnes et en particulier dans les montagnes européennes, le feu et les défrichements d'origine anthropique ont souvent abaissé la limite supérieure de la forêt de 300 mètres et la limite de l'arbre de 100 mètres en moyenne (Holtmeier, 2009; Ozenda, 1985; Tinner and Theurillat, 2003). Dans le cadre de ce travail de thèse, nos recherches s'inscrivent dans l'espace biogéographique compris entre la *timberline* (base de l'étage subalpin inférieur) et la *shrubline* (les derniers individus isolés de rhododendrons sont souvent situés autour de la base de l'étage alpin supérieur, voir Figure 8), incluant ainsi la majeure partie de l'aire de répartition des ligneux bas alpins et en particulier sa limite supérieure, où ces derniers sont en théorie particulièrement sensibles au réchauffement du climat. A travers les Alpes françaises, les limites altitudinales des étages subalpin et alpin varient en fonction du degré de continentalité. Située à une altitude d'environ 1800 m dans les Alpes externes soumises aux influences océaniques donc plus humides, la *treeline* s'élève à des altitudes avoisinant 2300/2400 m dans les Alpes internes, au climat plus continental (Ozenda, 1985).

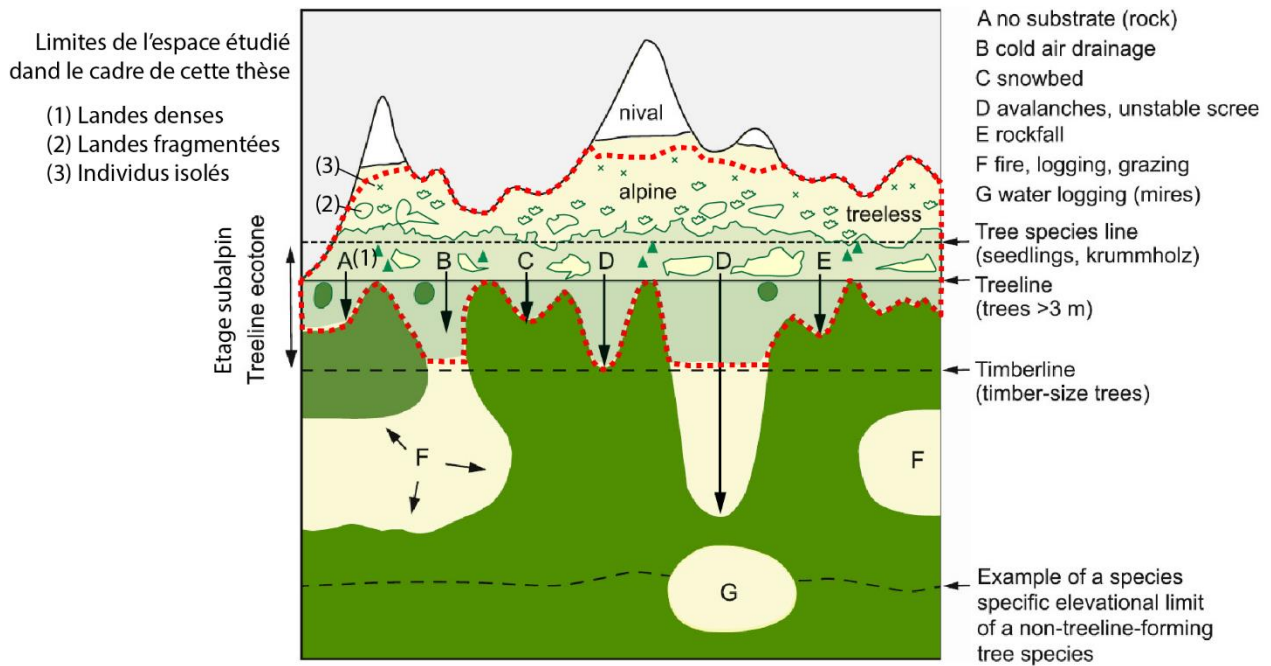
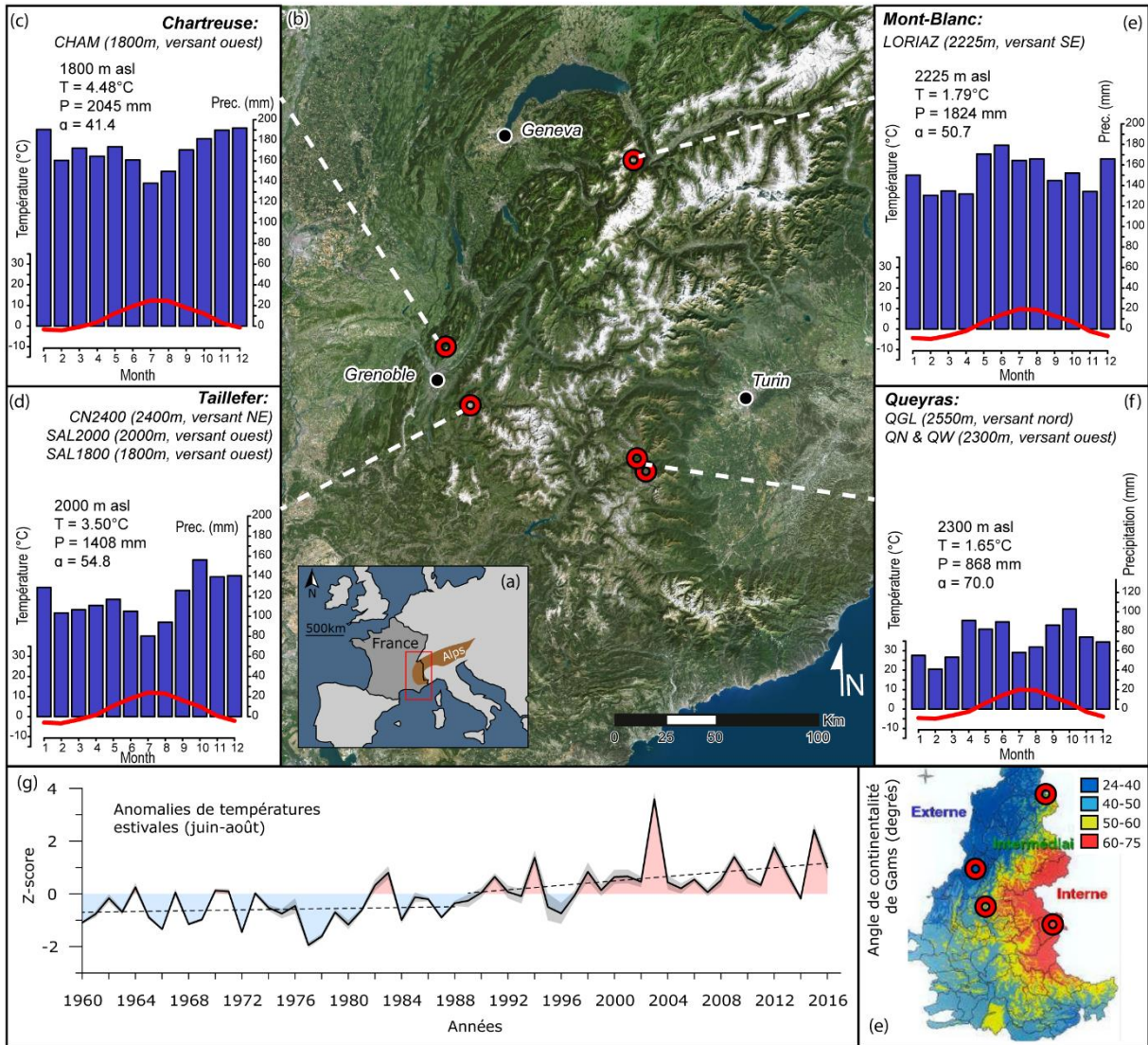


Figure 8 : Représentation schématique de l'étage subalpin et de l'étage alpin, avec délimitation de la bande altitudinale dans laquelle les ligneux bas ont été échantillonnés dans le cadre de ce travail de thèse. Adapté de Körner, (2012).

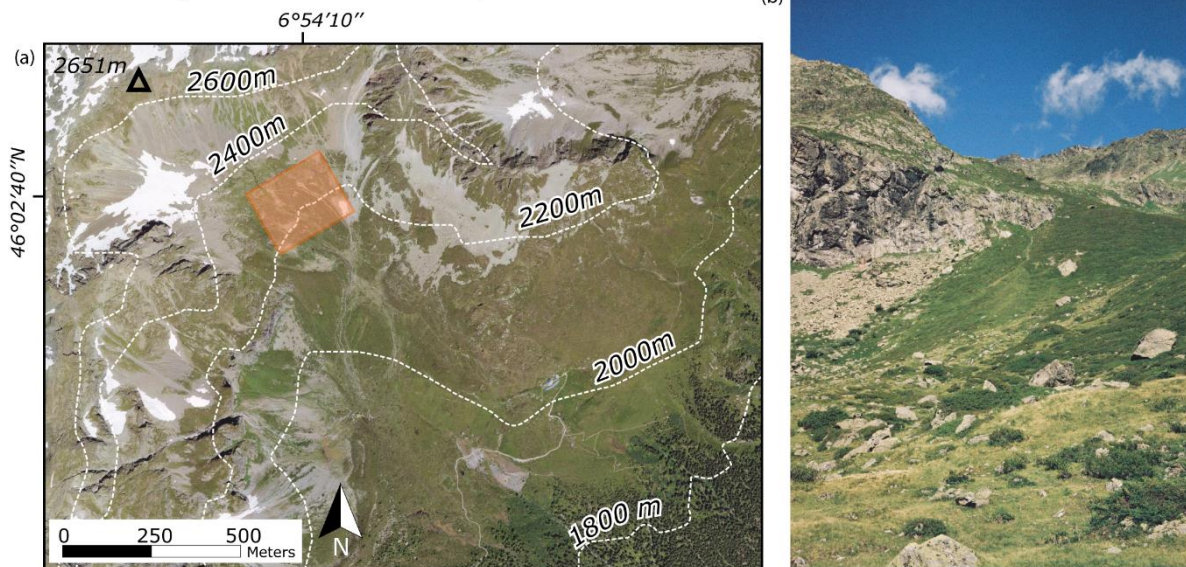
A l'échelle régionale, les sites d'étude (n=9) ont été sélectionnés pour prendre en compte la variabilité bioclimatique des Alpes françaises, depuis le massif du Queyras au sud jusqu'au massif du Mont-Blanc, au nord, en passant par l'Oisans et la Chartreuse, plus à l'ouest. Les caractéristiques climatiques de chaque massif sont présentées en figure 9a. Plus localement, à l'échelle du massif, ils ont été échantillonnés afin d'étudier les effets du gradient altitudinal (trois sites étagés dans le massif du Taillefer) ou du topoclimat (deux sites exposés N et O dans massif du Queyras) sur la croissance radiale (Figure 9 a, c, e).

Dans le cadre d'un travail de recherche de master (Francon, 2015), nous avons recensé l'ensemble des ligneux bas ayant une amplitude écologique suffisamment importante pour couvrir la tranche d'altitude décrite en figure 8 dans les Alpes. Sur la base de critères anatomiques (lisibilité des cernes de croissance), de longévité (potentiellement d'au moins 100 ans), d'abondance (large amplitude altitudinale et géographique) et d'importance écologique (espèce dominante au sein des communautés végétales alpines), nous avons identifié deux espèces, *Juniperus nana* et *Rhododendron ferrugineum*. Le potentiel dendroécologique de *J. nana* et plus généralement du genre *Juniperus* ayant été étudié dans différents contextes biogéographiques (Hallinger et al., 2010; Pellizzari et al., 2014, 2016), nous avons sélectionné *R. ferrugineum* L. (Ericaceae) pour tester nos hypothèses de recherche. Ce ligneux bas sempervirent, dont l'autoécologie est décrite en détail dans le chapitre 2, peut atteindre une taille de 70 cm. Il se développe en colonies clonales dont les individus peuvent atteindre potentiellement des âges supérieurs à 300 ans (Escaravage et al., 1998) ce qui le rend particulièrement intéressant pour une étude dendroécologique. Enfin *R. ferrugineum* forme des landes, classées d'intérêt communautaire (programme Natura 2000 : code 4060-4 ; CORINE biotope : code 31.42), localement très denses à l'étage subalpin dans les Alpes et dans les Pyrénées (Charrier et al., 2013; Larcher and Wagner, 2004; Pornon and Doche, 1995) mais on la retrouve également dans le nord des Apennins et dans le Jura.

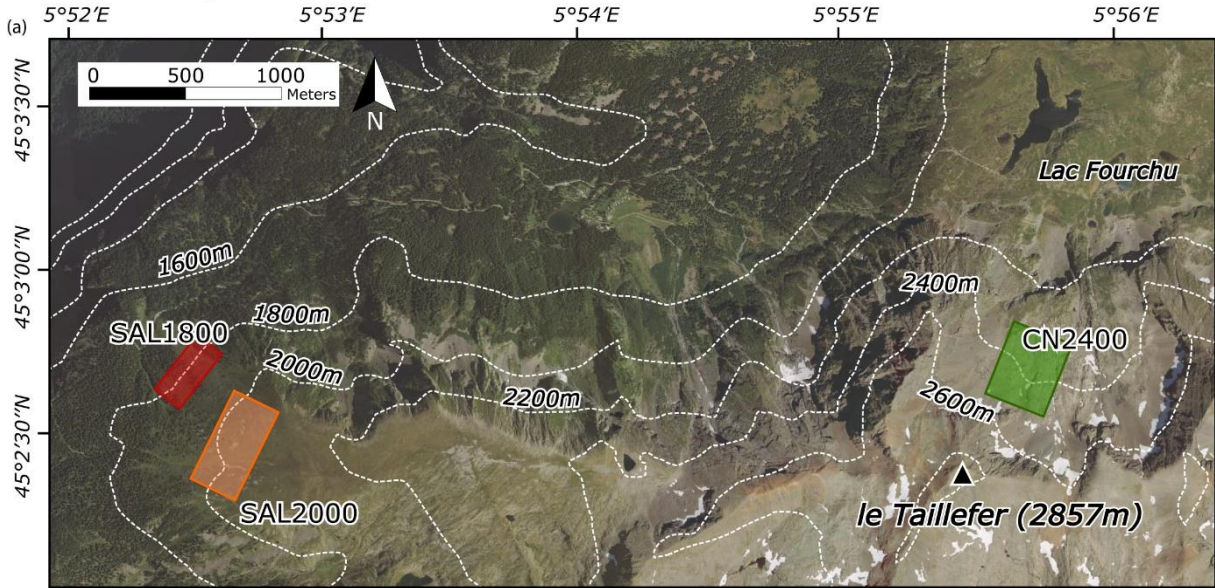
A- Localisation des sites d'étude et climat



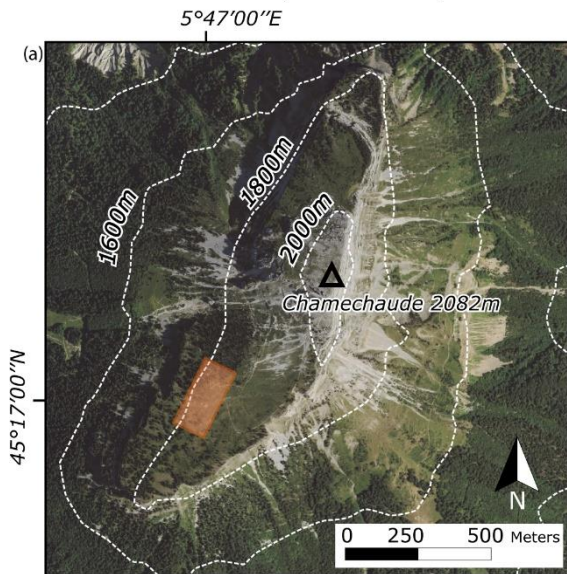
B- Loriaz (Massif du Mont-Blanc)



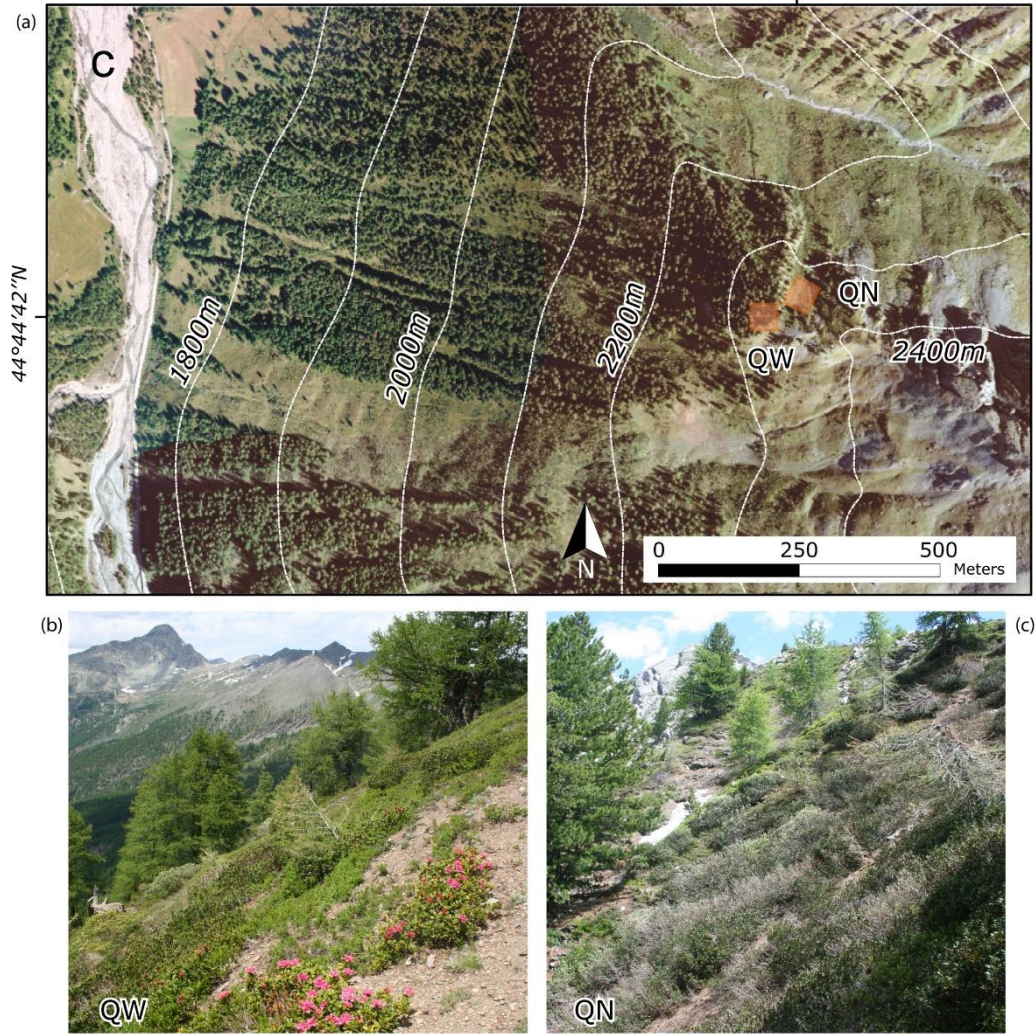
C- Taillefer (Oisans)



D- Chamechaude (Chartreuse)



E- Crête des Baysses (QW et QN, Massif du Queyras) 7°00'35"E



F- Crête de Gilly et sommet de la Lauzière (QGL, Massif du Queyras) 6°58'40"E

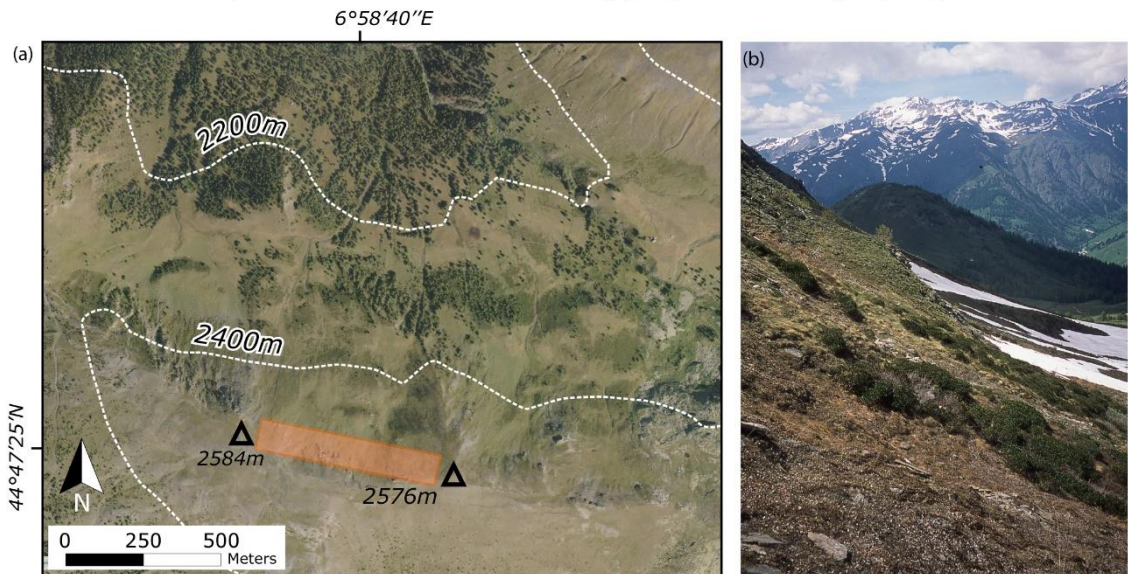


Figure 9 : Localisation et caractéristiques climatiques des huit sites étudiés

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Chapitre 1. Warm summers and moderate winter precipitation boost *Rhododendron ferrugineum* L. growth in the Taillefer massif (French Alps)

Les résultats présentés dans ce chapitre sont basés sur des échantillons récoltés dans le Massif du Taillefer. Les rhododendrons ont été récoltés à l'automne 2015 par Christophe Corona, Erwan Roussel, Séverine Finet, Jérôme Lopez-Saez, Robin Mainieri et moi-même. Les micro-sections ont été réalisées et photographiées à quatre mains, avec l'aide précieuse de Brigitte Girard, de l'UMR PIAF. J'ai également réalisé l'interdatation des différentes séries de largeurs de cernes, l'édification de la chronologie (la première chronologie de référence de *Rhododendron ferrugineum* pour les Alpes) et l'ensemble des analyses statistiques.

Ce chapitre est en totalité constitué de l'article publié dans la revue : *Science of the Total Environment* 586, 2017, 1020-1031.

Photographie de page précédente : échantillonnage d'un rhododendron, sur la Côte des Salières, dans le massif du Taillefer, à environ 2050 m d'altitude.

Warm summers and moderate winter precipitation boost *Rhododendron ferrugineum* L. growth in the Taillefer massif (French Alps)

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Abstract

Rhododendron ferrugineum L. is a widespread dwarf shrub species growing in high-elevation, alpine environments of the Western European Alps. For this reason, analysis of its growth rings offers unique opportunities to push current dendrochronological networks into extreme environments and way beyond the treeline. Given that different species of the same genus have been successfully used in tree-ring investigations, notably in the Himalayas where *Rhododendron* spp. has proven to be a reliable climate proxy, this study aims at (i) evaluating the dendroclimatological potential of *R. ferrugineum* and at (ii) determining the major limiting climate factor driving its growth. To this end, 154 cross-sections from 36 *R. ferrugineum* individuals have been sampled above local treelines and at elevations from 1800 to 2100m asl on northwest-facing slopes of the Taillefer massif (French Alps). We illustrate a 195-year-long standard chronology based on growth-ring records from 24 *R. ferrugineum* individuals, and document that the series is well-replicated for almost one century (1920-2015) with an Expressed Population Signal (EPS) >0.85. Analyses using partial and moving 3-months correlation functions further highlight that growth of *R. ferrugineum* is governed by temperatures during the growing season (May-July), with increasingly higher air temperatures favoring wider rings, a phenomenon which is well known from dwarf shrubs growing in circum-arctic tundra ecosystems. Similarly, the negative effect of January-February precipitation on radial growth of *R. ferrugineum*, already observed in the Alps on juniper shrubs, is interpreted as a result of shortened growing seasons following snowy winters. We conclude that the strong and unequivocal signals recorded in the fairly long *R. ferrugineum* chronologies can indeed be used for climate-growth studies as well as for the reconstruction of climatic fluctuations in Alpine regions beyond the upper limits of present-day forests.

Keywords

Tree-ring analysis; dwarf shrubs; *Rhododendron ferrugineum* L.; climate-growth correlations; winter precipitation.

1 Introduction

Tree-ring series are widely available at high latitudes and high altitudes across the northern hemisphere and represent the backbone of many annually resolved climate reconstructions of the Common Era (Intergovernmental Panel on Climate Change, 2014; Stoffel et al., 2015; Helama et al., 2016; Guillet et al., 2017). At the same time, and as a result of ongoing warming, arctic and alpine environments are also among the most sensitive regions when it comes to their reactions to climate change (Pauli et al., 2012; Gobiet et al., 2014). So far, however, assessments and time-series of changes in high altitude and high-latitude have been limited mostly to areas where trees (and their growth-ring series) are readily available. Despite the fact that beyond northern and alpine tree lines, other woody plants, such as dwarf shrubs, could be useful proxies for paleoclimate and paleoenvironmental reconstructions (Bär et al., 2008), their potential for dendroecological studies has only been explored more fully over the last decade (Myers-Smith et al., 2015b). Although the often extremely narrow rings and numerous anomalies in tree-ring formation making analysis of dwarf shrubs rather difficult and time-consuming (Bär et al., 2008), these pioneering studies also showed that shrub species indeed have a great potential to extend existing dendrochronological networks beyond limits and into extreme environments where trees cannot survive under the current climatic conditions (Liang and Eckstein, 2009). Annual growth rings in shrubs have thus been used among others to reconstruct the growing season climate in Arctic (Schmidt et al., 2006; Weijers et al., 2010; Rayback et al., 2012) or to explore the rapid climate warming in tundra biomes as a result of the increasing shrub dominance which in turn is related to the evolution of climate–growth relationships (Hallinger et al., 2010; Hollesen et al., 2015; Myers-Smith et al., 2015c).

By contrast to the large body of scientific literature on dwarf shrub studies using circumpolar species, one realizes that dendroecological work on high-elevation shrubs covering multi-decadal timescales remains scarce and that work exploring climate–growth relationships of dwarf shrubs in mountain environments is still largely missing. So far, published work focused mostly on the Tibetan plateau (Liang and Eckstein, 2009; Lu et al., 2015; Liang et al., 2012), the Central Norwegian Scandes (Bär et al., 2008) and the Sierra Nevada (Franklin, 2013). Only one dendroclimatological study has so far been dedicated to the detection of climate signals in shrub-ring chronologies in the Alps on *Juniperus communis* L. (Pellizzari et al., 2014a).

To fill this apparent gap and to explore the potential of European high-elevation dwarf shrubs for climate–shrub growth relationships, we directed our attention to *Rhododendron ferrugineum* L. (Ericaceae), an evergreen dwarf shrub with well-branched trailing stems and a height of up to 0.8 m. The species has a large geographic range of occurrence across the Alps (Ozenda, 1985) and is widespread at the subalpine level from about 1600 to 2200 m. In the northwestern Alps, it even forms large heathlands colonizing extensively grazed or abandoned meadows on north, west, and northwest-facing slopes (Escaravage et al., 1997) on which it apparently encounters the most favourable environmental conditions. Its abundance can also be explained by complementary sexual and vegetative

reproductive strategies (Doche et al., 2005), which enables *R. ferrugineum* to outcompete other plants (Pornon and Doche, 1996) and to reach a 90–100% cover after 150–250 years (Pornon and Doche, 1995). Based on a simple growth-ring count, (Schweingruber and Poschod, 2005) documented the existence of a 202-year-old *R. ferrugineum* individual in Central Switzerland, whereas genetic surveys have shown that some genotypes of this long-lived species are estimated to be >300 years old (Escaravage et al., 1998). Despite its (i) wide distribution, (ii) clearly identifiable annual rings as well as (iii) its longevity, neither its dendroecological potential nor its assumedly reliable climatic signal in its ring-width sequences has been studied so far.

In this context, the objectives of the study are threefold, and consist of (i) assessing the possibility to build a first, and reliable, *R. ferrugineum* ring-width chronology for the Alps; (ii) verifying the sensitivity of the species to climate; and of (iii) comparing *Rhododendron* growth to that of a typical high-elevation tree species in the Alps, namely *Picea abies* (L.) Karst., as this species is typically used in standard dendroecological investigations.

2 Material and Methods

2.1 Study site

Samples from *Rhododendron ferrugineum* L. and *Picea abies* (L.) Karst. were sampled at Côte des Salières (45°04'N, 5°88'E, Fig. 1), a site located in the Northern French Alps and within the northwest-facing slopes of the Taillefer massif. According to Ozenda et al. (1968) and Pautou et al. (1992), climate at the study site is reflective of a transition zone between the wettest oceanic pre-alpine environments (Chartreuse, Vercors), where the annual amount of precipitation exceeds 1600 mm at 1000 m asl, and the intra-alpine massif, characterized by a dryer continental climate with annual rainfall <800 mm at Briançon (1400 m asl) (Fig. 1). According to the HISTALP dataset (Chimani et al., 2011), precipitation at the gridded point closest to the study site (45°05'N, 5°85'E) is 1150 ± 200 mm yr⁻¹ for the period 1800–2003. At the same grid point, mean annual temperature is 3.3°C and mean May–August temperature is 9.9°C for the period 1780–2008 (Chimani et al., 2013). In the Taillefer massif, snow cover remains in place during 188 days on average, whereas mean snow depth is 66 cm at 1800 m asl. for the period 1959–2005 (Durand et al., 2009).

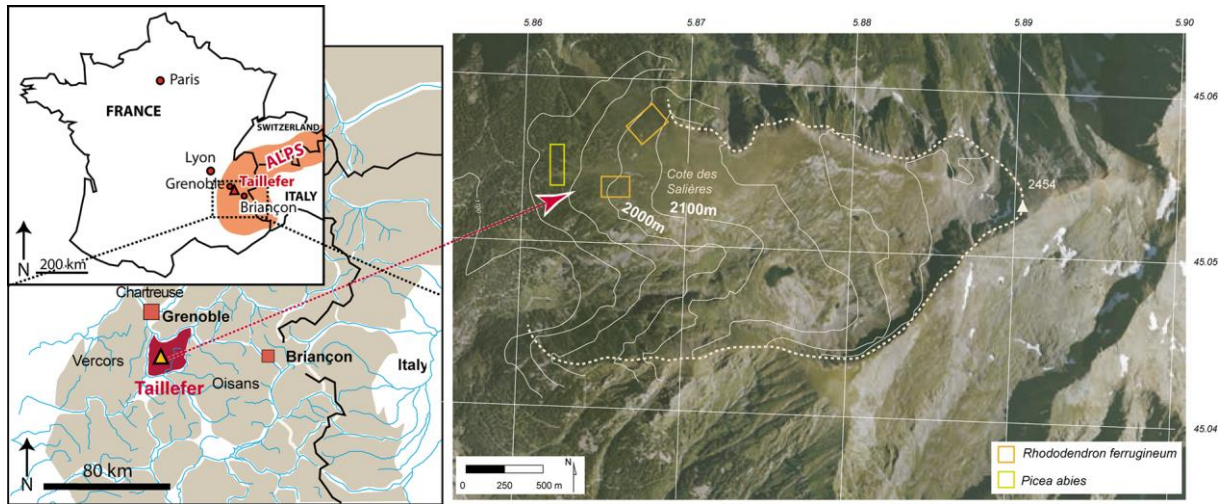


Figure 1: Location of the study site, called Côte des Salières (SAL, 45°04'N, 5°88'E) in the Massif du Taillefer (French Alps).

At Côte des Salières, *R. ferrugineum* and *P. abies* samples were collected within the upper subalpine belt, at the treeline ecotone (Holtmeier, 2009) between 1800 and 2100 m asl (Fig. 2). Slope angles range from 23° to 33°. Bedrock primarily consists of amphibolites and gneiss gabbros (Doche et al., 2005), whereas soils are stony ochre brown humic acid soils (Pornon et al., 1997). Monospecific stands of *Picea abies* dominate vegetation to elevations of up to 1850 m asl. The woody understory is mainly composed of *R. ferrugineum* and *Vaccinium myrtillus*. Above 1900 m asl, alpine dwarf shrub heathland has developed on abandoned pastures, dominated by a dense *R. ferrugineum* (80–100%) cover intermixed with individual *Sorbus aucuparia*, *Sorbus chamaemespilus*, and *Vaccinium myrtillus*, along with scattered *Picea abies* and *Pinus uncinata* trees. Significant geomorphic disturbances – related to e.g. snow avalanches or debris flows – are clearly absent.



Figure 2: (A) The sampling sites at treeline, more precisely between a *Picea abies* (L.) Karst. (black arrow head) and a *Rhododendron ferrugineum* L. heath. (white arrow head). (B) Illustration of the prostrate growth form of a *Rhododendron* individual growing at high elevation.

2.2 Sample collection and preparation

We randomly selected 36 *R. ferrugineum* individuals in fall 2015 above the treeline between 1900 and 2100 m asl. GPS coordinates with ± 1 m accuracy were recorded for each individual using a Trimble GeoExplorer. Two to six cross-sections per individual shrub were saw-cut with lengths each of 20–30 cm. Samples were taken from the main stems departing from the root collar, so that a so-called *serial-sectioning approach*, consisting of ring-width measurements and cross-dating at the intraplant level, can be applied. This approach has been first applied to shrub dendrochronology by Kolishchuk (1990) in an attempt to (i) improve ring-width dating through the identification of wedging and missing rings (Buchwal et al., 2013) as well as continuous missing outer rings which are more likely to occur in large sections of basal stems due to cambial age and growth forms (Wilmking et al., 2012); and to (ii) enhance the common signal and the correlation between individual tree-ring series. In addition, a total of 32 cores from 16 *P. abies* trees (two cores per tree) were taken at the same site using a Suunto increment borer at the lowest possible position on the tree in order to maximize the number of rings. Here, the purpose was to build a conventional tree-ring width chronology which could then be compared to the *R. ferrugineum* chronology.

In total, 106 *R. ferrugineum* micro-sections, with a thickness of ~ 15 – 20 μm , were obtained using a slide microtome, stained with a mixture of Safranin and Astra blue and permanently fixed on microslides using Canada balsam (Arbellay et al., 2012; Gärtner et al., 2015). High-resolution digital pictures were captured by a Carl Zeiss Axio Observer Z1 coupled to a Zeiss AxioCam MR R3 camera with 40–100 \times magnification. Individual images were then merged automatically to cover the entire cross-sections. This image merging has been performed with the Zeiss Zen 2011 software (<http://www.zeiss.com/microscopy/int/products/microscope-software/zen-lite.html>).

For *P. abies*, increment cores were mounted on a wooden support, air-dried and sanded with gradually finer sandpapers following standard dendrochronological procedures (Bräker, 2002), thus enhancing the appearance of ring borders and cell structures. Subsequently, the increment cores were scanned at a resolution of 1200 dpi with a high-resolution Epson 11000XL scanner.

2.3 Cross-dating and chronology development

For both species, tree-ring widths were measured from scanned images with the CooRecorder 7.6 software (Larsson, 2003). In the case of *R. ferrugineum*, ring widths were measured at two to three radii so as to detect wedging or missing rings, but also to enhance the cross-dating between different sections within the same individual. During this procedure, the fact of having as large as possible images of the entire section (rather than images of thin transects) greatly facilitated analysis and helped quite substantially in the detection of partially missing rings.

Radial measurements along chosen radii on individual *R. ferrugineum* samples were supplemented by a careful visual inspection of each cross-section so as to eliminate the risk of growth underestimation caused by partially missing rings. The principal three stages of cross-dating were based on a comparison of growth curves (i) between 2–3 radii measured within a single cross-section, (ii) among the mean growth curves of all the sections within the same individual and finally (iii) between the mean growth curves of all individual shrubs was done using Cdendro 7.3 (Larsson, 2003). Alignment of growth

curves was based on a visual comparison of positive and negative pointer years as described by Schweingruber (1988). Pointer years refer to cross-dated growth rings presenting common, yet conspicuous ringwidths such as exceptionally narrow or wide rings (Schweingruber et al., 1990). The visual cross-dating was then checked statistically in COFECHA (Holmes, 1994).

For *P. abies*, individual series coming from the same tree were cross-checked visually and statistically using Cdendro (Larsson, 2003), so as to check for potential counting errors or missing rings; samples were then corrected if necessary. Individual corrected series were then averaged into a single mean series per tree. In a second step, mean series of different trees were crossdated with one another and also checked for counting errors or missing rings using Cdendro and COFECHA.

Mean tree ring-width series were then detrended using the dplR package (Bunn, 2008) for R software (R Core Team, 2016) in order to eliminate non-climatic trends (e.g., age related growth trend and/or effect of natural or human-induced disturbances) and to maximize climatic information. The ring-width data from both species were standardized (Fritts, 1976; Cook and Kairiukstis, 1990) following an identical two-step procedure: a double-detrending process was applied based on (i) a negative exponential or linear regression, followed by (ii) a fitting of a cubic smoothing spline with a 50% frequency response at 32 years (Cook and Peters, 1981). Dimensionless indices were obtained by dividing the observed ring-width value by the predicted value. This process allowed the creation of stationary time series for each individual tree with a mean of 1 and a homogeneous variance. Finally, and for each species, growth indices were averaged by year using a bi-weight robust mean which reduces the influence of outliers (Cook and Peters, 1981). They also allowed the development of mean standardized chronologies (SalRf and SalPa for *Rhododendron ferrugineum* L. and *Picea abies* (L.) Karst., respectively) which represent the common high-frequency variation of the individual series (Cook, 1987).

By means of several descriptive statistics – commonly used in dendrochronology – the two species chronologies were compared. These statistics included standard deviation (SD), which estimates the variability of measurements for the whole series; mean sensitivity (MS), which is an indicator of the mean relative change between consecutive ring widths and is calculated as the absolute difference between consecutive indices divided by their mean value, mean RBAR, which is a measure of the common variance between the single series in a chronology and first order autocorrelation (Auto Corr), a measure of the influence of previous year's conditions on the following ring formation (Fritts 1976). The Expressed Population Signal (EPS) was calculated for both the SalRf and SalPa chronologies to indicate the level of coherence of the constructed chronology and to illustrate how it portrays the hypothetical perfect population chronology that has been infinitely replicated from the individual series composing the chronology (Briffa, 1995). The running RBAR and running EPS were computed using a 30-year moving window for both species. Their values illustrate changes in the strength of common patterns of tree growth over time. The commonly accepted EPS threshold of 0.85 (Wigley et al., 1984) is the limit at which tree-ring widths chronologies were considered as reliable and well replicated.

2.4 Climate-growth analysis

The *R. ferrugineum* and *P. abies* chronologies were regressed against mean monthly air temperature (°C) and monthly precipitation totals (mm) using values from the HISTALP dataset. At the grid point

45°05'N, 5°85'E, monthly mean temperature and precipitation totals exhibit statistically significant correlations (wrt. 1920-2003, $p < 0.01$) in May (-0.76), June (-0.73), July (-0.77), August (-0.75), September (-0.76) and October (-0.70).

The exploration of climate–growth relationships between climatic parameters and the *R. ferrugineum* and *P. abies* chronologies was conducted in three methodological steps. First, partial and moving 3-months correlation functions were computed using the seasonal correlation procedure (SEASCORR) developed by Meko et al. (2011) to disentangle confounding influences of correlated climatic variables. SEASCORR in fact correlates tree-ring series with a primary climate variable (i.e., temperature) and uses partial correlations to investigate a secondary variable (i.e., precipitation) controlling for the influence of the primary variable. We selected temperature as the primary variable because previous works examining climate controls on trees at high-altitude sites in the Alps have identified temperature as a key driver (Büntgen et al., 2006; Corona et al., 2011; Saulnier et al., 2011). We then used individual monthly as well as seasonal values integrating three consecutive months (e.g. DJF, MAM, JJA, SON). We considered a 14-month window, thus assessing a period extending from September of the year preceding growth-ring formation ($n-1$) to October of the year of actual ring formation (n); this approach therefore results in a dataset of 28 climatic variables being analyzed. Confidence intervals for all correlations were estimated by using Monte Carlo simulations of the tree-ring series (Percival and Constantine, 2006). The Bonferroni method was used for multiple comparison correction of the significance levels (Hochberg, 1988).

In a second step, we (i) tested whether the significant growth-climate relationships detected during the SEASCORR analyses are indeed reliable across regional-scale climate variability and (ii) identify potential large-scale forcing effects on tree growth. To this end, we correlated the tree and shrub chronology data with mean monthly temperature and precipitation totals from the HISTALP gridded dataset for all grid cells available in a user-defined region (43-46°N, 4-18°E) and over the time period 1920–2003. Analyses were conducted with the KNMI Climate Explorer (Royal Netherlands Meteorological Institute; <http://www.climexp.knmi.nl>, van Oldenborgh et al. (2009)).

Lastly, we categorized calendar years as pointer years if at least 50% of the cross-dated *R. ferrugineum* and *P. abies* individuals presented an absolute value of radial growth variation exceeding 40% (Mérian and Lebourgeois, 2011). In this study, radial growth variation (RGV) is an expression of the degree to which the ring of the current year (n) is narrower (negative value) or wider (positive value) than the previous ring ($n-1$). The RGV was calculated using the following equation:

$$RGV_n = 100 * \frac{RW_n - RW_{n-1}}{RW_{n-1}} \quad (1)$$

where RW_n is the ring width in year n , and RW_{n-1} indicates ring width of the previous year. The negative pointer years detected in SalRf and SalPa were compared to records of temperature and precipitation from the HISTALP database for the period extending from September ($n-1$) to October (n).

3 Results

3.1 Wood anatomical characteristics of *Rhododendron ferrugineum* L.

High-resolution digital pictures from cross-sections display distinctly visible growth rings are annual as a result of the strong climatic seasonality in this alpine ecotone. Growth-ring boundaries are clearly visible and can be discriminated by a band of radially aligned, thick-walled latewood fibers, flattened along the ring boundary. The flattened fibers are in a sharp contrast to the high density of vessels in the remainder of the ring. Ring widths range between 0.1 and 0.3 mm and are rather uniform around the circumference, thus revealing that one-sided, mechanical stress had a rather weak influence on radial growth, at least in the stems selected for this analysis. Despite this concentricity, wedging rings – which often correspond to missing ring in some other parts of the same plant – were rather common. The proportion of completely missing rings was, by contrast, much smaller and only accounted for 2.3%.

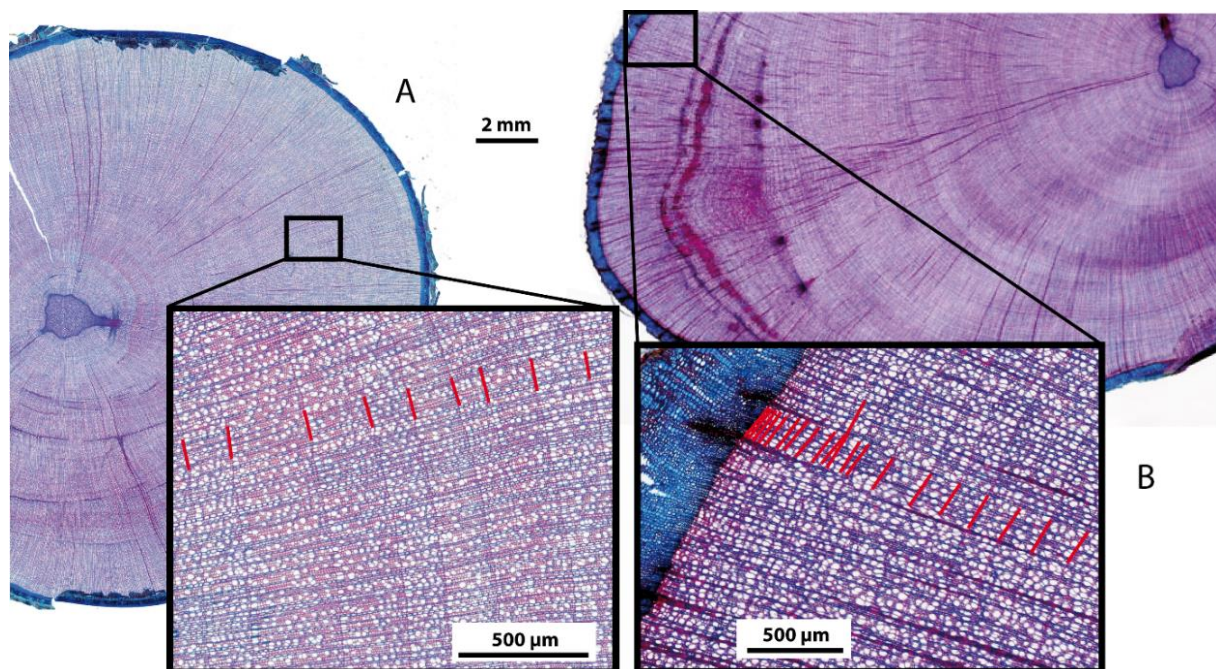


Figure 3 : Examples of cross-sections of *Rhododendron ferrugineum* L.. (A) Individuals showing wide, distinct, and concentric rings as well as (B) eccentric, narrow and wedging rings, in the latter case on a cross-section exhibiting 195 growth rings.

3.2 Cross-dating and chronology statistics

Based on the assessment of 24 individuals (69 sections, rejection rate: 33%), we were able to build a *R. ferrugineum* chronology for the Côte des Salières covering the period 1821–2015 (Fig. 4A). The mean age of individuals included is 91 years, but we counted 195 growth rings on the oldest *R. ferrugineum* individual. By comparison, the *P. abies* chronology was obtained from 16 trees (rejection rate: 0%, mean age of trees: 144 years) and spans 216 years, i.e. the period from 1800–2015, with SalRf being characterized by a high common signal represented by an overall RBAR of 0.41 and an average mean sensitivity of 0.3. The expressed population signal (EPS), which is a function of the mean inter-series correlation and series replication, varied from 0.71 to 0.96 (mean = 0.88) and exceeds the threshold of

0.85 ever since 1920 (Fig. 4A). Figure 4B denotes the temporal signal strength of SalPa. Except for the period 1800–1887, during which the sample replication is <10 series, EPS (mean: 0.89) and RBAR (mean: 0.44) values point to internal consistency (EPS>0.85) in common variance between 1887 and 2015. The mean sensitivity (MS) of the SalPa series shows values of 0.17, which are significantly lower than those obtained for SalRf. The correlation coefficient between SalRf and SalPa is 0.4 ($p<0.05$) for the 1920-2015 common period characterized by EPS values >0.85.

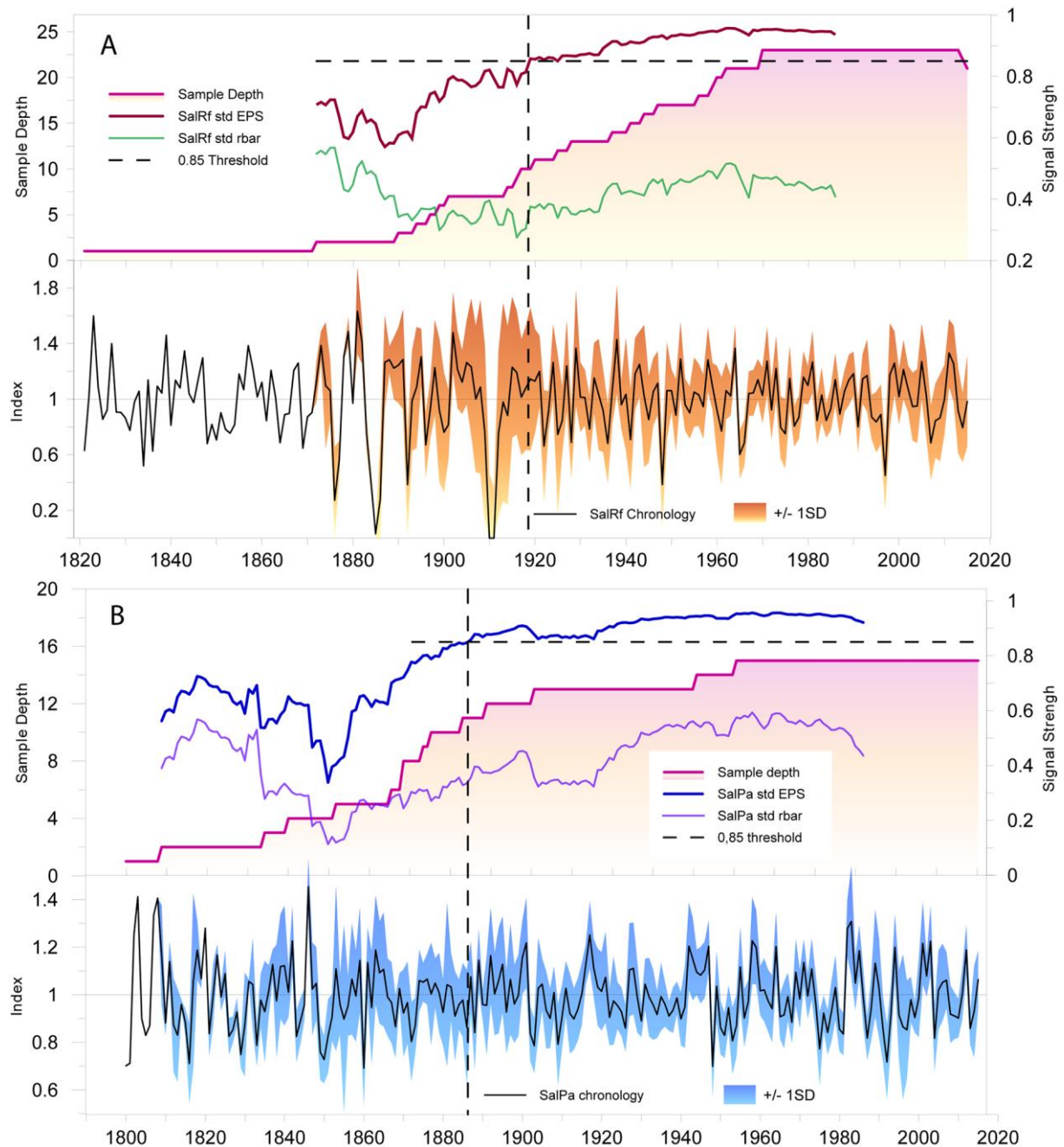


Figure 4: Standard growth-ring chronology of (A) *Rhododendron ferrugineum* L. and (B) *Picea abies* (L.) Karst at Côte des Salières. Sample depth, running Expressed Population Signal (EPS) and common variance between single tree-ring series in a chronology (RBAR) are computed using a 30-year moving window. Horizontal lines indicate sample depth. The EPS threshold value of 0.85 is passed to the right of the dashed vertical lines (For values exceeding 0.85, a chronology is considered well replicated and reliable).

Table 1: Characteristics of standard *R. ferrugineum* and *P. abies* ring-width chronologies: length, standard deviation, mean sensitivity, first order autocorrelation and signal strength along the entire chronology (i.e. Rbar and EPS).

Species	First Year	Last Year	Year EPS > 0.85	Mean length	Length	Stand. Dev.	Mean Sens.	Auto Corr.	Rbar	EPS
<i>R. ferrugineum</i>	1821	2015	1919	81	195	0.27	0.30	0.224	0.41	0.88
<i>P. abies</i>	1800	2015	1887	144	216	0.14	0.14	0.165	0.44	0.89

3.3 Monthly and moving 3-months climate correlations

Partial and moving 3-months correlation functions using monthly mean temperature and monthly totals from September of the year preceding ring formation (n-1) to October of the year of ring formation (n) as climatic variables are presented for *R. ferrugineum* and *P. abies*, respectively (Figs. 5A and 5B). With respect to monthly values, a significant positive correlation ($p < 0.05$; 1920-2003) is observed between the *R. ferrugineum* ring-width chronology and current May (0.29) and July (0.23) mean temperatures. Significant seasonal (3-months) correlations are also consistently identified for growing season temperatures (MJJ, 0.33). In addition, correlation profiles evidence positive values between SalRf and temperature for September (n-1) (0.24, $p < 0.05$). With respect to monthly and seasonal precipitation totals, significant negative correlation coefficients are found between the standardized *R. ferrugineum* chronology and precipitation totals of January (-0.25, $p < 0.05$) and more generally of early winter (i.e. NDJ and DJF, -0.29 and -0.29 respectively, $p < 0.05$).

P. abies and *R. ferrugineum* correlation profiles are similar for the current (i.e. April-September) growing season. Significant positive correlations between *P. abies* radial growth and mean air temperature are computed for June (n) and July (n), peaking in July (n) (0.44, $p < 0.05$). In sharp contrast to *R. ferrugineum*, *P. abies* does neither show any sensitivity towards winter and summer precipitation nor does it react to conditions occurring at the end of the growing period (i.e. in autumn of year n).

3.4 Existence of a regional climatic signal in the SalRf chronology

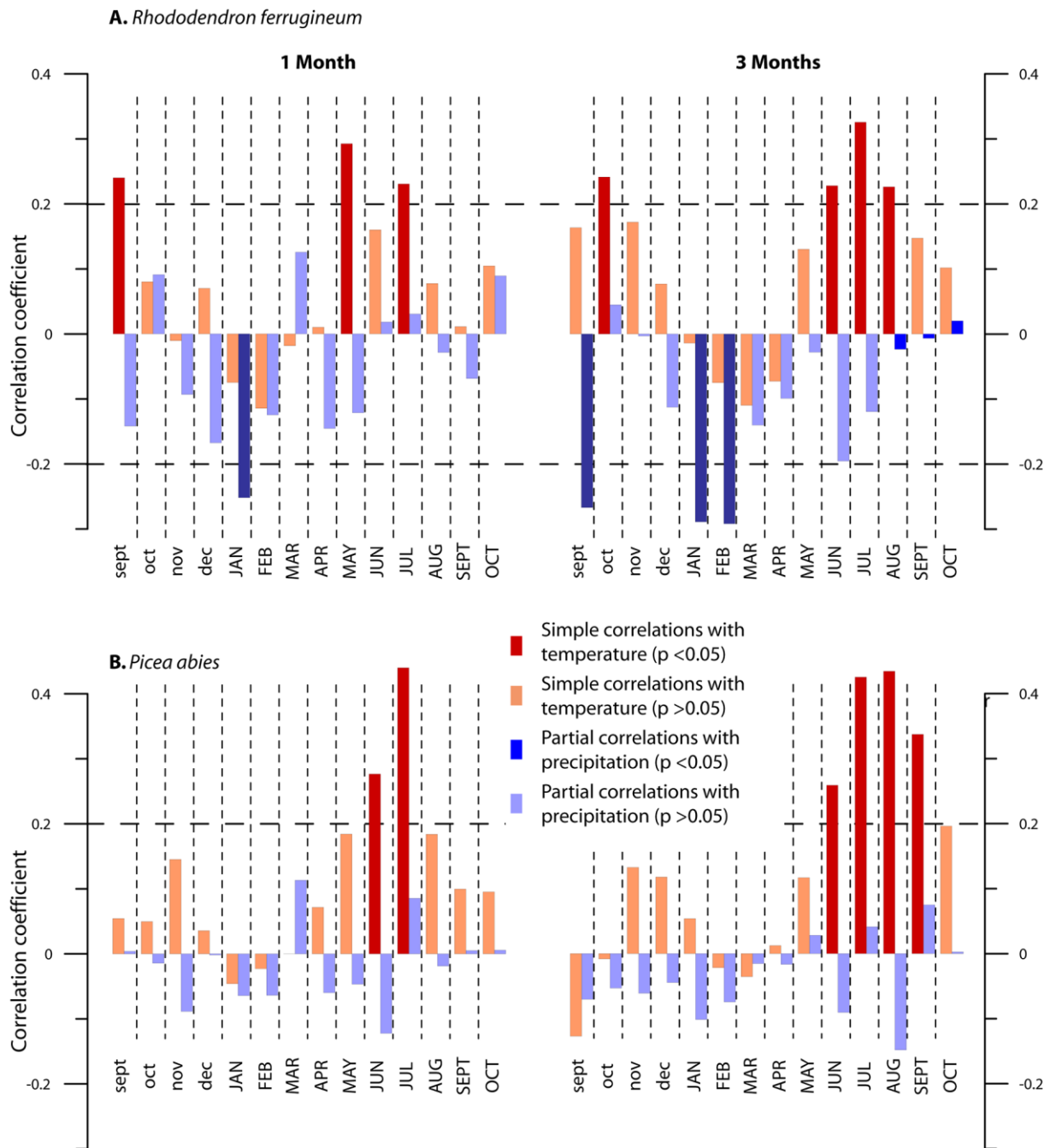


Figure 5 : Monthly and moving 3-months correlation functions (SEASCORR) analysis between the *R. ferrugineum* (A, top panel) and *P. abies* (B, bottom panel) chronologies, with monthly mean temperatures and monthly precipitation totals for the period 1920–2003. Simple correlations of tree-ring indices were computed for the primary climate variable (temperature), whereas partial correlations were determined for the secondary climate variable (precipitation).

Correlations coefficients ($p < 0.05$) computed between the SalRf and SalPa chronologies and the gridded HISTALP (43–46°N, 4°–18°E) current May (n)–July (n) mean air temperatures, as well as previous December (n–1)–current February (n) and current May (n)–July (n) precipitation totals are mapped for the period 1920–2003 (Fig. 6). Longer-range correlations obtained with mean air temperatures exceed those derived from precipitation totals. Both chronologies show similar correlation patterns with current May–July mean temperatures throughout a large part of the Greater Alpine Region (Fig 6A, B). In the case of SalPa, a stronger temperature signal ($0.4 < r < 0.5$) extends from the French Alps to the westernmost parts of the Austrian Alps, this signal ($0.4 < r < 0.3$) is weaker for SalRf.

The precipitation field represented by the SalRf and SalPa data shows generally lower correlations as compared to those derived for mean air temperatures. The spatial correlation patterns with gridded precipitation also differ between species. The SalRf chronology is associated with a winter precipitation field north of approximately 43–49° latitude and with a 4–10°E west-east extension; the core region of the precipitation field is slightly smaller (44–46.5°N, 4–6°E) and centered over the French Alps ($r > 0.3$, $p < 0.05$, Fig. 6C). The SalPa chronology does not, by contrast, show any significant correlation with previous December (n–1) – current February (n) precipitation totals (Fig. 6D).

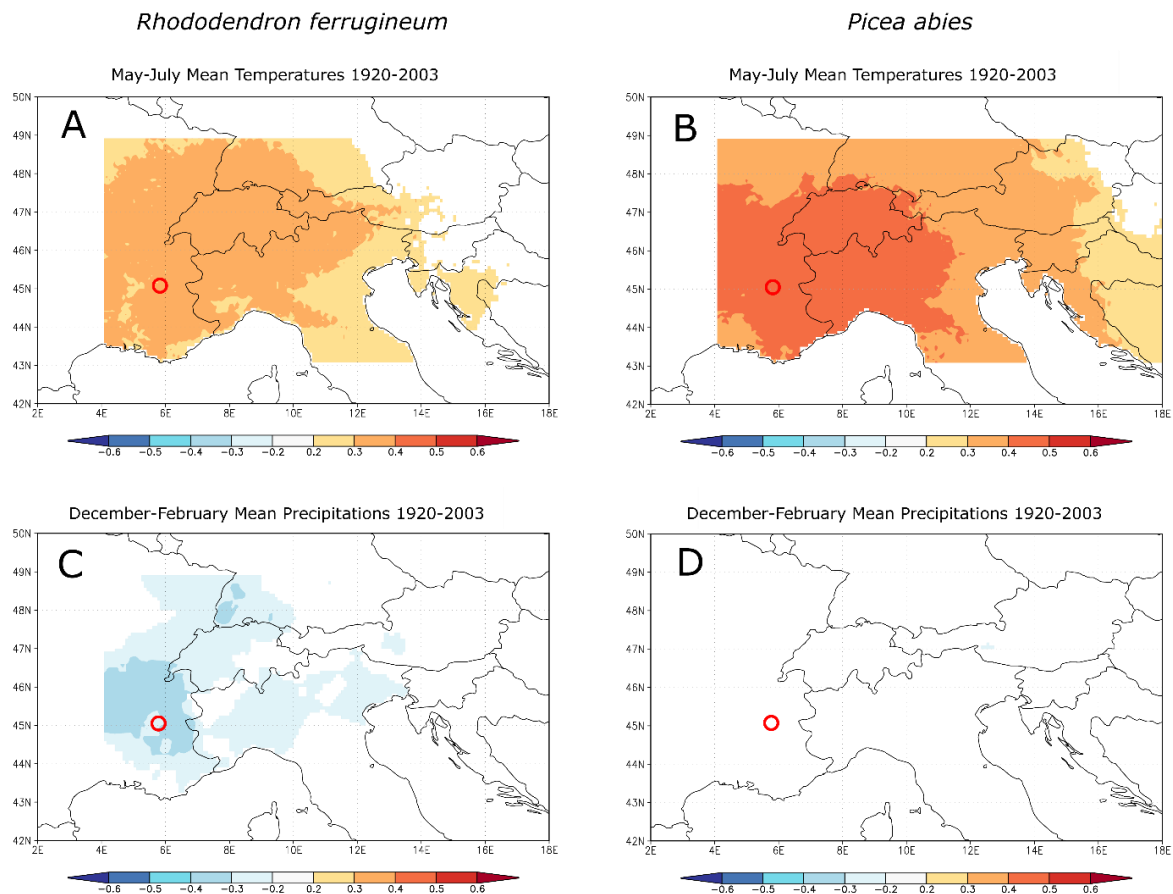


Figure 6: Spatial correlations ($p < 0.05$) between *R. ferrugineum* (left panel) and *P. abies* (right panel) standard ring-width chronologies and current (n) May–July temperatures (A–B), previous (n–1) December – current (n) February (C–D). Red dots correspond to the location of the study site SAL. Data consist of gridded (5' × 5' lat/long) surface temperatures and have been extracted from the HISTALP dataset (available at <http://www.zamg.ac.at/histalp>).

3.5 Climate during extreme years

For either chronology, years with negative indices – i.e. years where at least 50% of the cross-dated trees presented an absolute value of radial growth variation exceeding 40% – were categorized as extreme and compared to meteorological records of the HISTALP database. The SalRf chronology shows negative pointer years in 1922, 1928, 1948, 1965, and 1997 (Fig. 7). Conversely, the *P. abies* population only shows 1948 as a negative pointer year. Both species exhibit the sharpest and most widespread growth decline in 1948 when 76.5% of the *R. ferrugineum* individuals show a mean RGV of -62.1% and half of the *P. abies* individuals show a RGV of -41%. When compared with monthly data from the HISTALP database, these extremes can be explained by below-average precipitation totals during at least 2–3 winter months. By way of example, precipitation deficits were most significant in 1997 (February-March: -156 mm, February-April: -197 mm), 1948 (February-March: -180 mm), 1965 (January-February: -97 mm) and 1928 (November-December: -161mm). For the years 1948 and 1997, the effect of precipitation deficits was further enhanced by above-average mean air temperatures between January and May (+1.6 and +1.8°C, respectively).

Temperature during the growing season did not apparently have a significant impact on radial growth in the years mentioned above, as no specific climatic parameter could be isolated to explain these pointer years. Whereas negative growing season (May-September) mean air temperature anomalies prevailed in 1948 (-0.7°C wrt 1961-1990) and 1965 (-0.75°C), we note fairly mild conditions during the extreme pointer year of 1928 (+0.6°C) and 1997 (+0.7°C).

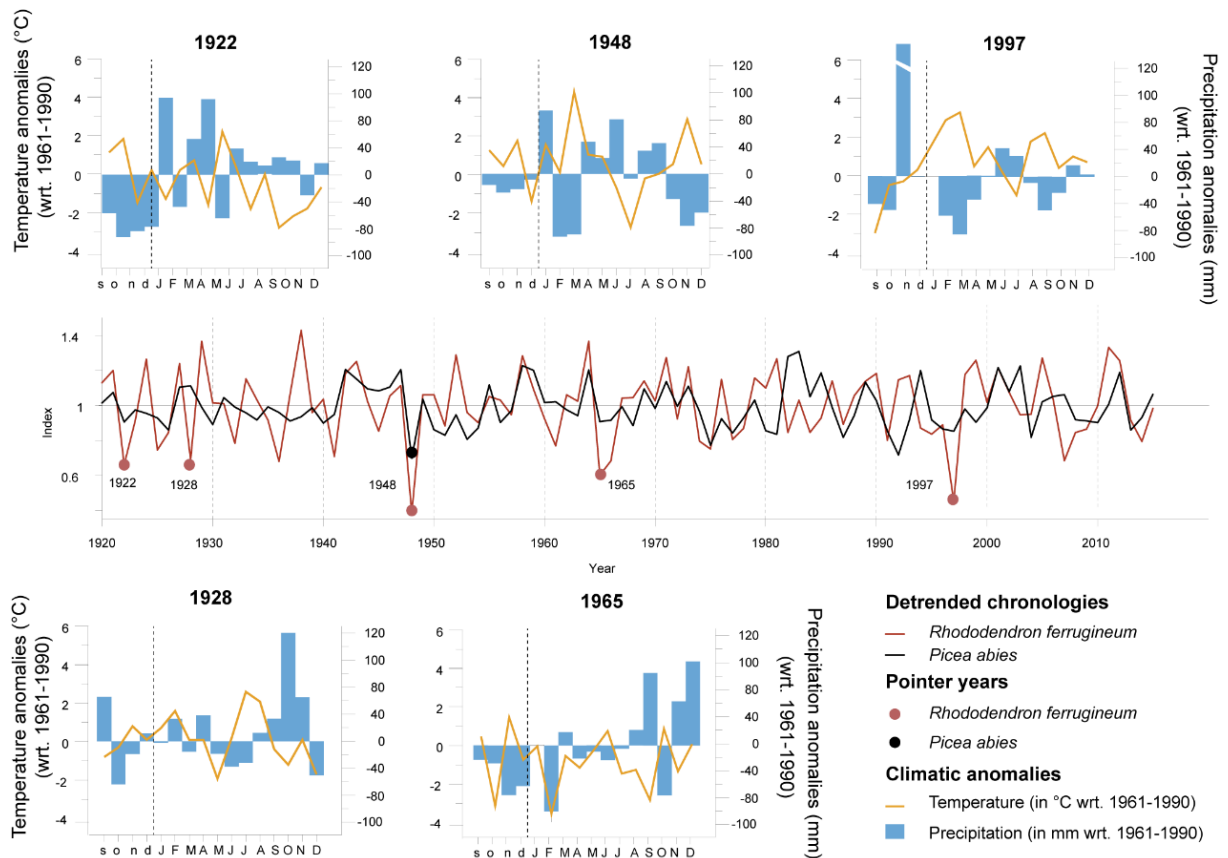


Figure 7: *Rhododendron ferrugineum* and *Picea abies* detrended chronologies and climatic diagrams of negative extreme years.

4 Discussion

4.1 Chronology quality

We present one of the first dendroclimatic investigations from a dwarf shrub in the European Alps and the longest record for a Western European high-altitude species so far. From 24 individuals of *Rhododendron ferrugineum* L., a rather widespread dwarf shrub growing close and above treeline we were able to build a solid reference chronology ($EPS > 0.85$) extending back to the early decades of the 20th century (1920-2015) and responding to summer temperatures and early winter precipitation totals.

At our study site, located around 2000 m asl in the French Alps, *R. ferrugineum* is characterized by rather low growth rates, even lower than those obtained for *R. przewalskii* in the Miyaluo Forest Region (Li et al., 2013), *R. aganniphum* (Lu et al., 2015) or *R. nivale* on the south-eastern Tibetan Plateau (Liang and Eckstein, 2009). In addition, we observe that wedging or completely missing rings are common in our samples and likely related to the limited length of the growing season as well as to limited resource availability during certain years (Hallinger et al., 2010). Despite these difficulties, a detailed serial sectioning and cross-dating analysis at the shrub level enabled the development of a robust ring-width chronology with relatively high values for the mean inter-series correlation ($RBAR = 0.41$), therefore confirming a common high frequency variance (Fritts, 1976) in the SalRf record. Interestingly, the mean sensitivity of SalRf is significantly larger than that of SalPa and also exceeds values obtained for other

Rhododendron spp in the Himalaya (0.21, 0.14-0.19 and 0.12 for *R. przewalskii*, *R. aganniphum* and *R. nivale*, respectively). MS at our study site is comparable to values reported for the only other dwarf shrub chronology published for the Alpine space, *Juniperus communis* (Pellizzari et al., 2014a). Nevertheless, it remains generally lower than those of the majority of other shrub chronologies assembled to date in subarctic regions, where e.g. *Salix* spp (Schmidt et al., 2006; Blok et al., 2011), *Betula nana* (Blok et al., 2011), or *Juniperus nana* (Hallinger et al., 2010) exhibited mean sensitivity values $MS > 0.4$, thereby suggesting that tree-ring width in the Taillefer massif did not vary to the same degree from year to year as in the subarctic shrublands.

4.2 Radial growth sensitivity to growing season temperatures and length

We realize that radial growth of *R. ferrugineum* in the Taillefer massif portrays a statistically significant coherence with average temperatures during the growing season on a regional scale. A rather similar dependence on average temperatures during the growing season is observed for SalPa, but also for other networks of conifer tree chronologies sampled at treeline sites across the French Alps (Corona et al., 2010; Petitcolas, 1998; Rolland et al., 1998; Saulnier et al., 2011). The same coherence with growing season temperatures is also apparent in various *R. ferrugineum* chronologies from the Himalayas (Li et al., 2013; Liang and Eckstein, 2009; Lu et al., 2015) as well as for dwarf shrub chronologies sampled across 37 arctic and alpine sites across the Northern Hemisphere (Myers-Smith et al., 2015a). Table 2 synthesizes the monthly climate-growth correlations (from previous (n-1) September to current (n) October) found in previously published dendroecological studies and classify results according to study regions going from driest to wettest. The data in Table 2 confirm the strong correlations between shrub growth and summer temperatures at the much colder and drier Arctic sites (Myers-Smith et al., 2015a), but also points to much weaker correlations between shrub chronologies and summer temperatures in typically wetter mountain environments (Li et al., 2013; Pellizzari et al., 2014b).

Partial correlations reveal the predominant role of temperature (May) in driving radial growth of *R. ferrugineum*. This statistical evidence is in good agreement with observations on *Rhododendron aganniphum* cambial activity (Li et al., 2016) and shoot development. In fact, Pornon et al. (1997) demonstrated that shoot development started around mid-June in 1991 and 1992 in the Taillefer massif. Furthermore, higher temperatures in May will favor faster snowmelt. We thus hypothesize that snowmelt indeed modulates the length of the growing season in *R. ferrugineum* and that early snowmelt can effectively boost radial growth. Similar beneficial effects of early snowmelt have been reported for other dwarf shrub species, such as *Juniperus communis*, in the Italian Alps (Pellizzari et al., 2014a). Based on data from experimental plots, in which advanced snowmelt was simulated artificially, *Vaccinium myrtillus* reacted with increased growth to mild winter conditions as well (Rixen et al., 2010), therefore adding further evidence to our hypothesis.

Table 2 : Comparisons of shrub chronology responses to climate parameters as published in past studies. The different types of environments are named DA (dry Arctic), HM (high mountain), and O (oceanic). The annual amounts of precipitation are given as well (in mm). Very significant, positive correlations, significant positive correlations and significant negative correlations are respectively indicated with (++; +; -). Grey boxes point to lacking data.

Authors - Year of publication - studied species		Zalatan and Gajewski, 2006 <i>Salix alaxensis</i>	Buchwal et al. 2013 <i>Salix polaris</i>	Block et al. 2011 <i>Salix puchra</i>	<i>Betula nana</i>	Hollesen 2015 <i>Betula nana</i>	Hallinger et al. 2010 <i>Juniperus nana</i>	<i>Empetrum hermaphroditum</i>	Forbes et al. 2010 <i>Salix lanata</i>	Au and tardif, 2007 <i>Dryas integrifolia</i>	Jorgensen et al. 2014 <i>Alnus viridis</i>	<i>Salix glauca</i>	Ropars et al. 2015 <i>Betula glandulosa</i>	Liang et al. <i>Juniperus</i> spp	Lu et al. 2015 <i>Rhododendron</i> . Spp.	Li et al. 2013 <i>Rhododendron</i> . Spp.	Liang and Eckstein 2009. R. spp.	Pellizzari et al. 2014 <i>Juniperus communis</i>	Franklin 2013 <i>Linarthus pungens</i>	Bei et al. 2015 <i>Calluna vulgaris</i>	Our study <i>R. ferrugineum</i>			
Type of env.		DA	DA	DA	DA	DA	DA	DA	DA	DA	DA	DA	DA	HM	HM	HM	HM	HM	HM	O	HM			
mean annual prec.		162	184	203	same study	273	310	300 to 400	419	432	445	same study	460	312	672	600 to 1000	836	600 to 1200	1500	1330	1200 to 1800			
MONTH	S	T																						
		P											+						+				+	
	O	T																						
		P											+											
	N	T																						
		P		+															+					
	D	T																						
		P	+				+																	
	J	T																						
		P																						
	F	T																						
		P																						
	M	T																						
		P	+											++										
	A	T																						
		P												+										
M	T																							
	P																							
J	T		++	+	+	+	++	++					+	+	+								+	
	P		-																					
J	T		++	+	+	+	++	++	++				+	+	++								+	
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The climatic conditions prevailing at the end of the summer and in early fall (temperature in September) are also determinant for radial growth during the next growing season. A similar dependence of radial growth on fall temperatures have been reported for *Rhododendron nivale* growing on the Tibetan Plateau (Liang and Eckstein, 2009). The authors state that negative correlations between growth-ring width – along with cold and dry conditions in preceding November should be attributed to frost damage to leaves and buds which in turn would reduce root activity or increase the risk of frost-induced desiccation. As a consequence, subsequent defoliation and bud mortality would thus deplete the carbon reservoirs and growth hormones and thereby reduce the shrub’s potential for further growth and photosynthetic activity.

Apart from *R. nivale*, sensitivity of dwarf shrubs to climatic conditions in early fall have been reported for no other species growing in mountain regions, and thus have to be investigated in future work. Even if comparable studies lack for dwarf shrubs, some literature on the positive effect of previous fall temperatures on radial growth exist in studies focusing on different European conifer species

(Oberhuber, 2004; Carrer et al., 2010; Babst et al., 2012). In the alpine treeline ecotone, Oberhuber (2004) and Oberhuber et al. (2008), for instance demonstrated that *Pinus cembra* trees indeed benefit of warm autumns as unusually mild temperatures will promote mycorrhizal association by maintaining soils above freezing, and will thus also favor maturation of buds against detrimental effects of winter stress. Moreover, some authors assume that high photosynthesis rates late in the fall could lead to high carbon storage and thus to increased growth in the following year (Fritts, 1976; Babst et al., 2012).

4.3 Contrasted impacts of winter precipitations on radial growth of *R. ferrugineum*

We have also shown that significant negative correlations exist between SaIRf and early winter precipitation totals (i.e. previous (n-1) December-January), both at the local and regional scales. Similar responses have been reported for shrub species and chronologies, such as *Salix arctica* in Greenland (Schmidt et al., 2006, 2010), *Linanthus pungens* in the Sierra Nevada, (Franklin, 2013), or *Juniperus communis* in the Italian Alps (Pellizzari et al., 2014a) (Table 2). We assume that the extensive and long-lasting snow cover could have a detrimental effect on radial growth of *R. ferrugineum* at our site through (i) cooler soil temperatures (Pellizzari et al., 2014), (ii) a shortening of the growing season and (iii) possible delays in the onset of cambial activity at the start of the new growing season, or (iv) even through lower amounts of growing degree-days (Vaganov et al., 1999; Blok et al., 2011), which will then be traceable in reduced radial growth of *R. ferrugineum*. In our study, the tree-ring width chronology of *Picea abies* trees does not exhibit this winter signal which tends to validate the hypothesis of physical effects of the snow cover which in fact filter incoming solar radiation (blocking photosynthesis), rather than the collateral reduction in soil temperature (Pellizzari et al., 2014a).

As a consequence, the sensitivity of our dwarf shrub species to winter precipitation differs quite sharply from studies in the very dry Arctic (162 mm.yr^{-1}) and Himalayan (210 mm.year^{-1}) environments (Zalatan and Gajewski, 2006; Liang et al., 2012) (Table 2) where the positive effects of a thicker snowpack will favor radial growth in shrubs (*Salix alaxensis* and *Juniperus pingii*) as a result of the thermic protective effect against frost (Neuner, 2007) and/or winter desiccation (Sakai and Larcher, 1987). Other studies from these dry sites interpreted the positive effects of a thicker snow cover on radial growth as a result of increased active permafrost layer depth and soil nutrient concentrations during the spring season (Nowinski et al., 2010) which may in turn favor further shrub growth and could thus create positive feedback loops (Sturm et al., 2005; Hallinger et al., 2010; Blok et al., 2011). In the absence of permafrost, however, the mechanisms described above cannot be used to explain enhanced or reduced radial growth in dwarf shrubs in the Alps.

Nevertheless, we observe that several years with very narrow rings in the SaIRf chronology coincide with extremely dry winters. Compared to the 1920-2003 mean December-February (DF) precipitation totals, this observation is particularly true for the three last pointer years (1948, 1965 and 1997) for which DF precipitation was significantly lower (131mm vs 234 mm, $p < 0.05$). In 1922 the occurrence of a pointer year is coherent with negative precipitation anomalies in November-December months. Only 1928 does not show a dry winter. One should, however, keep in mind that (i) this pointer year is least marked in terms of radial growth variations of the all five pointer years described, (ii) the chronology in 1928 is built with only 13 individuals, and (iii) the precipitation dataset could be

inaccurate due to the quality of the measurements back in time and heterogeneity of the precipitation distribution.

For the 1922, 1948, 1965 and 1997 pointer years, we explain this apparent discrepancy with monthly correlations by the increase of winter stress during periods with insufficient snow cover. As winter stress cannot be regarded simply as a number of single stressor-response incidents (Neuner et al., 1999), it is difficult to disentangle, based on pointer analyses alone, the interrelated climatic events inducing an extremely narrow ring. We thus hypothesize that during periods with insufficient snow cover, winter desiccation and freezing damage (Neuner et al., 1999) can occur simultaneously if evergreen *R. ferrugineum* leaves are exposed to excess irradiation, and that limited radial growth can thus occur during the subsequent growing season.

5 Conclusions

We built one of the first dwarf shrub growth-ring chronologies for the European Alps and tested the suitability of the widespread Alpine shrub species *Rhododendron ferrugineum* L. for dendroclimatological investigations. Despite the many challenges encountered during cross-dating, we were able to extract a unique, annually resolved, and statistically solid retrospective of >90 years of *R. ferrugineum* growth variability for a site in the French Alps. The construction of the chronology was facilitated by the well-defined and distinctly visible growth-ring boundaries and by a comprehensive serial sectioning of microcuts from 24 individuals. Results show that a clear climatic signal exists in the growth-ring variability in the growth-ring series. In particular, we observe that the *R. ferrugineum* chronology displays a climate-growth association similar to that observed in treeline *Picea abies* (L.) Karst. trees, with monthly mean May-July temperatures of the current year being the key unifying growth-limiting factors at the study site. In the case of *R. ferrugineum*, warm climatic conditions during previous fall and current May seem to be further influential factors and indeed affect shrub growth, thus pointing to a clear dependence of ring widths in this dwarf shrub species on the length of the growing season. The early winter (December-February) precipitation signal observed in our *R. ferrugineum* chronology appears to be more complex, as both an extensive and long-lasting snow cover and extremely dry winters seem to have detrimental effects on radial growth.

Given the wide geographic distribution of *R. ferrugineum* and its occurrence above treeline in the Alps, this dwarf shrub species should clearly become a promising candidate and a valuable proxy for the development of multi-centennial, annually resolved ring-width chronologies, even more so as these areas void of trees are typically also lacking meteorological records. In this perspective, we are calling for more research on climate-growth relationships of *R. ferrugineum* and are confident that climate reconstruction from growth-ring records of alpine shrubs can indeed become a standard, high-elevation proxy, even more so if the current study and other initiatives will be enlarged through (i) the development of extensive and dense *R. ferrugineum* chronology networks (Lu et al., 2015), (ii) the use of new anatomical indicators (von Arx et al., 2016), or (iii) the combination of newly-developed shrub chronologies with other highly resolved proxy data (e.g. lake sediments, glacier mass balance).

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Chapitre 2. Assessing the effects of earlier snow melt-out on Alpine shrub growth: the sooner the better?

Les résultats présentés dans ce chapitre sont basés sur les échantillons récoltés dans le Massif du Taillefer à l'automne 2015 dans le cadre du chapitre premier, échantillonnage complété à plus basse et à plus haute altitude, à l'automne 2016. Christophe Corona, Erwan Roussel, Jérôme Lopez-Saez, Arthur Messerli et moi-même ont participé à cette seconde campagne de terrain. Les microsections ont été réalisées et photographiées en laboratoire avec l'aide Brigitte Girard. Les données météorologiques, provenant du modèle SAFRAN-Crocus de Météo-France, ont été extraites par Samuel Morin et Carlo Maria Carmagnola (CEN, Météo-France). J'ai fait les analyses dendrochronologiques, et j'ai fait le choix et la réalisation des analyses statistiques.

Ce chapitre est en totalité constitué de l'article soumis à la revue *Ecological Indicators*, actuellement (25.01.2020) en révision mineure.

Photographie de page précédente : échantillonnage d'un individu isolé en limite altitudinale, autour de 2500m, sur la combe nord du Taillefer.

Assessing the effects of earlier snow melt-out on Alpine shrub growth: the sooner the better?

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Abstract

In contrast to Arctic ecosystems, the impacts of increasing temperatures and resulting changes in snow cover on low stature vegetation changes have received only limited consideration in the context of temperate mountains. Enhanced shrub growth in a warming alpine climate has potential far-reaching implications, including soil nutrient cycling, carbon storage, or water and surface energy exchanges. Growth ring analysis can yield mid- to long-term, annually-resolved records of shrub growth, and thereby offer valuable insights into how growth is driven by interannual climate variability. In the European Alps, dendroecological approaches have shown that dwarf shrub productivity is influenced by interannual variations of growing season temperature but results also point to a negative effect of winter precipitation on radial growth. However, as past work lacked snow cover data, links between snow cover duration, growing season length, energy availability and inter-annual shrub growth remain poorly understood. In this paper, we combined multi-decadal shrub-ring series sampled along a 600-m elevational gradient in the Taillefer massif, located in the French Alps, in order to assess the growth sensitivity of long-lived and widespread *Rhododendron ferrugineum* shrubs to both snow cover dynamics and temperature changes. We computed SEMs to track the response of shrub radial growth to extending growing season at different elevations and different period of times. At the high-elevation site, our results demonstrate a positive effect of increasing growing season length on shrub growth, which is strongly dependent on snowpack depth and snow cover duration. Conversely, at lower

elevations, earlier melt-out dates and associated late frost exposure are shown to lead to radial growth reduction. Moreover, the climate signal in ring-width chronologies of *R. ferrugineum* portrays a weakening since 1988 – similar to a phenomenon observed in series from circumpolar and alpine tree-ring sites and referred to as “divergence”. By analyzing long-term records of radial growth along an elevation gradient, our work provides novel insights into the complex responses of shrub growth to climate change in alpine environments. This paper demonstrates that *R. ferrugineum*, as a dominant alpine shrub species, behave as an ecological indicator of the response of alpine ecosystem to global warming.

Keywords

dendroecology; divergence; dwarf shrubs; elevation gradient; frost; snow cover

1 Introduction

Temperatures in Arctic and Alpine regions have been increasing twice as fast as the global average over the last decades (Stocker et al., 2013), with potential far-reaching consequences for ecosystem functioning due to feedbacks between vegetation and climate (Bjorkman et al., 2018). Rapid climate warming is also driving changes in the structure and composition of cold ecosystems and has been associated with changes in plant diversity and richness (Boscutti et al., 2018; Grabherr et al., 1994; Steinbauer et al., 2018), poleward and upslope shifts in species geographic distribution (Chen et al., 2011; Elsen and Tingley, 2015; Parmesan and Yohe, 2003) and thermophilization (Dolezal et al., 2016; Elmendorf et al., 2015; Gottfried et al., 2012). At high-latitude sites, increasing vegetation productivity (Pearson et al., 2013) associated with a widespread shrub expansion (Elmendorf et al., 2015; Tape et al., 2006) has resulted in a greening trend, characterized by increasing canopy cover, height, abundance, and biomass (Forbes et al., 2010; Hollesen et al., 2015; Myers-Smith et al., 2011, 2015). Conversion of tundra to shrubland is driven by ongoing warming, and modulated by soil moisture (Ackerman et al., 2017; Elmendorf et al., 2012), but also by changes in snow cover duration (Gamm et al., 2018; Niittynen et al., 2018; Weijers et al., 2018a; Young et al., 2016). Recent warming and related shrubification (i.e. increasing shrub cover and biomass) in Arctic systems has also been shown to drive climate feedbacks, for instance by altering surface albedo, energy, water balance, or permafrost (Blok et al., 2011; Chapin, 2005; Liston et al., 2002; Sturm et al., 2001). Although comparable changes can be expected at high altitudes, shrubification has hitherto received very little consideration in temperate mountain systems.

In the European Alps, documentation of upslope advancement of shrub species remains scarce and spatially limited (Anthelme et al., 2007; Cannone et al., 2007; Dullinger et al., 2003). At the regional scale, Carlson et al., (2017) provided remote sensing-based evidence linking the observed greening of alpine vegetation (increased productivity) to increasing air temperatures and decreasing snow cover duration. Snow manipulation experiments, designed to simulate the expected advance of melt-out dates in a warmer climate (Gerdol et al., 2013; Rixen et al., 2010; Wipf and Rixen, 2010) confirm the strong control of snowpack duration on shrub phenology and growth via indirect effects on soil temperature, nutrient availability and frost exposure. Despite the indisputable value of these studies to improve understanding of climate–growth linkages, experimental studies typically cover relatively short periods

(1-2 years; Wipf and Rixen, 2010) and cannot capture longer-term shrub growth responses to climate change.

By contrast, growth-ring analyses have the potential to provide uninterrupted mid- to long-term, annually-resolved records of shrub growth, thereby revealing responses to interannual climate variability (Bär et al., 2006; Buchwal et al., 2013; Forbes et al., 2010; Hollesen et al., 2015; Weijers et al., 2010; Young et al., 2016). Still underused in high-altitude environments, the limited number of existing dendroecological studies tends to confirm that dwarf shrub productivity is influenced by interannual variations of growing season temperature (Francon et al., 2017; Liang et al., 2012; Liang and Eckstein, 2009; Lu et al., 2015; Pellizzari et al., 2014). In the Alps, initial results point to a negative effect of winter precipitation on the radial growth of shrubs (Carrer et al., 2019; Francon et al., 2017; Pellizzari et al., 2014; Rixen et al., 2010), a phenomenon that has been observed only rarely in circum-Arctic tundra ecosystems (Bär et al., 2008; Hallinger et al., 2010; Ropars et al., 2015; Zalatan and Gajewski, 2006; but see Schmidt et al., 2010, who found snow to correlate negatively with *Salix arctica* growth). Several hypotheses have been proposed to explain this phenomenon, such as the detrimental effect of late-persisting snow on the onset of cambial activity, growing season length or soil temperatures (Pellizzari et al., 2014). However, most of these studies relied on monthly-resolved meteorological time series and lacked snow cover data, thereby precluding a precise assessment of the relationships between snow cover duration, growing season length and energy availability during the snow free period. We argue that by ignoring the impact of changes in snow cover alongside temperature, shrub ring–climate studies focusing on plant growth in temperate mountain ecosystems will likely dismiss an obvious mechanistic pathway, which could potentially regulate shrub growth in response to winter snow accumulation. This knowledge gap is particularly pressing given the wealth of studies documenting a warming-induced decrease of snow cover duration in temperate alpine regions of North America (Mote et al., 2005) and Europe (Beniston et al., 2018; Hantel et al., 2000, 2012; López-Moreno, 2005). Ongoing and future climate change will likely accelerate warming, but also favor earlier melt-out dates and decreased snowpack depths at altitudes comprised between 1500 and 3000 m above sea level (asl; Beniston et al., 2018; Marty et al., 2017; Steger et al., 2013; Verfaillie et al., 2018).

Here, we sampled *Rhododendron ferrugineum* individuals along a 600-m elevational gradient from a site where shrub growth is expected to be influenced by snow cover dynamics (Francon et al., 2017) and where plants are likely to be vulnerable to climate change. In order to test the hypothesis that shrub growth is directly influenced by the accumulation of degree days received during the snow free period (SFGDD), we (i) developed a multidecadal shrub-ring series from long-lived *Rhododendron ferrugineum* individuals; (ii) evaluated recent climatic trends in atmospheric temperature and snow cover obtained from a locally calibrated meteorological model, specifically designed for the mountain environment and spanning the period 1958-2017 (Durand et al., 2009a, 2009b) and (iii) investigate climate–growth relationships using structural equation models (SEMs) designed to disentangle the effects of the above-mentioned climate variables on radial growth. We computed SEMs for the periods 1959-1988 and 1989-2016 to test for the potential change in shrub sensitivity to climatic drivers in the context of recent climate changes.

2 Material and methods

2.1 Study species

Rhododendron ferrugineum L. is the dominant mountain shrub of the subalpine belt in the siliceous Alps (Ozenda, 1985). It is distributed from about 1600 to 2500 m asl, where it can form large heathlands or grow in localized patches (Escaravage et al., 1997). The high local abundance of the species can be attributed to complementary sexual and vegetative reproductive strategies (Doche et al., 2005) which enable *R. ferrugineum* to outcompete other plants (Pornon and Doche, 1996) and to reach a 90–100% cover after 150–250 years (Pornon and Doche, 1995). *R. ferrugineum* provides an ideal model to study the long-term effects of climate on radial growth due to its high longevity, estimated to be up to three centuries (Escaravage et al., 1998), as well as its clearly identifiable annual rings discriminated by a band of radially aligned, thick walled latewood fibers, flattened along the ring boundary (Francon et al., 2017).

2.2 Study area

The study area is situated in the northern French Alps (Fig. 1), on a northwest-facing slope in the Taillefer massif. At Taillefer, *R. ferrugineum* is the dominant species (80–100% cover) of above-treeline dwarf shrub heathlands. The species developed on abandoned pastures between 1900 and 2100 m asl and is intermixed with *Sorbus* sp. and *Vaccinium* sp. along with scattered *Picea abies* and *Pinus uncinata* trees. Beyond this altitude, heathlands become more fragmented and are mixed with patches of alpine meadows and scree. Isolated patches of *R. ferrugineum* are observed up to ~2500 m asl. Shrub individuals were sampled along an elevational gradient, at three sites located at (i) 1800–1850 m (SAL1800), (ii) 1950–2050 m (SAL2000) and (iii) 2300–2500 m asl (CN2400). SAL1800 and SAL2000 are located at the Côte des Salières (SAL, 45°02'N, 5°52'E, Fig. 1) on a northwest-facing slope with slope angles ranging from 23° to 33°. CN2400 is located in the Combe Nord (3 km east of SAL, 45°02'N, 5°55'E, Fig. 1) on a north-facing slope (25°). At SAL1800 and SAL2000, bedrock consists of amphibolite and gneissic gabbro (Doche et al., 2005). SAL1800 and SAL2000 heathlands have developed on stony, ochre-brown humic acidic soils (Pornon et al., 1997). At CN2400, *R. ferrugineum* individuals grow on shallow and discontinuous soils developed on talus slopes and weathered rock outcrops.

Climate of the Taillefer massif reflects a transition between the wet oceanic Pre-Alps (Chartreuse, Vercors) and the intra-alpine Oisans massif, with the latter being characterized by a more continental climate with drier summers (Pautou et al., 1992). Daily reanalysis from the SAFRAN meteorological system (Durand et al., 2009a) was used to characterize climatic conditions along the elevational gradient (Fig. 1B). Over the period 1959–2016, mean annual air temperatures were 4.2°C, 3.3°C, and 1.4°C at SAL1800, SAL2000 and CN2400, respectively. The melt-out date occurred on average on May 2 at 1800 m asl, and roughly one month later at 2400 m asl (June 6).

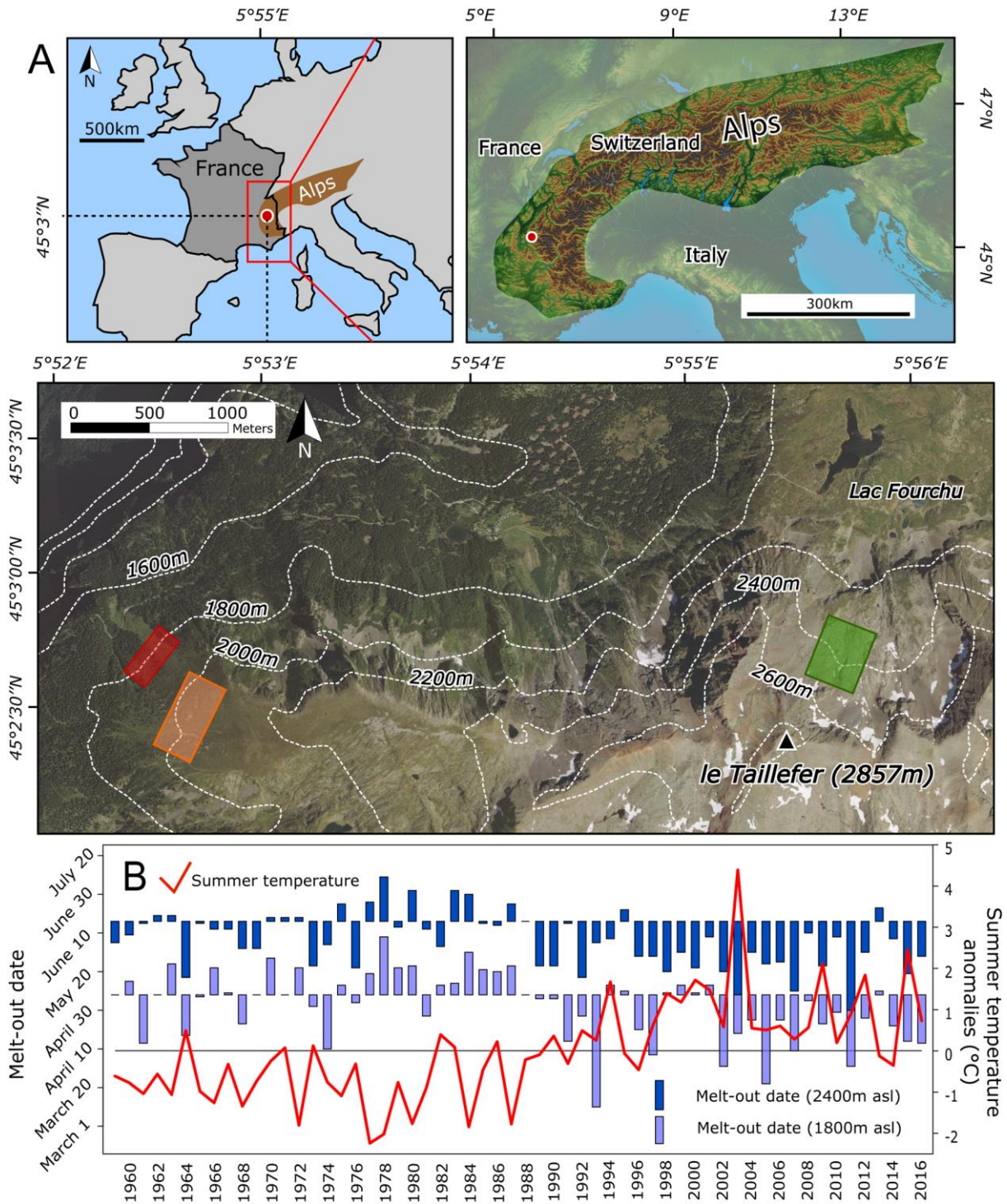


Figure 1: (A) Location of the study sites, Côte des Salières (SAL1800, red; SAL2000, orange) and Combe Nord (CN2400, green) in the Taillefer massif (French Alps). (B) Summer (May–August) temperature anomalies (1959–2016) as well as melt-out dates at 1800 (light blue) and 2400 m asl (dark blue) for the 1959–2017 period. Meteorological data were extracted from the SAFRAN-Crocus re-analysis datasets (Durand et al., 2009a, 2009b).

2.3 Sample collection and preparation

A total of 80 randomly selected *R. ferrugineum* individuals were sampled at the three sites: 36 at SAL2000 in October 2015, 17 at SAL1800, and 27 at CN2400 in October 2016. Individuals were sampled at a minimum distance of four meters from each other to avoid the sampling of the same clone (Escaravage et al., 1998). Locations were recorded with metric precision using a Trimble GeoExplorer GNSS (Global Navigation Satellite System) unit. Three to six wood sections were cut per individual on the main stems, starting at the root collar and then every 10-20 cm to the stem extremity. This approach was used in order to apply the serial-sectioning method, consisting of repeated growth-ring width measurements and cross dating at the intra-stem level (Kolishchuk, 1990).

To ensure precise detection of all rings, 20 μm thick cross sections were prepared from each sample using a slide microtome. Cross sections were then stained using Safranin and Astra Blue, and permanently fixed on microslides with Canada balsam (Schweingruber et al., 2011). High-resolution digital pictures were taken using a Carl Zeiss Axio Observer Z1 coupled to a Zeiss AxioCam MR R3 camera under 40–100 magnification. Individual images were merged automatically to cover the whole cross-sections by using the Zen 2011 software.

2.4 Crossdating and chronology development

Width of individual growth rings were measured from digital images with CooRecorder 7.6 (CYBIS Elektronik & Data AB) along three radii of the cross-sections to detect wedging rings. Radial measurements along the chosen radii were supplemented by careful visual inspection of each cross section to eliminate annual growth underestimation caused by partially missing rings. Cross-dating was based on a three-step procedure involving a comparison of growth curves (i) between three radii measured within a single cross section, (ii) among the mean growth curves of all sections within individual plants, and finally (iii) between the mean growth curves of all shrubs of a given site. The output of visual crossdating was statistically checked with COFECHA (Holmes, 1994).

After cross-dating, each individual mean series was standardized (Cook and Kairiukstis, 1990; Fritts, 1976) with a double-detrending process in ARSTAN (Cook, 1987). We first selected a negative exponential function to eliminate non-climatic trends (e.g. age-related growth trend and other potential biological effects) referred to as Neg-Exp chronologies. In addition, we fitted a cubic smoothing spline, preserving 50% of the variance at a wave-length of 32 years so as to remove the effect of localized disturbance events (Cook and Peters, 1981) hereafter referred to as detrended chronologies. In both approaches, outputs referred as growth indices were averaged by year using a bi-weighted robust mean aimed at reducing the influence of outliers and at developing mean standardized site chronologies (Cook and Peters, 1981). The resulting growth indices are referred to as ring-width indices (RWI).

Several descriptive statistics were then applied to detrended chronologies using the *dplR* package, including standard deviation (SD), first-order autocorrelation (AC), mean sensitivity (MS), mean inter-series correlation (R_{bar}), and expressed population signal (EPS; Bunn, 2008) in R 3.3.2 (R Core Team, 2016). Running R_{bar} and EPS were computed at each site using a 30-year moving window with a 29-year overlap to illustrate changes in the strength of common patterns of radial growth over time. We used the commonly applied quality threshold of $\text{EPS} \geq 0.85$ to determine the reliability of our

chronologies. As shrubs may potentially retain climate-driven, low frequency variations in the raw data (decadal growth variations), Neg-Exp chronologies were used to detect potential impacts of decadal-scale climatic fluctuations on radial growth. Indices from the double-detrending procedure were used for climate-growth correlations and climate-growth modeling in relation to high-frequency (interannual) growth variations.

2.5 Meteorological series

At each plot, daily meteorological and snow time series were obtained from the SAFRAN- Crocus coupled snowpack-atmosphere model. The SAFRAN reanalysis combines *in-situ* meteorological observations with synoptic-scale meteorological fields to provide continuous time series of meteorological variables at hourly resolution and for elevation bands of 300 m within areas, referred to as “massifs” (Oisans in the case of this study), assumed to be horizontally homogenous (Durand et al., 2009a). The dataset extends back to 1958. SAFRAN meteorological fields are used to drive a land surface model, the ISBA-Crocus soil and snowpack model. This tool provides corresponding reanalysis of snow conditions and underlying ground temperature for the same time span as SAFRAN reanalysis (Durand et al., 2009b; Vionnet et al., 2012). To quantify ground temperature, we extracted values for the uppermost soil layer with a thickness of 1 cm.

SAFRAN meteorological fields corresponding to the sampling sites were extracted according to their elevation, aspect, and slope angles (Lafaysse et al., 2013). Meteorological data were interpolated from the neighboring 300-m elevation bands, and incoming shortwave radiation data was adjusted by using the prevailing aspect and slope angle. The ISBA-Crocus models runs were performed specifically for the sites. Vegetation was represented in a simplified manner in the simulations, assuming grassy conditions so as to simulate typical snow conditions and underlying ground temperature for open areas, therefore neglecting small-scale interactions between vegetation, topography, and snowpack. We then extracted hourly air temperature and precipitation sums as well as daily snow depth and uppermost ground layer temperatures (6:00 UTC) for the period 1959-2017. The data were carefully visually checked to detect extreme temperature events that could be linked with marked growth reduction. Monthly minimum, mean, and maximum air temperature, monthly precipitation sums, snow depth, and duration, melt-out date, sum of snow-free growing degree days (SFGDD) and daily uppermost ground layer temperature series were computed from the same datasets. The snow melt-out date was defined as the last day when snow cover reached the mean height of the shrub canopy at *c.* 50 cm for SAL1800 and SAL2000, and at *c.* 30 cm for CN2400. SFGDD were calculated for periods with snow-free ground and daily air mean temperatures above zero degrees. SFGDD series were calculated from melt-out date to August 31.

Given that previous work identified a shift toward earlier snow melt-out in the study region occurring during the late 1980s (Dedieu et al., 2016); we applied a breakpoint analysis to the meteorological record. This preliminary analysis points to a significant tipping point in 1988, which is consistent with regional-scale studies (Reid et al., 2016). At 2400 m asl, the melt-out date thus advanced on average from June 14 (1959-1988) to May 28 (1989-2016). At the same time, mean May temperatures increased from 1.7°C to 3.5°C. At 1800/2000m, a shift of 19 days is observed for the melt-out date and an increase

of 25% in SFGDD is observed. As a consequence, climate-growth analyses were systematically performed separately for the subperiods 1959-1988 and 1989-2016.

2.6 Statistical analysis of climate-growth relationships

Structural Equation Models (SEMs, Grace, 2006; Kline, 2011) enable (i) decomposition of total effects into direct and indirect types, and (ii) comparison of alternative models using indices of goodness of fit (Kline, 2011; Mitchell, 1992). SEMs have been used in previous ecological studies to investigate e.g. the impacts of shrub expansion on species richness and plant diversity (Boscutti et al., 2018), the relation between climate and mountain plant productivity (Choler, 2015; Jonas et al., 2008; Madrigal-González et al., 2017, 2018) or the relation between tree-ring width and sea surface temperature in Mexican dry forests (Brienen et al., 2010). Here, SEMs were developed to gain insights into the concurrent effects of climatic variables (especially snowmelt timing and the amount of growing degree days, susceptible to influence radial growth) and to compare the partition of covariance among variables along the elevation gradient and over time (before and after 1988). In order to develop a robust conceptual model for each site and each sub-period, we developed a two-step statistical procedure (Fig. 2):

(i) bootstrapped correlation functions (BCFs) between the detrended chronologies, mean monthly air temperature (°C), monthly precipitation sums (mm), melt-out dates, and SFGDD series were computed with the *Treeclim* package (Zang and Biondi, 2015) in R (R Core Team, 2016) to identify climate variables that are significantly correlated ($P < 0.05$) with radial growth. To identify direct and indirect drivers of radial growth, we also computed partial correlation functions (PCFs); and

(ii) SEMs were developed with the “*Lavaan*” package (Rosseel, 2012) in R. The structure of the hypothetical SEM path structure (see Fig. 2) requires the incorporation of available *a priori* knowledge (Pérez-de-Lis et al., 2016). In this study, direct effects are given as standardized path or partial regression coefficients. According to the hypothesis formulated in the introduction, we considered SFGDD as a direct driver of radial growth, while melt-out timing was incorporated as an indirect parameter through its mediating effect on growing season length. The latter parameters formed the backbone of the SEMs at each site, while additional climatic variables significantly correlated ($p < 0.05$) with radial growth (steps 1-2) were added as explanatory variables. To derive comparable estimates, we standardized all quantitative predictors to a mean of zero and to a standard deviation of one. To prevent any effect of multicollinearity among explanatory variables, we used variance inflation factors (VIF). Collinearity was assessed with a cut-off value of 3 (Zuur et al., 2010). To compare the competing models, each model was first evaluated with the Akaike Information Criterion (AIC, Akaike, 1981) for which lower values correspond to more parsimonious models. We thereafter employed the Chi-square (χ^2) difference statistic to control the overall fit and to verify whether the model was consistent with the data covariance matrix (p cut-off ≥ 0.05) (Kline, 2011). In addition, we computed the CFI (Comparative Fit Index, Bentler, 1990) with a CFI cut-off ≥ 0.90 . Assumptions of normality and homogeneity of variance were controlled for every endogenous variable in the SEMs using qq-plots and standardized residuals vs. fitted values plots (see Fig. S1 in supplementary material).

Step 1 Bootstrapped Correlation Functions (BCFs), Partial Correlation Functions (PCFs)

treeclim

ppcor

- 1- Selection of **significant monthly or seasonal climatic parameters**
- 2- Checking for correlations between:
 - RWI and SF-GDD
 - RWI and melt-out timing

Identification of direct, indirect and confounding influences between variables

Step 2 Structural Equation Models (SEMs)

lavaan

SEMs building according to:

- **The main hypothesis**
- Climatic parameters selection procedure (**step 1**)
- **Parcimony (delta AIC)**
- **Goodness of fit (Chi-square, χ^2)**

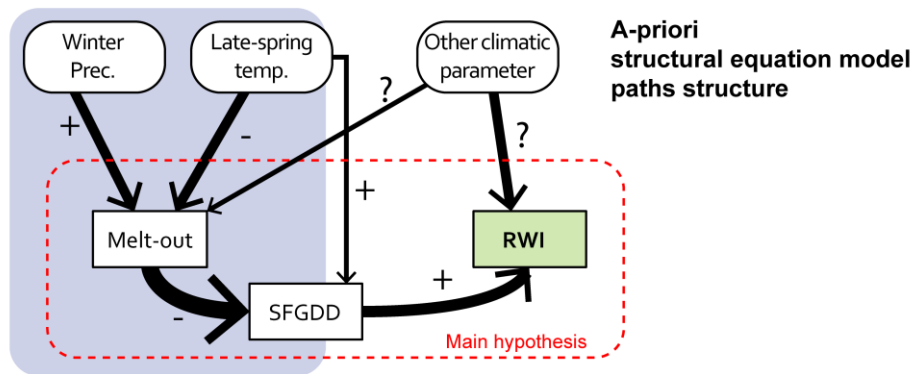


Figure 2: Diagram of the 2-step procedure adopted for the development of the Structural Equation Models (SEMs). First (step 1), Bootstrapped Correlation Functions (BCFs) are used to identify climatic variables that potentially have a direct or indirect effect on Ring-Width Indices (RWI) at the monthly or seasonal scales. Relationships with SFGDD and Melt-out dates were also tested. Climatic variables were then tested using Partial Correlation Functions (PCFs) for direct, indirect or confounding effects on RWI. Second (step 2), SEMs are built according to the main hypothesis (Melt-out timing \rightarrow SFGDD \rightarrow RWI) and with other climatic parameters selected in step 1.

3 Results

3.1 Chronology statistics

A total of 11, 24, and 14 *R. ferrugineum* individuals were included in the SAL1800 (1826-2016), SAL2000 (1821-2015) and CN2400 (1896-2016) chronologies, respectively (Fig. 3 A, B) corresponding to rejection rates (e.g. the percentage of misdated individuals) of 35, 33, and 48% of the samples. Cross-correlations between standardized chronologies over the period 1960-2016 yielded r values of 0.80 (SAL1800-SAL2000), 0.46 (SAL2000-CN2400) and 0.30 (SAL1800-CN2400). Wood productivity – estimated as the mean annual growth between cambial age 20 and 39 – was 0.17 mm at SAL1800, 0.16 mm at SAL2000, and thus significantly larger than the values obtained at CN2400 (0.12 mm, ANOVA $p < 0.001$). Descriptive statistics computed for the detrended chronologies (Fig. 3B) are given in Table 1. Mean sensitivity values were comparable at SAL1800 (0.34) and CN2400 (0.31), but lower at SAL2000 (0.26). The highest inter-series correlations ($R_{bar} = 0.41$), EPS (0.94) and AC values (0.22) were

observed at SAL2000. At SAL1800 and CN2400, lower Rbar and EPS values (slightly below the 0.85 threshold at CN2400) were found for the period covered by meteorological series (1959-2016), thereby pointing to higher inter-individual ring-width variability.

Table 1: Characteristics of *R. ferrugineum* raw ring-width chronologies: length, mean age, median ring-width. Statistics computed for detrended chronologies: standard deviation (Std. dev.), signal strength (Rbar and EPS, computed only from 1959 onwards), mean sensitivity (MS) and first order autocorrelation (AC).

Chronology	Raw ring-width chronologies				Detrended ring-width chronologies				
	First year	Last Year	Mean age	Median ring-width	Std. dev.	Mean Rbar (1959-2016)	Mean EPS (1959-2016)	MS	AC
SAL1800	1862	2016	81	0.171	0.281	0.321	0.86	0.338	0.136
SAL2000	1821	2015	86	0.159	0.246	0.412	0.94	0.257	0.221
CN2400	1896	2016	56	0.117	0.265	0.278	0.82	0.314	0.008

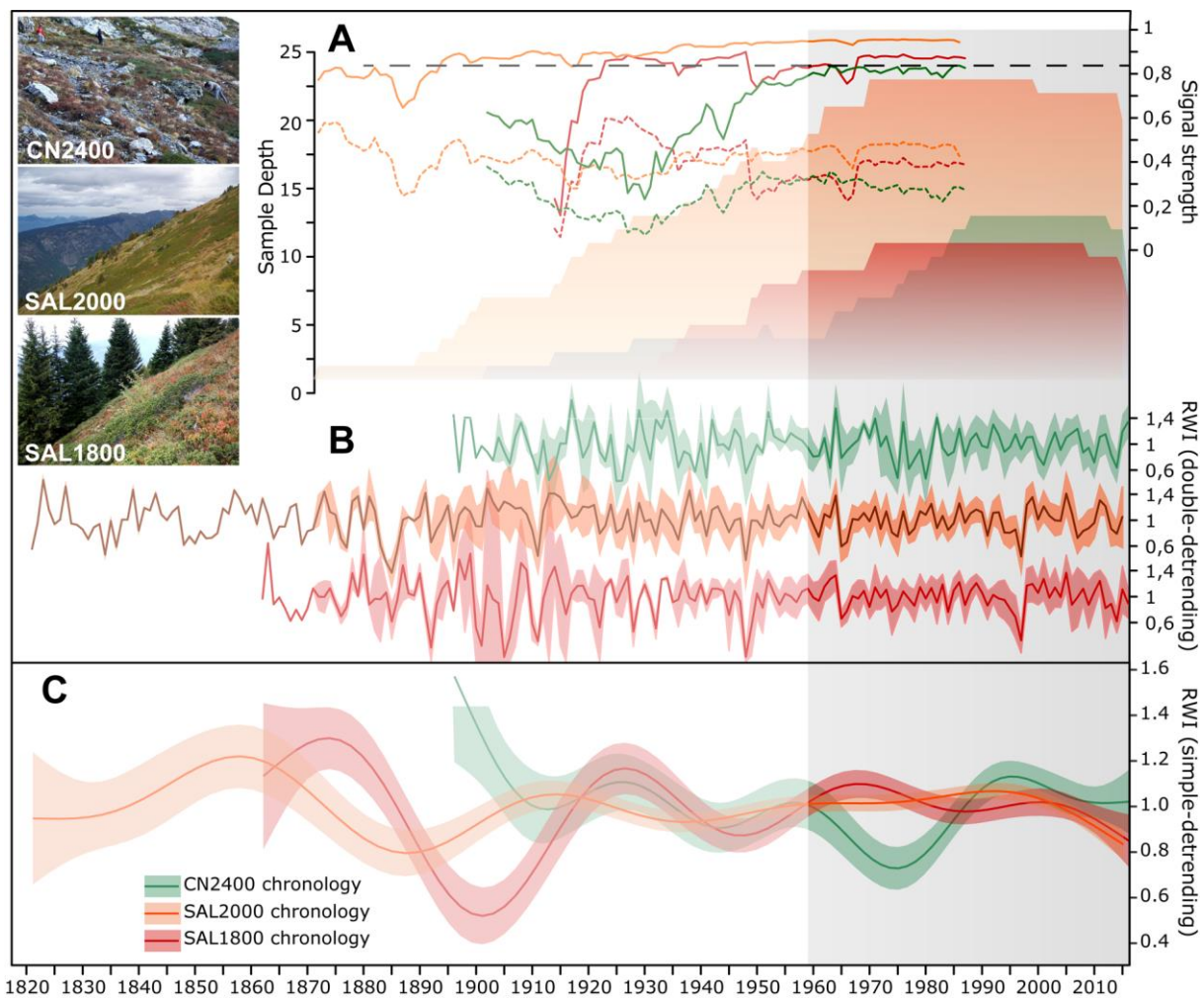


Figure 3: (A) Sample depth (colored areas) and running detrended chronologies signal strength: Expressed Population Signal (EPS, solid lines) and common variance between single growth-ring series in a chronology (Rbar, dotted lines) were computed using a 30-year moving window. Colored

areas indicate sample depth. The EPS threshold (0.85) is shown by the black dotted line. (B) Standard growth-ring chronologies of *R. ferrugineum* with ribbons designating Ring-Width Indices (RWI) \pm 1 SD. (C) Neg-Exp chronologies smoothed with a GAM-smoothing, ribbons indicate the 95% confidence intervals. The grey area corresponds to the period analyzed.

3.2 Bootstrapped correlation functions (BCFs) and partial correlation functions (PCFs)

Results from the bivariate bootstrapped correlation function analyses are summarized in Fig. 4. May temperatures (year N; $r = 0.33, 0.34, 0.40$ at 1800, 2000, and 2400 m asl, respectively, all with $p < 0.05$) were the only statistically significant climatic driver of radial growth observed in all *R. ferrugineum* chronologies. More generally, positive correlations (albeit not significant) were observed between summer temperature of year N (June, July, and August) and radial growth at each site. Similar BCF profiles were observed at SAL1800 and SAL2000, characterized by positive significant correlations with September (year N-1) temperatures ($r = 0.26$ and $r = 0.35, p < 0.05$) and April precipitation sums ($r = 0.28, r = 0.28, p < 0.05$). By contrast, at CN2400, the response to fall (N-1) temperature was delayed to October ($r = -0.28, p = 0.06$) and November ($r = -0.30, p < 0.05$). The response of *R. ferrugineum* to snow melt-out date and SFGDD was particularly acute at 2400 m asl. The correlation between ring-width indices and SFGDD increased from low to high elevation sites, with $r = 0.18$ ($p = 0.18$) at SAL1800, $r = 0.28$ ($p < 0.05$) at SAL2000, and $r = 0.51$ at CN2400 ($p < 0.001$). Radial growth also appeared to be more limited by melt-out date at CN2400 ($r = -0.56, p < 0.001$) and winter precipitation ($r = -0.41, p < 0.01$) as compared to $r = 0$ at SAL1800 (Fig. 4).

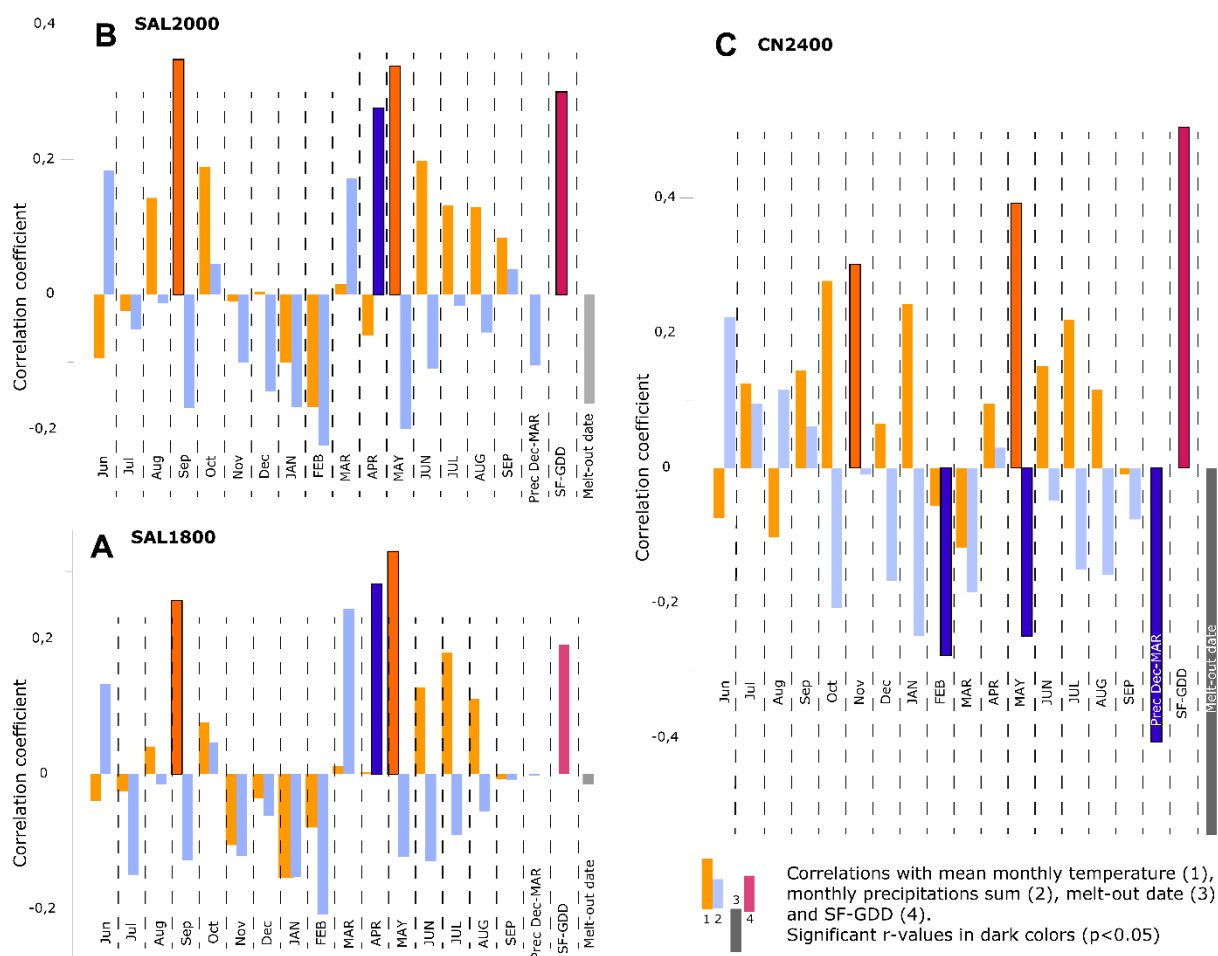


Figure 4: Monthly bootstrapped correlation functions analysis between *R. ferrugineum* radial growth chronologies at SAL1800 (A); SAL2000 (B); and CN2400 (C), monthly mean temperatures, monthly precipitation sums, previous December to current March precipitation sums (Prec dec-MAR), SFGDD and snow melt-out date for the period 1959–2016. Months of the year preceding ring formation (N-1) are given with lowercase letters, and months of the year (N) of ring formation are shown with capital letters.

At our study sites, melt-out timing, late winter precipitation and May temperature are correlated, therefore partial correlations between tree-ring growth and the latter variables were performed. At CN2400, PCFs computed between radial growth, May temperature and precipitation or winter precipitation were not significant when melt-out timing was included as a control variable (Table 2). In other words, this indicates that the latter climatic variables have no impact on radial growth when melt-out-timing is held constant. Conversely, at SAL1800 and SAL2000, correlations between shrub chronologies, May temperature and March/April precipitation totals remain highly significant in the absence of melt-out timing fluctuations (Tab. 2). One can thus conclude that the correlations between our shrub ring width chronology and May temperature and late winter precipitation totals are 0.33 and 0.47 ($p < 0.05$), respectively at SAL1800 if adjusted for the effects of melt-out timing. At SAL2000, the partial coefficients reveal the critical influence of May temperature ($r = 0.32$, $p < 0.05$) and Mar-Apr precipitation ($r = 0.48$, $p < 0.001$) on radial growth.

Table 3: Partial Correlations Functions (PCFs) and their significance computed between climatic parameters and ring width indices (RWI) at SAL1800, SAL2000 and CN24000 controlling for melt-out timing. Significant relationships ($p < 0.05$) are given in bold. "na" means that the partial correlation was not computed, as no effect on radial growth was detected in the Bootstrapped Correlation Functions for the corresponding climatic variable.

Effect	SAL1800		SAL2000		CN2400	
	Corr.	Signif.	Corr.	Signif.	Corr.	Signif.
May temperature	0.33	0.01	0.32	0.02	0.03	0.84
March + April precipitation	0.47	0.00	0.48	0.00	na	na
Winter precipitation	na	na	na	na	-0.10	0.45
May precipitation	na	na	na	na	-0.08	0.56

3.3 Structural equation modeling

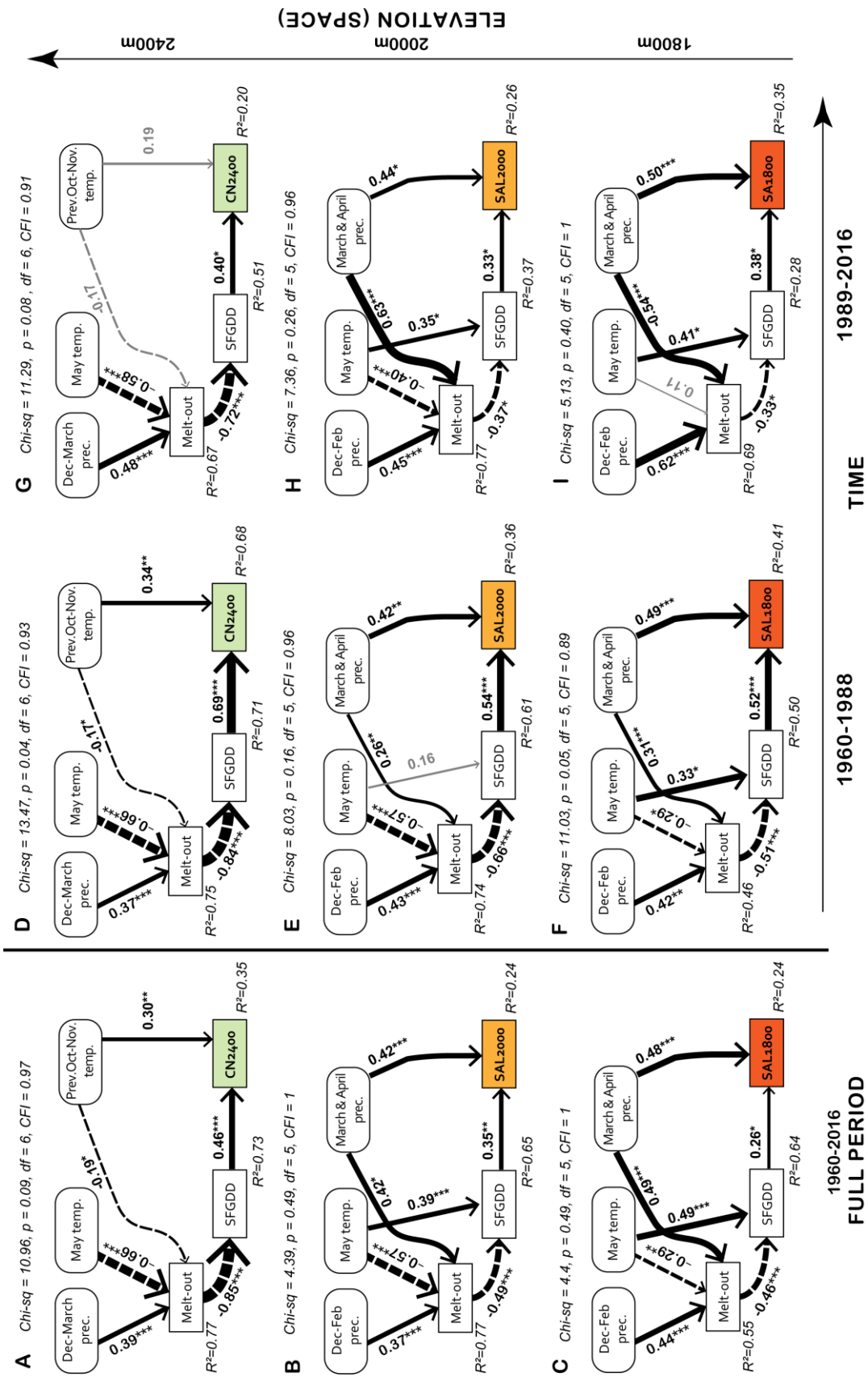


Figure 5 : Structural equation model results exploring the effects of spring snow-cover duration (Melt-out) on SFGDD, and the effects of SFGDD and other climatic parameters (March and April precipitation totals at SAL1800/2000, previous September temperature at SAL2000 and previous October-November temperature at CN2400) on shrub ring width indices (RWI) at different sites (A, D, G: 1800 m asl, SAL1800; B, E, H: 2000 m asl, SAL2000 and C, F, I: 2400 m asl, CN2400). SEMs were performed for the period 1960-2016 (A, B, C) and two sub-periods: 1960-1988 (D, E, F) and 1989-2016 (G, H, I). Winter precipitation totals and May temperature effects on Melt-out timing as well as the direct effect of May temperature on SFGDD are also represented. Colored boxes represent measured RWI, white boxes represent intermediate climate parameters and rounded white boxes represent monthly or seasonal meteorological data. Black solid (or dotted) arrows indicate unidirectional positive (negative) significant relationships (at $p < 0.05$) among variables. Grey arrows indicate non-significant relationship ($p > 0.05$). The thickness of the paths was scaled to the magnitude of the standardized regression coefficient (shown besides the arrows). Multiple R^2 are given next to the box of the respective response variable. Significance levels are denoted by *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$). Chi-square and CFI values indicate goodness of fit.

Results from BCFs and PCFs were used to determine the direction and strength of correlations between climate variables and the shrub ring chronologies implemented in the path diagrams of each structural equation model over the period 1960-2016 (Figs. 5A-C). At each site, as stated in our initial hypotheses (Fig. 2), path diagrams were designed to disentangle the respective impacts of SFGDD, melt-out timing, winter precipitation and spring temperatures on shrub radial growth. In addition to the latter variables, fall temperatures (N-1, CN2400, SAL2000) and spring precipitation (SAL1800, SAL2000), significantly correlated to shrub ring records (BCFs), were added as direct predictor variables. SEMs computed for the periods 1960-2016 displayed Chi-square p-values above 0.05 and CFI higher than the 0.9 cut-off. At the three sites, the proportion of the variance in the dendrochronological series that could be explained by the climatic variables increased with elevation ($R^2 = 0.35, 0.24, 0.24$ at CN2400, SAL2000 and SAL1800, respectively). However, the effect of SFGDDs on shrub ring records increased from 0.26 standard deviation units as a result of change of one standard deviation in SFGDD at 1800 m ($p < 0.05$) to 0.35 ($p < 0.01$) at 2000 m and to 0.46 ($p < 0.001$) at 2400 m asl. Significant relations between climatic variables and radial growth differed along the elevational gradient. At CN2400, SFGDD variability is the main driver of radial growth, which is significantly related to melt-out-timing (path coefficient of -0.85, $p < 0.001$). Melt-out was in turn directly conditioned by May temperature (-0.66, $p < 0.001$), winter precipitation (0.39, $p < 0.001$) and – to a lesser extent – by previous late-autumn temperature (-0.19, $p < 0.05$).

At SAL2000, SFGDD, spring precipitation and previous fall temperature show comparable, statistically significant impacts on shrub radial growth. Interannual variability of SFGDD remains dependent on melt-out timing but is also directly driven by May temperature (Fig. 5B). Finally, at 1800 m asl, the SEM differs from those obtained for the higher elevation sites. Albeit significantly related to radial growth at SAL1800, SFGDD is not the main driver for shrub ring width which appears to depend more strongly on March-April precipitation totals (0.48, $p < 0.001$). At this elevation, SFGDD is driven by melt-out timing and May temperature (-0.46, $p < 0.001$ and 0.49, $p < 0.001$, respectively).

3.4 Stationarity of radial growth-climate relationships over time

To evaluate the stationarity and consistency of radial growth-climate relationships, SEMs were computed for the two sub-periods 1960-1988 and 1989-2016 (Fig. 5 D-I). The SEMs presented good overall performances by passing the goodness of fit cutoffs of Chi-square $p > 0.05$ and CFI > 0.90 except for the SEMs computed at CN2400 and SAL1800 for the period 1960-1988 ($\chi^2 = 13.47$, $p = 0.04$, CFI = 0.93 at CN2400 and $\chi^2 = 11.03$, $p = 0.05$, CFI = 0.89 at SAL1800).

Strikingly, we observe a loss of the explanatory powers of the SEMs for the recent period, especially at CN2400 where the amount of variance in radial growth explained by climatic variables decreased from 0.69 for the period 1960-1988 to 0.20 between 1989 and 2016. For both subperiods, the dependence of radial growth on SFGDD thus decreased from 0.69 ($p < 0.001$) to 0.40 ($p < 0.05$), from 0.54 ($p < 0.001$) to 0.33 ($p < 0.05$), and from 0.52 ($p < 0.001$) to 0.38 ($p < 0.05$) at 2400, 2000, and 1800 m asl, respectively. In addition, the models illustrate nicely that the dependence of SFGDD on melt-out dates and May temperatures remain highly significant ($p < 0.001$) at CN2400, whereas their influence strongly decreased at SAL2000 and SAL1800 after 1988. Similarities exist between the SEM computed at SAL2000 for the period 1960-1988 and at CN2400 for the period 1989-2016 (Fig. 5 E, G), especially with respect to the correlations between May temperatures, melt-out timing, SFGDD and radial growth. Similarly, comparable impacts of winter precipitations and May temperatures on melt-out dates were observed in Fig. 5F and 5H. This evolution suggests a 200-400 m shift of the climatic conditions and, to a lesser extent, of radial growth response to climate over the last 30 years.

4 Discussion

In this paper, we disentangled the impact of recent climate change on radial growth in the widespread mountain shrub species *Rhododendron ferrugineum* by sampling a total of 80 stems along an elevation gradient. The three multi-decadal growth-ring chronologies developed from individuals sampled at 1800, 2000, and 2400 m asl (referred to as SAL1800, SAL2000, and CN2400) provide a unique perspective on mountain shrub responses to climate variability in the context of recent climate changes (Myers-Smith et al., 2015). We used Structural Equation Models (SEMs) to disentangle direct and indirect drivers of radial growth, which clearly demonstrate an elevation-dependent response of *R. ferrugineum* to snow cover duration. Our results also provide evidence for a divergence of radial growth responses to climate during recent decades, given that climate-growth correlations have weakened since 1988.

4.1 Radial growth responses along the snow melt-out timing gradient

At CN2400, results support the initial hypothesis that the amount of growing degree days during the snow-free period (SFGDD) would impact *R. ferrugineum* radial growth strongly whereas melt-out dates would act only as an indirect limiting factor on radial growth by conditioning the length of the growing season. Results from SEMs show that SFGDD – controlled by melt out dates – explained about 46% of radial growth variability over the period 1960-2016 and about 70% of the variability between 1960 and 1988. At this elevation, the growing season is short (85 days on average prior to August 31) and SFGDD totals are low (823°C on average for the period 1959-2016). Snowmelt frequently occurs between early

and mid-June and coincides with peak annual temperatures and photoperiod, i.e. when the carbon gain of a single bright day is at its maximum. Consequently, any variation in melt-out dates, even by a few days, can affect SFGDD totals strongly, and can thus also explain the strong correlation between both variables ($r = -0.85$, $p < 0.001$).

R. ferrugineum is an evergreen shrub that has developed an opportunistic growth strategy, able to photosynthesize within two hours after snow removal (Larcher and Siegwolf, 1985). We can therefore reasonably assume that the species will also benefit from an earlier growing season, consistent with the correlation between SFGDD and radial growth. Our results are in line with numerous studies from Arctic and Alpine environments, which demonstrated that the accumulation of temperature above a certain threshold is a key factor driving growth through cell division and differentiation (Hoch, 2015; Körner, 2003; Wheeler et al., 2016; Wipf, 2010) and phenological transitions (Kudo and Suzuki, 1999; Molau et al., 2005). Results are also consistent with (i) dendrochronological studies that demonstrated the negative effect of snowpack duration on radial growth at the upper shrub limit in the Alps (Carrer et al., 2019; Francon et al., 2017; Pellizzari et al., 2014) and (ii) manipulation experiments (Stinson, 2005; Wheeler et al., 2016) showing increased productivity in case of artificial snow removal at sites where melt-out dates occurred after late-May (Wipf and Rixen, 2010). Results from the Alps differ from the wealth of studies in the Arctic, where a positive effect of snowpack was highlighted. We can explain this discrepancy by the fact that, in the Arctic, the positive winter precipitation effect is mostly related to snowpack thermal insulation, which protects plants from the harsh external conditions but also promotes higher winter soil surface temperatures with greater decomposition and nutrient release (Chapin, 2005; Hallinger et al., 2010). Furthermore, Alpine snowpack tends to be deeper and winter temperatures milder compared to the Arctic, and accordingly soil temperatures less sensitive to a slight change in snow accumulation. In the context of our study sites, root and vegetative shrub tissues are likely more protected from persistent negative temperatures in the Alps than in the Arctic (Domine et al., 2016; Ernakovich et al., 2014).

By contrast, at the lower sites (SAL1800, SAL2000), our results indicate that the weaker effects of (i) snow cover duration on SFGDD and (ii) SFGDD on ring width can be explained by earlier melt-out dates, occurring at these elevations between early and mid-May, when GDDs (4.9°C and 6.4°C in May on average for the 1960-2016 period at 2000 and 1800m asl respectively) and solar radiation have not yet attained peak values and are insufficient for shrub growth. In addition, SFGDD at SAL1800 and SAL2000 (1316°C on average) are significantly higher than those estimated at CN2400 and thus certainly less constraining for plants to complete the phenological cycle and a complete carbon storage at the end of the growing season. These hypotheses are consistent with experiments showing neutral to negative impacts of early (i.e. late-April) artificial snow removal (Dorrepaal et al., 2006; Wipf et al., 2006, 2009) at sites where natural early melt-out date would occur before mid-May. In the specific case of mountain shrub species, Wipf et al. (2009) found a general decrease in shoot growth in *Empetrum nigrum*, *Vaccinium myrtillus* and *V. uliginosum* under earlier melt-out dates due to higher frost exposure. In our case, the positive effect of a longer growing season can be similarly offset by the detrimental impact of spring frost (Choler, 2015; Jonas et al., 2008) or drought (Wheeler et al., 2016). Accordingly, we hypothesize that the positive correlations observed between low-elevation chronologies and March-April precipitation sums could either reflect the protective effect of late snowfalls against late frost

(Choler, 2015; Jonas et al., 2008), irradiation (Neuner et al., 1999) or limited drought stress during the subsequent growing season (Buchner and Neuner, 2003; Daniels and Veblen, 2004).

In the case of the Taillefer massif, a detailed analysis of meteorological conditions and radial growth in 1997 is relevant in order to illustrate the detrimental effects of late frost. According to the SAFRAN-Crocus reanalysis, melt-out occurred on approximately April 14 at lower elevations (SAL1800 and SAL2000,) and on May 31 at CN2400. At lower elevations, spring 1997 was the coldest since 1959 at the ground level. Immediately after melt-out, two cold episodes with two extreme freezing periods occurred between April 14 and 24 and between May 6 and 9. Ground level temperatures reached their absolute minimum on April 17 at -7.3°C . The same year, a majority of *R. ferrugineum* individuals from the two lower elevation sites formed extremely narrow rings, whereas no significant growth reduction was observed at 2400 m asl where plants were still under snow. This suggests that very low productivity at SAL1800 and SAL2000 is linked to cellular damage associated with intense late frost which likely damaged fine roots, leaves, buds, and the cambium (Inouye, 2000; Wipf et al., 2006; Wipf and Rixen, 2010). However, the absence of other events comparable to 1997 in meteorological or ring width series does not allow inference of robust relationships between late frost and radial growth. Here, experimental testing using ecophysiological monitoring could be used to further explore the effects of frost events on radial growth (Charrier et al., 2017).

4.2 Climate warming, trend analysis and the divergence problem

Our study demonstrates diverging effects of growing season length and snowmelt timing on radial growth along the elevational gradient. At CN2400, the decadal growth trend follows that of SFGDD, in line with findings from the Arctic (Myers-Smith et al., 2015). In addition, at lower elevation sites, our results also point to a divergence of radial growth as radial growth did not track the SFGDD increase during more recent decades. These results concur with the growth decline detected since the 1990s in shrub rings of *B. nana* and *S. glauca* from Western Greenland, where reduced ring width was attributed to increasing moisture limitation (Gamm et al., 2018). In the Taillefer massif, a weakening of the climatic signal is observed in shrub-ring chronologies after 1988, a year that can be considered as a tipping point in the meteorological series. Interestingly, comparable trends were reported for *B. nana* and *E. hermaphroditum* in the central Norwegian Scandes, where the positive influence of summer conditions was replaced by a negative response to May temperatures, over the last decades (Weijers et al., 2018a, 2018b). These findings echo the “divergence problem” reported in trees growing at circumpolar, northern latitudes (Briffa et al., 1998; D’Arrigo et al., 2008; Driscoll, 2005) and high-elevation sites (Büntgen et al., 2006, 2008). This body of evidence suggests more complex and nonlinear growth responses of trees to a changing climate, thereby leading to a decrease in year-to-year sensitivity of tree growth in previously temperature-limited sites (D’Arrigo et al., 2008; Vaganov et al., 1999; Wilmking, 2005). Potential causes for this divergence include warming-induced thresholds of tree growth (D’Arrigo et al., 2004; Jochner et al., 2018), limitation of growth by nutrient availability (Fajardo and Piper, 2017) or drought stress (Büntgen et al., 2006) or interactions between these factors. In the case of low-stature alpine vegetation, frost damage (Phoenix and Bjerke, 2016; Treharne et al., 2019) could also be assumed as a cause divergence, and merits further investigation.

5 Conclusion

In this paper, we analyzed annually resolved, statistically solid multi-decadal chronologies of *R. ferrugineum* shrubs sampled along an elevational gradient in the French Alps. Results show that a clear, elevation-dependent climatic signal exists in the growth-ring series. Growing degree days during the snow-free period emerge as a key unifying, growth-limiting factor at the study sites at 1800, 2000, and 2400 m asl. The positive response of radial growth to decreases in snowpack depth and duration is particularly acute at the highest site (2400 m asl) where both parameters strongly constrain SFGDD. Conversely, at lower elevations (1800 and 2000 m asl), we observe no positive effect of earlier snowmelt on radial growth, and further found that radial growth in this context is less sensitive to increases in summer temperature. In addition, our study provides evidence of a recent divergence in radial growth, insofar as the increase in SFGDD results in a weakening of the climatic signal in shrub ring-width chronologies since 1988, similar to the divergence observed in trees at circumpolar and alpine sites. Conversely, at lower elevations (1800 and 2000 m asl), an extremely narrow ring was formed in 1997 following late frost. Albeit unique in the dendrochronological series, it illustrates the potential detrimental effects of early melt-out dates on frost risk and productivity. Accordingly, 1997 might well be an example of extreme events that can be expected to become more frequent in a warmer climate.

Given the wide geographic distribution of *R. ferrugineum* and its large occurrence above treeline in the Alps, this species represents a promising candidate and a valuable proxy to document precisely, at decadal to centennial scales, the response of dwarf shrubs to recent climate change. To improve our understanding of processes governing shrub growth in mountainous environments further, including the potential impact of extreme climatic events, we recommend future work combining field-based ecophysiological and microclimatic monitoring, as performed in Charrier et al. (2017), with remote sensing of landscape-scale vegetation dynamics in alpine regions.

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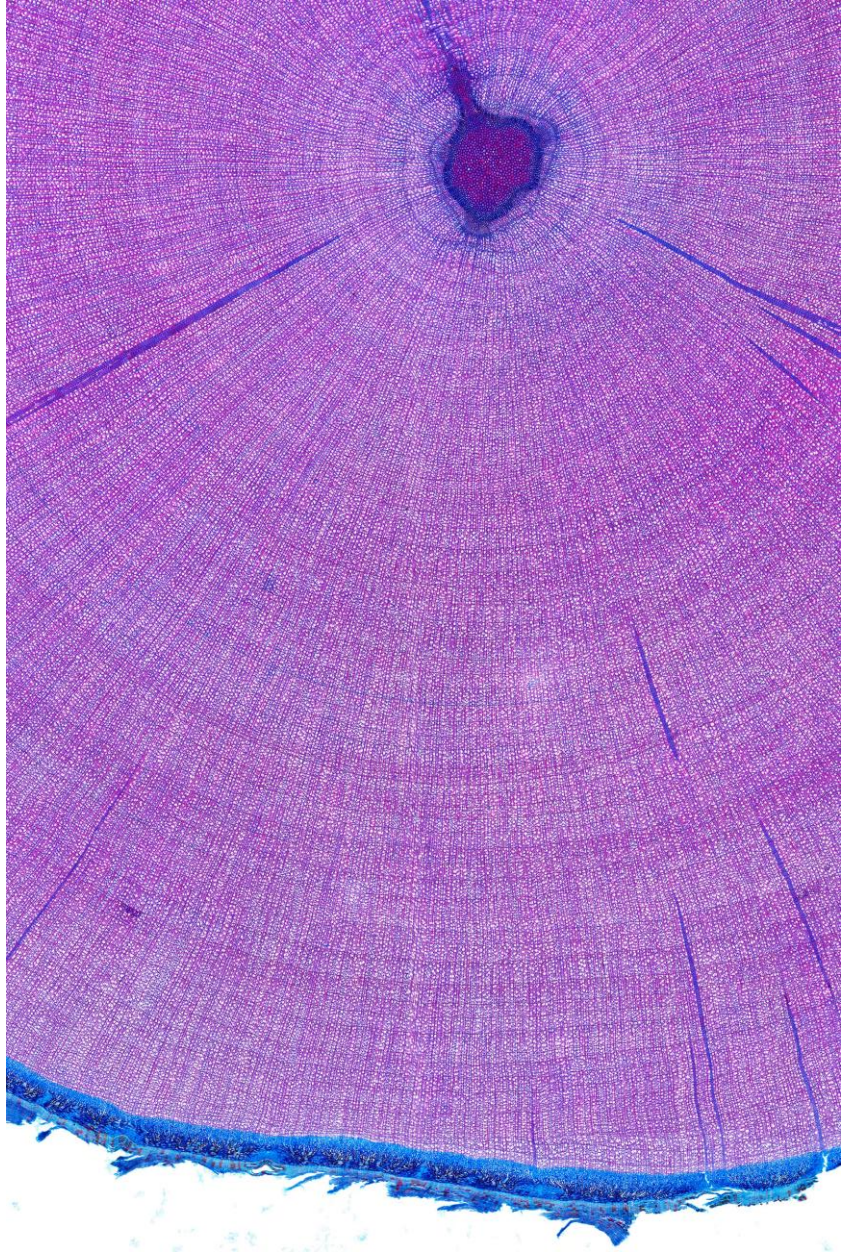
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Chapitre 3. Some (do not) like it hot:
shrub growth is hampered by heat
and drought at the Alpine treeline in
recent decades

Les résultats présentés dans ce chapitre sont basés sur des échantillons récoltés en juin 2017 dans le Massif du Queyras. Christophe Corona, Sébastien Guillet et moi-même ont participé à cette troisième campagne de terrain. Les micro-sections ont été réalisées avec le support de Brigitte Girard (UMR PIAF, INRA). Les données météorologiques, provenant du modèle SAFRAN-Crocus de Météo-France, ont été extraites par Samuel Morin et Carlo Maria Carmagnola (CEN, Météo-France). J'ai fait les analyses dendrochronologiques, le choix et la réalisation des analyses statistiques.

Ce chapitre est en totalité constitué de l'article accepté pour publication dans la revue : *The American Journal of Botany*, 2020.

Photographie de page précédente : Microsection d'une tige d'un individu échantillonné sur la face nord de la Crête des Baysses, dans le Queyras.

Some (do not) like it hot: shrub growth is hampered by heat and drought at the Alpine treeline in recent decades

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Abstract

Premise of the study: Mountain ecosystems are particularly sensitive to climate change. However, only a very small number of studies exist so far using annually-resolved records of alpine plant growth spanning the past century. This paper aims to identify the effects of heat waves and drought, driven by global warming, on annual radial growth of *Rhododendron ferrugineum*.

Methods: We constructed two century-long shrub ring-width chronologies from *R. ferrugineum* individuals located on two adjacent, north and west-facing slopes, located in the southern French Alps. We analyzed available meteorological data (temperature, precipitation and drought) over the period 1960-2016. Climate-growth relationships were evaluated using (i) bootstrapped correlation functions and (ii) structural equation models to identify the effects of rising temperature on shrub growth.

Key results: The analysis of meteorological variables over the 1960-2016 period reveals a shift occurring in the late 1980s, after which heat waves and drought have increased in both intensity and frequency. In response to these extreme climate events, shrubs have experienced significant changes in their main limiting factors. Between 1960 and 1988, radial growth on both slopes was strongly controlled by the sum of growing degree days during the snow free period. Between 1989 and 2016, August temperature and drought have emerged as the most important

Conclusions: Increasing air temperatures have caused a shift in the growth response of shrubs to climate. The recently observed negative effect of high summer temperature and drought on shrub growth can, however, be buffered by topographic variability, supporting the macro- and microrefugia hypotheses.

Keywords

Shrub-ring analysis; dwarf shrubs; *Rhododendron ferrugineum*; Standardized Precipitation-Evaporation Index, drought, heat wave, dendroecology, Structural equation model

1 Introduction

Mountain regions are warming at a rate twice as fast as the global average, and are thus expected to undergo a greater relative temperature increase over the next century (Mountain Research Initiative EDW Working Group, 2015; Stocker et al., 2013). In the European Alps, recent warming is not linear, and a sharp increase in annual temperature has started to emerge in meteorological records since the end of the 1980s (Beniston et al., 2018; Gobiet et al., 2014). A growing body of evidence documents changes in mountain vegetation in response to longer and warmer growing seasons, such as (i) an upward shift of species distribution (Lenoir et al., 2008), (ii) increasing biodiversity on summits (Pauli et al., 2012; Steinbauer et al., 2018), (iii) phenological shifts (Choler, 2015), (iv) increasing plant productivity and long-term greening (Carlson et al., 2017; Filippa et al., 2019), as well as (v) a reshuffling and thermophilization of alpine communities (Gottfried et al., 2012). However, and in sharp contrast to the Arctic, where widespread shrub expansion has been identified (Myers-Smith et al., 2011, 2015a), evidence remains scarce for a similar large-scale shrub expansion in the European Alps, even if some regional studies have documented a denser shrub cover above treeline during recent decades (Anthelme et al., 2007; Cannone et al., 2007; Carlson et al., 2017).

Although alpine and arctic ecosystems both experience short and cold growing seasons, Ernakovich et al. (2014) recently predicted alpine ecosystems to be more drought-sensitive than their arctic counterparts under the influence of climate change. According to the authors, alpine plants will potentially experience earlier senescence as a result of reduced water availability and will thus be unable to extend their growing season, despite earlier snow melt out. At the same time, however, non-linear responses to rising summer temperatures have been locally observed in dry arctic landscapes, where soil moisture seems to buffer the positive effect of higher temperatures on shrub growth (Ackerman et al., 2017; Bjorkman et al., 2018; Gamm et al., 2018; Myers-Smith et al., 2015a).

In the European Alps, the frequency and intensity of summer heat waves and extreme drought events have increased in recent decades, and this increase is expected to continue with increasing temperatures (Corona-Lozada et al., 2019; Easterling, 2000; Orsenigo et al., 2014; Russo et al., 2014). To date, only a handful of studies have documented responses of alpine ecosystems to heat waves and drought, leading to contrasting results (Corona-Lozada et al., 2019; Cremonese et al., 2017; De Boeck et al., 2016; Jolly et al., 2005). Corona-Lozada et al., (2019), De Boeck et al. (2016) and Cremonese et al. (2017) documented a negative effect of summer drought on alpine plant productivity, which was clearly aggravated in the case of heat waves. In the Swiss Alps, Jolly et al. (2005) reported that the 2003 heat wave would have had positive effects on plant growth above treeline through an extension of the growing season, but negative impacts at lower elevations, where the higher evaporative demand increased drought sensitivity.

Shrub dendroecology, which analyzes radial stem growth over time, allows us to contextualize the response of woody vegetation to climate variability in a longer term context (Myers-Smith et al., 2015b). For this reason, the approach has been used widely across the Arctic biome to assess climatic drivers of shrub expansion. In comparison, only a handful of chronologies have been constructed so far for shrubs in alpine regions (e.g. Franklin, 2013; Liang and Eckstein, 2009; Lu et al., 2015). Dendroecological studies carried out in the European Alps hitherto identified that increasing summer temperatures and earlier snow melt-out dates would have a positive effect on shrub growth (Carrer et al., 2019; Francon et al., 2017; Pellizzari et al., 2014). By contrast, in the Mediterranean mountain ranges of south-eastern Spain, juniper shrubs were shown to experience a change in their main limiting factors, shifting from temperature and growing season length to water availability (García-Cervigón et al., 2018). The authors further demonstrated that contrasting micro-climates – induced by topography – could modulate the response of junipers to ongoing climate change.

Here, we investigate long-term climate-growth relationships for the widespread and dominant alpine shrub species, *Rhododendron ferrugineum* L., using samples within the Queyras massif located in the southern French Alps. We hypothesize that the recent increase in drought and heat waves could counteract the beneficial effects that rising temperatures have on shrub radial growth, but that this buffering could be different and/or modulated according to slope aspect. In order to test this hypothesis, we: (i) identified the main climatic parameters controlling *R. ferrugineum* radial growth at the study site by using a bootstrap correlation analysis; (ii) included these parameters in structural equation models (SEM) to disentangle their respective effects on two adjacent slopes of different aspects and (iii) attempted to detect potential shifts in the climatic drivers of shrub growth, resulting from climate changes since the late 1980s.

2 Methods

2.1 Study site and climate

The study site is located in upper Guil valley, in the French southern intra-alpine Queyras massif, (Fig. 1a, b, c). Geology of the region is dominated by Mesozoic *schistes lustrés* (Tricart and Lemoine, 1986), a tectonic stack of blue schist to green schist-facies carbonate metasediments on which acidic soils have developed. More precisely, the site is located at treeline (2350 m asl) and dominated by the Crête des Bayssees, in the vicinity of the French-Italian border. The site was chosen to minimize effects other than slope aspect (geographical proximity for similar bedrock conditions, climate and slope inclination). *Rhododendron ferrugineum* individuals were sampled on two adjacent, west (Queyras West, QW, Fig. 1c, d) and north-facing (Queyras North, QN, Fig. 1c, e) slopes. The landscape is dominated by a *Rhododendron ferrugineum* heathland intermixed with *Vaccinium* sp. and *Salix* sp. shrubs as well as isolated *Larix decidua* and *Pinus cembra* trees. Slope angles (30°) are comparable on both slopes. Microtopography is very regular at QW but slightly more heterogeneous at QN, with the latter being situated in the catchment area of the Nalbert torrent. Climate is characterized by a mix of montane-Mediterranean and continental influences (Touflan et al., 2010). According to the SAFRAN-Crocus meteorological data (1960-2016) downscaled to the location of our study sites, annual precipitation is

873 mm. Monthly precipitation totals are smallest in winter and summer (P-February = 51 mm, P-July = 58 mm) and largest in spring and autumn (P-June = 84 mm, P-October = 98 mm). July (9.4°C) is the warmest month and snow cover remains until May 24 (+/- 12 days) at QW and June 1 (+/-12 days) at QN.

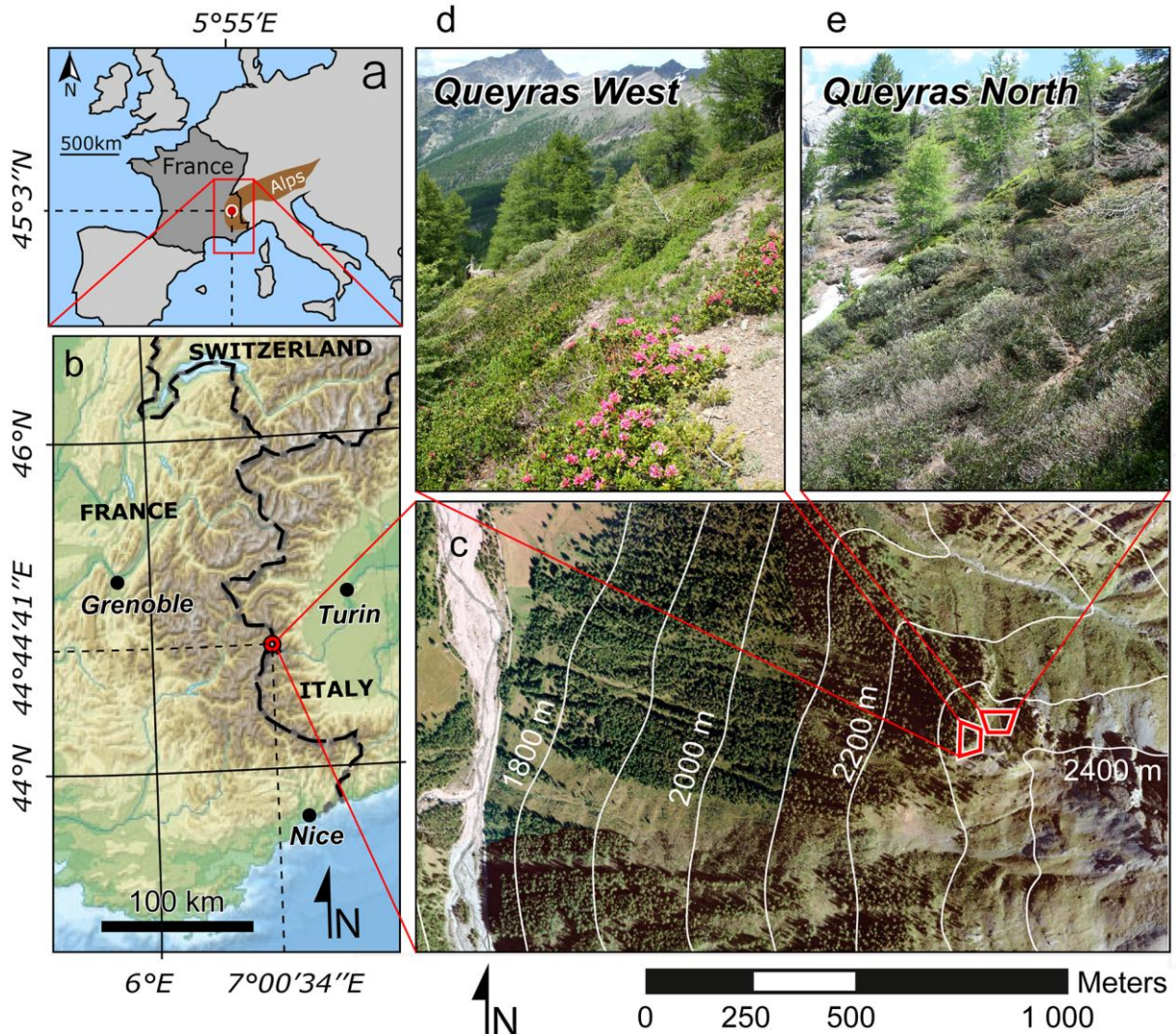


Figure 1: (a, b, c) Location and overview (d, e) of the west- (QW: Queyras West) and north-facing slopes (QN: Queyras North) selected for sampling in the Queyras massif (Southern French Alps). Photographs of QW (d) and QN (e) were taken on June 15, 2017.

2.2 Sample collection and preparation

Rhododendron ferrugineum is a dominant mountain shrub in the siliceous Alps from about 1600 to 2500 m asl (Ozenda, 1985), where it is often found as the dominant species in sub-alpine dwarf shrubs communities (Pornon and Doche, 1996). It can form large heathlands colonizing grazed or abandoned grasslands on north, west, and northwest-facing slopes of the central and southern Alps (Escaravage et al., 1997). High longevity as well as clearly identifiable annual rings – discriminated by a band of radially aligned, thick walled latewood fibers, flattened along the ring boundary – make *R. ferrugineum* a promising model to study shrub response to long-term climate variability (Francon et al., 2017).

In this study, a total of 36 randomly selected *R. ferrugineum* individuals were sampled in June 2017 at a minimum distance of five meters between each other, 18 at QW and 18 at QN. The main stem of each specimen was cut at the level of the root collar. In the lab, two to three 20 µm-thick cross sections were prepared for each stem, a first sample at the root collar and further samples at 10 to 20 cm steps along the stem, so as to apply an approach known as serial-sectioning method (Kolishchuk, 1990). Cross sections were then stained with Safranin and Astra Blue, and permanently fixed on microslides with Canada balsam (Schweingruber et al., 2011). High-resolution digital pictures were taken using a Carl Zeiss Axio Observer Z1 coupled to a Zeiss AxioCam MR R3 camera under 40–100 magnification. Individual images were merged automatically to cover the whole cross-sections by using the Zen 2011 software.

2.3 Chronology development

Ring widths were measured along three radii on each section from digital images with CooRecorder 7.6 (CYBIS Elektronik & Data AB). Radial measurements along the chosen radii were supplemented by careful visual inspection of each cross section to eliminate annual growth underestimation caused by partially missing rings. Crossdating was based on a three-step procedure involving a comparison of growth curves (1) between the three radii measured within a single cross section, (2) among the mean growth curves of all sections within individual plants, and finally (3) between the mean growth curves of all shrubs on each of the slopes sampled (Francon et al., 2017; Shetti et al., 2018). The output of the visual cross-dating was checked statistically with COFECHA (Holmes, 1994).

After cross-dating, the mean series of each section was standardized (Cook and Kairiukstis, 1990; Fritts, 1976) in ARSTAN (Cook, 1987). To remove age-related growth trends and other possible biological effects, we standardized each growth curve at the section scale using a negative exponential function, so as to obtain detrended chronologies. A negative exponential function was chosen as a rather conservative growth trend model to keep as much climatic signal as possible in the series. Growth indices (referred to as ring-width indices, RWI) were averaged to mean standard individual and site chronologies, on a year-by-year basis, and by using a bi-weighted robust mean that reduces the influence of outliers (Cook and Peters, 1981). In addition to the standard chronologies, we also computed so-called residual chronologies in which auto-correlation was removed.

Descriptive statistics including standard deviation (SD), mean sensitivity (MS) and autocorrelation (AC), were computed for both detrended chronologies. In addition, the Expressed Population Signal (EPS, Wigley et al., 1984), Subsample Signal Strength (SSS, Wigley et al., 1984; Buras, 2017) and mean inter-series correlation (\bar{r}) were computed using the ARSTAN software, with the aim to evaluate the robustness of each chronology. The EPS and SSS statistics quantifies the strength of the common climate signal in the tree-ring proxies by calculating how well a finite sub-sample represents an infinite (EPS) or finite sample (SSS) (Buras, 2017; Wigley et al., 1984). For both SSS and EPS, a threshold of 0.85 was used to guarantee robustness of the chronologies.

2.4 Meteorological and climatic data

Monthly temperature, precipitation sums and snow-related parameters were extracted from the SAFRAN-Crocus reanalysis. The SAFRAN analysis system combines *in-situ* meteorological

observations with synoptic-scale meteorological fields to provide continuous time series of meteorological variables at hourly resolution, for elevation bands of 300 m, different slope aspects and angles within spatial units, referred to as “massifs” (Queyras in the case of this study), for which meteorological variables are assumed to be horizontally homogenous (Durand et al., 2009). In addition, the Crocus model was run specifically for QW and QN. The Crocus model provides corresponding reanalysis of snow conditions and underlying ground temperature for the same time span as SAFRAN reanalysis (Durand et al., 2009; Vionnet et al., 2012). Vegetation was represented in a simplified manner in the simulations, assuming grassy conditions to simulate typical snow conditions and underlying ground temperature for open areas. The dataset extends back to August 1958.

From the hourly outputs, we extracted (i) monthly temperature and precipitation sums, (ii) dates of snow melt-out (defined as the last day when snow cover reached at mean height of the shrub canopy located at ca. 50 cm), (iii) snow-free growing degree days (hereafter referred to as SF-GDD and computed as the sum of positive air temperature from the melt-out date to the end of growth period arbitrarily fixed at August 31) as well as (iv) heat wave index (HWI). HWI series accounting for the magnitude and the duration of heat waves (Russo et al., 2014) were computed from July 1 to September 10 over the 1960–2016 period. In a first step, we computed a daily temperature threshold defined as the 80th percentile of the daily maxima over the period 1959–2016. This threshold was calculated by considering a 30-day window centered on the day of interest. In a second step, we extracted episodes with at least three consecutive days during which the maximum air temperatures exceeded the threshold. These episodes were considered as heat waves. Finally, we summed daily maximum temperatures of each episode to obtain a measure of the magnitude of the heat wave.

We used the Standardized Precipitation–Evapotranspiration Index (SPEI) developed by Vicente-Serrano et al. (2010) as a metric to quantify drought. SPEI combined precipitation, temperature, wind, nebulosity and relative humidity series from the SAFRAN analysis system for the period 1960–2016 at time intervals of 2 (SPEI2) and 12 months (SPEI12, September to August). SPEI2 was used for climate-growth analyses, whereas SPEI12 was employed to identify dry years.

2.5 Climate-growth modelling

We used Structural equation models (SEM) to unravel the direct and indirect effects of interrelated climatic variables, in particular heat waves and drought, on *R. ferrugineum* growth. SEM is an extension of a path analysis and represents a relevant statistical framework to model multivariate effects of driving factors on a response variable (Grace and Bollen, 2005).

As a preliminary analysis to determine the nature of causal relations between climate variables and the shrub ring chronologies implemented in the path diagrams of each structural equation model, we computed correlations between the standard and residual chronologies and monthly climatic variables using Bootstrapped Correlation Functions (BCF) using the *Treeclim* package (Zang and Biondi, 2015) in R (R Core Team, 2016). The climatic dataset included monthly temperature, precipitation sums, snow melt-out timing, SF-GDD, and SPEI2 sequences. For each variable, we included values from July of the year preceding growth-ring formation ($n - 1$) to September of the year of actual ring formation (n), thereby analyzing a set of 51 predictors. The relationships between the HWI and the shrub-ring

chronologies was evaluated using Spearman's rank correlation. Significance was assessed at $p < 0.05$ through a 1000 bootstrap replicate approach.

Based on this pre-selection of variables and to unravel the potential impacts of rising temperatures on shrub growth, we computed SEMs for two distinct periods, namely 1960-1988 and 1989-2016. The splitting of the record in two subsets of equal length was motivated by the fact that the meteorological series, especially HWI, indicate a threshold around 1989. In addition, as shown in Fig. 2, statistically significant differences are observed in mean summer temperature, SPEI12 and HWI between both sub-periods (see Results section and Fig. S1). In the resulting models, the set of causal assumptions are represented as arrows on diagrams and the values of standardized path coefficients quantify the relative impact of a driving variable on a response variable (Jonas et al., 2008). Prior to analyses, we verified that the diagrams did not include any feedbacks and that relationships among variables could be described using linear models. We checked the data for goodness-of-fit by using the Chi-square statistic with a $p > 0.05$ cut-off (Grace, 2006) and the comparative fit index ($CFI > 0.90$, Bentler, 1990). To perform and control SEMs, we used the *Lavaan* package (Rosseel, 2012) running in R. Akaike information criterion (AIC) was used to compare performance among competing SEMs.

3 Results

3.1 Evolution of summer climate in the Queyras massif

Figure 2 synthesizes the evolution of summer conditions in the Queyras massif with a specific focus on dry conditions and heat waves. The linear regressions show significant increasing trends ($P < 0.001$) for mean summer (June-August) temperature over the period 1960-2016. For the same period, we observed a significant decrease in the annual SPEI computed from September of the previous ($n-1$) to August of the current (n) year ($P < 0.001$), pointing to an increasing frequency of years with water deficit. Mean values of SPEI12 thereby decreased from 0.41 to -0.41 for the sub-periods 1960-1988 and 1989-2016, respectively. At the same time, mean summer (June-August) temperatures increased from 7.9°C to 9.2°C. In addition, HWI values reveal an increase in the frequency of extremely warm summers since 1989 (see Fig. S1). The two strongest heat waves in the record occurred during the summers 2003 and 2015. They were of comparable magnitude with a HWI of 138.5 and 139.4, respectively. Very warm

summers were also recorded in 2016 (HWI = 123.2) and 2012 (HWI = 104.8). However, no significant trend was observed in the summer rainfall series over the same period.

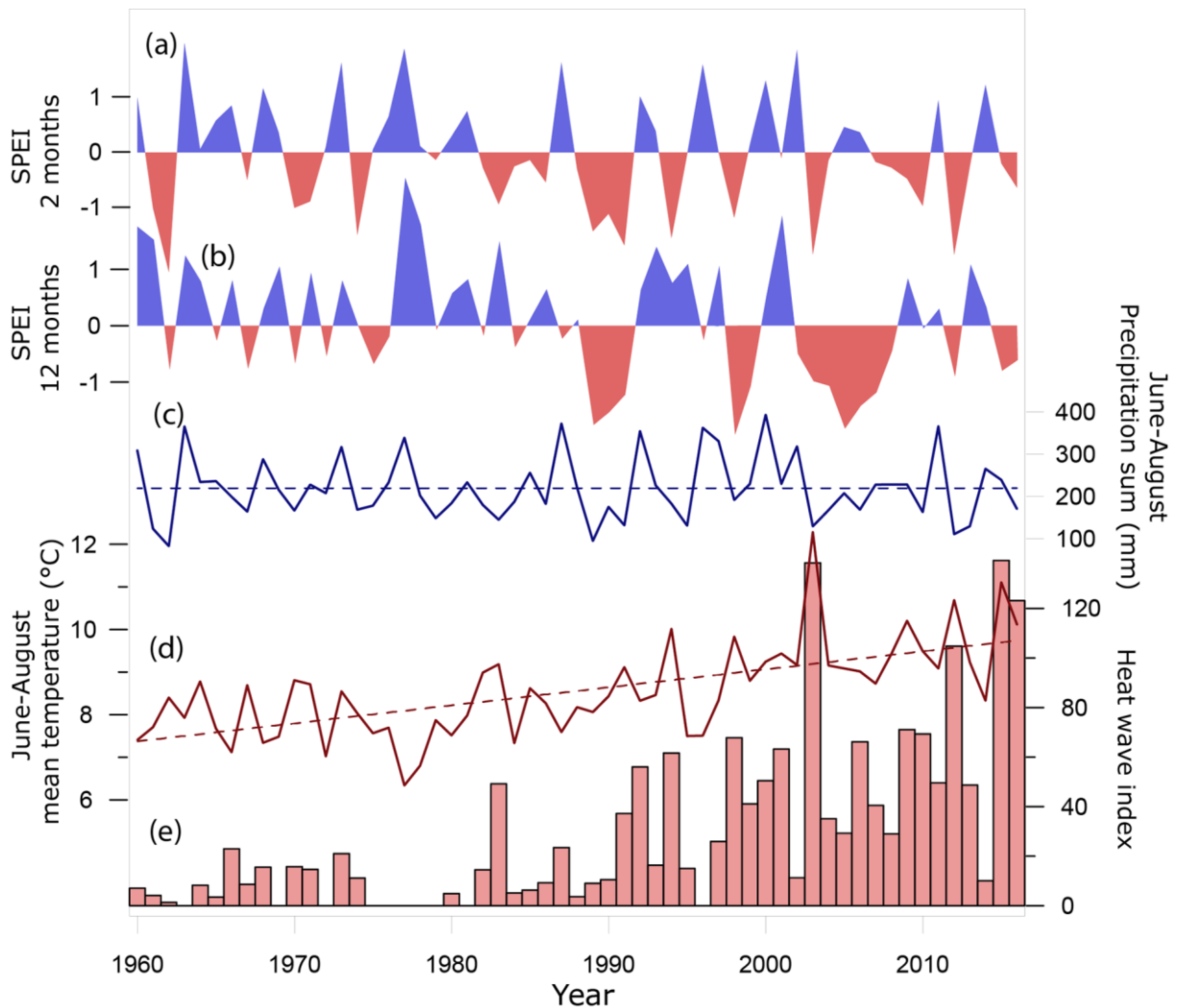


Figure 2: Synthesis of climate evolution during summers in the Queyras massif for the period 1959-2016, and with a specific focus on dry conditions and heat waves. (a-b) Evolution of the 2- (i.e. July and August) and 12-months (September-August) Standardized Precipitation-Evapotranspiration Index (SPEI). Negative SPEI values correspond to dry conditions. The evolution of (c) summer (June-August) precipitation sums are indicated with a blue line, (d) summer (June-August) mean temperature are shown with a red line. (e) Unscaled values of the heat wave index over the period 1959-2016. The dotted blue and red lines indicate linear trends for summer precipitation sums and mean temperatures, respectively.

3.2 Statistics of the chronologies

Cross-dating was successful for 10 individuals at QN and 14 individuals at QW (Fig. 3; Tab. 1). On average, shrubs at QN were significantly older (mean age: 83 years) than at QW (50 years). Annual radial increment between cambial ages at 20 and 39 years was, on average, 0.09 mm at QN and significantly higher at QW (0.14 mm, $P < 0.001$). Rbar values computed between the detrended ring width series are 0.42 and 0.56 for QN and QW, respectively. EPS values of 0.89 at QN and 0.93 at QW attest

to the strong coherence of growth between individuals selected within both chronologies. Noteworthy, the SSS (and EPS computed for 30 year moving periods) values exceeded the 0.85 threshold from 1949 (1959) at QW, and from 1938 (1952) onward at QN. Autocorrelation (0.13 at QW and 0.22 at QN) is limited at both sampling sites. Mean sensitivity at QN (MS = 0.33) is slightly higher than at QW (MS = 0.30).

Table 1: Characteristics of *R. ferrugineum* ring-width chronologies: Length, mean age, median ring-width computed for raw chronologies and standard deviation (SD), signal strength (Rbar and EPS for the period 1960–2016), mean sensitivity (MS) and first order autocorrelation (AC) (calculated over the entire periods covered by the chronologies. Values refer to series after detrending.

Chronology	First year	Last Year	Mean age	SD	Rbar	EPS	MS	AC
QN	1906	2016	83	0.30	0.42	0.89	0.33	0.24
QW	1918	2016	50	0.27	0.56	0.93	0.30	0.13

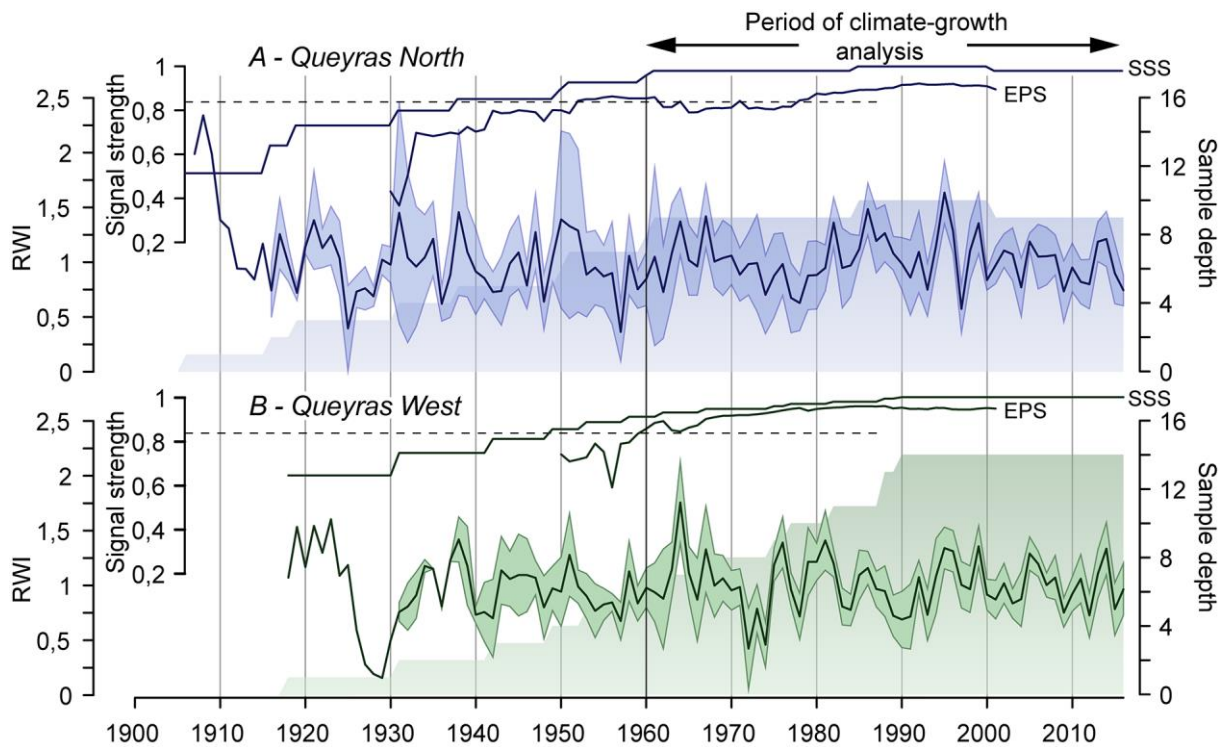


Figure 3: Detrended *R. ferrugineum* ring width chronologies and the Subsample Signal Strength (SSS) from Queyras North (panel a) and Queyras West (panel b) with their confidence intervals (± 1 SD). The Expressed Population Signal (EPS) is computed with a 30-year moving window (solid line above the chronologies). The horizontal dotted black lines denote the 0.85 signal strength threshold. The vertical continuous line indicates 1960, the starting year for climate-growth analyses. Colored background surfaces represent sample depth.

3.3 Climate-growth relationships

Bootstrapped correlation functions (BCFs, Fig. 4) showed significant positive correlations between RWI and SPEI2 for July and August at QW ($r=0.41$, $P<0.01$) whereas no significant relationship was found at QN. At QW, shrub ring width is inversely correlated with August temperature (N) ($r=-0.29$, $P < 0.01$)

and positively associated with summer (July-August) precipitation sum ($r=0.30$, $P<0.01$). At QN, we found positive relationships of RWI with October (N-1, $r= 0.20$, $P<0.05$) and July (N, $r=0.22$, $P<0.05$) mean temperatures. Radial growth was negatively correlated with precipitation sums in October (N-1, $r=-0.26$, $P<0.05$), but no significant correlation could be found with respect to precipitation sums during the growing season. The Spearman correlation between the heat wave index and RWI was negative and stronger at QW than at QN, but again not significant at either of the slopes ($\rho = -0.26$, $P = 0.06$ and $\rho = -0.04$, $P = 0.76$ at QW and QN, respectively). The four heat waves of 2003, 2012, 2015 and 2016 have systematically been associated with ring widths that were smaller than average at QW (RWI = 0.836, 0.727, 0.784 and 0.964, in chronological order) and with average or small rings at QN (RWI = 1.072, 0.800, 0.899 and 0.743, in chronological order). With regard to winter conditions, RWI was significantly limited by above-average precipitation sums at QN ($r=-0.34$, $P<0.01$) and by snow melt-out dates ($r=-0.27$, $P<0.05$) at QW.

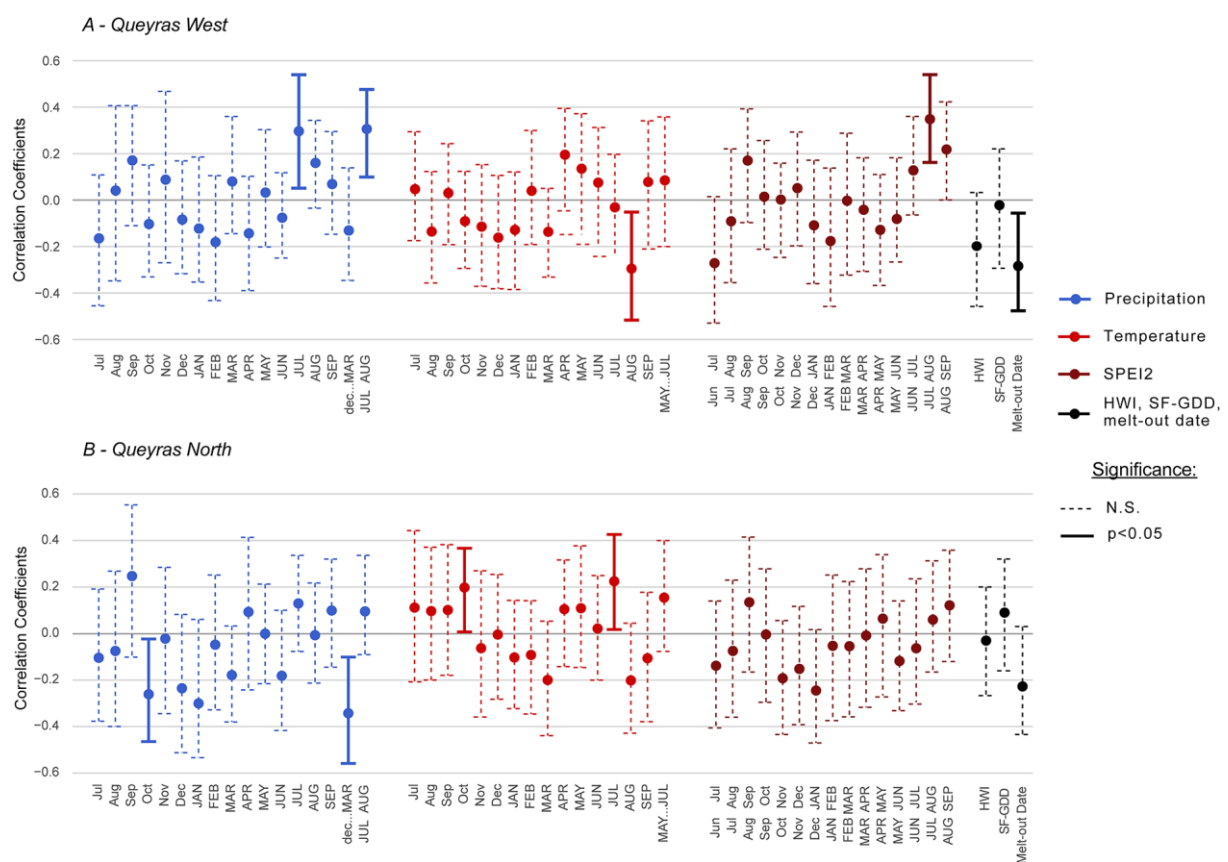


Figure 4: Bootstrapped correlations computed between *R. ferrugineum* detrended chronologies (a: Queyras West, b: Queyras North) and monthly (seasonal) precipitation sums, mean temperatures, 2-months (July-August) Standardized Precipitation-Evapotranspiration Index (SPEI2), heat wave index (HWI), Snow-Free Growing Degree Days (SF-GDD) and snow melt-out dates for the period 1960–2016. Months of the year preceding (N-1) ring formation (N) are shown with lowercase letters, current (N) year periods are shown with capital letters.

Based on these initial results, we hypothesized that shrub growth would depend on SF-GDD which in turn depended on melt-out dates, and thus possibly mitigated by the negative effects of drought (Fig. 5). The SEMs computed over the period 1960-2016 explain 24 and 14% of inter-annual variations in ring width of *R. ferrugineum* at QW and QN, respectively, and present a good performance ($\chi^2 = 14.87$, $df = 15$, $P=0.47$, $CFI = 1.00$ at QW and $\chi^2 = 19.2$, $df = 14$, $P=0.16$, $CFI = 0.98$ at QN). Modelling results

confirm that SF-GDD is a strong driver of radial growth at QN (path coefficient of 0.40, $P < 0.05$) and to a lesser extent at QW (0.29, $p < 0.1$). At both sites, SF-GDD are controlled by snow-free period temperatures and melt-out dates which in turn will depend significantly on December-March precipitation sums and on spring temperature (April temperature at QW and May temperature at QN).

SEMs support the hypothesis of SPEI2 having a significant effect on RWI at QW with a path coefficient of 0.34 ($P < 0.01$), whereas no such effect was detected between SPEI (July + August) and RWI at QN. August mean temperature had a negative effect on RWI at QW (-0.32, $P < 0.05$) and at QN (-0.42, $P < 0.01$). The SEM computed for QW indicates that the latter parameter, in combination with summer precipitation sums, would also have an indirect effect on radial growth as it controls SPEI2. The inclusion of July (N) as well as October (N-1) temperatures and precipitation sums – parameters that were shown to be significantly correlated to *R. ferrugineum* growth according to BCFs – did not improve the robustness of our SEMs significantly (Table S2). Therefore, we present here only the best performing path model at each site. The SEMs based on the residual chronologies provide comparable results (Fig. S3).

3.4 Stationarity of shrub growth-climate relationships over time

SEMs computed for the periods 1960-1988 and 1989-2016 all display Chi-square p-values exceeding 0.05 and CFI values above the 0.9 cut-off. Between 1960 and 1988, the SEMs were comparable and confirmed the crucial impact of SF-GDD on RWI at both sites (0.52 and 0.70, $P < 0.01$ and $P < 0.001$ at QW and QN, respectively). Correlations between August temperatures and radial growth were not significant. A limited effect of SPEI2 is detected at QW (0.31, $P < 0.1$). The SEM computed for the QN ring-width chronology has greater explanatory power ($r^2 = 0.41$) than the one computed for QW chronology ($r^2 = 0.29$).

After 1989, the overall impact of SF-GDD on RWI strongly decreased and are no longer significant at the investigated slopes. At the same time, the path coefficients between August temperature and radial growth decreased from -0.15 to -0.45 ($P < 0.05$) at QW and -0.16 to -0.56 ($P < 0.05$) at QN. Similarly, the influence of SPEI increased at QW (0.38, $P < 0.05$).

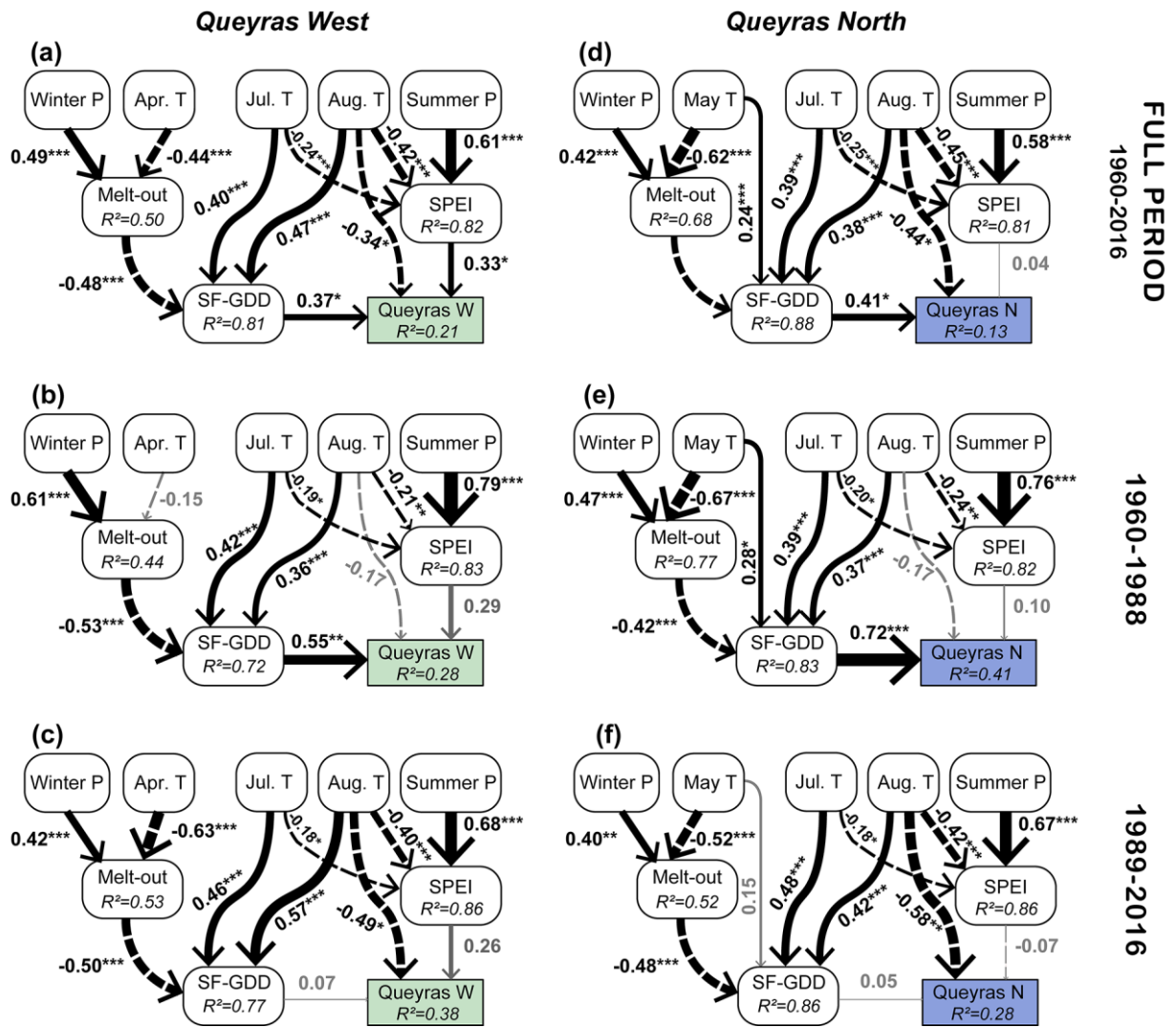


Figure 5: Structural Equation Models (SEMs) showing all climatic variables expected to have a direct or indirect influence on shrub growth as well as their respective effects on shrubs ring width indices for the Queyras West (left panel, a, b, c) and Queyras North (right panel, d, e, f) sites between 1960 and 2016 (a, d), as well as for the sub-periods 1960-1988 (b, e) and 1989-2016 (c, f). Black solid arrows denote positive while dotted arrows represent negative significant relationships ($P < 0.05$) between variables. Grey arrows indicate non-significant relationships ($P > 0.05$). The thickness of arrows is proportional to the standardized path coefficient. Multiple R^2 are given in the box of each response variable. *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$), ($P < 0.1$) indicate the significance level of each effect.

4 Discussion

Shrub dendroecology entails challenging cross-dating due to the often thin, wedging or missing rings (Hollesen et al., 2015; Myers-Smith et al., 2015b), which renders assigning growth rings to an exact year of formation sometimes difficult. Despite these challenges, we were able to build two long-term chronologies in this paper. The North (QN) and West (QW) chronologies presented here are well replicated ($n > 6$) and robust ($EPS > 0.85$) over the period covered by meteorological data (i.e. 1960-2016). The rejection rate (33%: 4 out of 18 and 8 out of 18 individuals at QW and QN, respectively) is mainly related to the occurrence of sequences with extremely narrow, wedging or missing rings, difficult to detect and measure. The occurrence of complex samples was larger at QN than at QW.

On average, *R. ferrugineum* ring widths were significantly (33 percent) thinner at QN than at QW for cambial ages between 20 and 39 years. Similarly, the correlation between both growth-ring chronologies was rather limited ($r=0.57$ for the period 1960-2016), despite the fact that sampling sites were located next to each other. Differences in shrub productivity and asynchronous signals at both sites are likely related to differences in aspect which have been shown to induce different exposition to photosynthetically active radiation, wind and snow accumulation (Körner, 2003). These differences are likely leading to colder temperatures and shorter growing seasons at QN. Significantly higher inter-series correlations (r_{bar}) on the west-facing slope also suggest (Dearborn and Danby, 2018), that growth patterns at QW would be more governed by broad-scale climatic patterns influencing growth of all individuals. At QN, by contrast, we hypothesize that microtopography may induce substantial spatial variability in shrub growth as previously observed in topographically complex regions (Danby and Hik, 2007; Dearborn and Danby, 2018; Leonelli et al., 2009; Ropars et al., 2015; Young et al., 2016).

Despite these differences, Bootstrapped Correlation Functions (BCFs) profiles and Structural Equation Models (SEMs) computed for both slopes show comparable results for the period 1960-2016. They demonstrate that SF-GDD which is largely determined by snow melt-out dates, which constitutes a strong limiting factor for *R. ferrugineum* radial growth in both topoclimatic contexts. A similar positive effect of increased growing season length and/or temperature has been found at many northern and high-elevation locations worldwide (Blok et al., 2011; Forbes et al., 2010; Myers-Smith et al., 2015a; Pellizzari et al., 2014), where plant growth is temperature limited (Körner, 2003; Wheeler et al., 2016; Wipf, 2010). The negative correlations between radial growth, melt-out timing and winter snowfalls observed in the BCF profiles at QW and QN are congruent with other dendroecological studies carried out in the Alps (Carrer et al., 2019; Francon et al., 2017; Pellizzari et al., 2014). Our results differ from most Arctic studies, however, where the positive effect of snowpack on shrub growth (Hallinger et al., 2010; Hollesen et al., 2015; Ropars et al., 2015; Zalatan and Gajewski, 2006) has been attributed to its thermal insulation effect (Chapin, 2005; Hallinger et al., 2010; Sturm et al., 2005). In the Queyras massif, SEMs reveal that the relationship between winter precipitation and *R. ferrugineum* radial growth is not direct but instead affects available SF-GDD totals by regulating snow cover accumulation and duration.

Analysis of the meteorological series shows (1) an increase in summer temperatures between 1960 and 2016 as well as (2) stronger annual water deficits and (3) more frequent and severe heat waves since the early 1990s. These changes have apparently led to a clear shift in the climate-growth relationships since the late 1980s. In that sense, we observe that *R. ferrugineum* radial growth was controlled mainly by SF-GDD (with the latter depending on snowpack duration) until 1989, but has ever since been limited by August temperatures at both sites and by summer drought at QW. Comparable shifts have been reported in the Mediterranean mountains and at a dry Arctic tundra site. It was shown that junipers from south-eastern Spain exhibit a strong drought signal as a response to increasing evapotranspiration rates (García-Cervigón et al., 2018), whereas in Greenland, the growth decline of dwarf birch coincides with a shift in the correlations between growing season air temperatures and neutral to strongly negative plant growth rates (Gamm et al., 2018). Noteworthy, responses to August temperatures comparable to those observed in the Queyras massif since 1989, have remained exceptional and hitherto only observed in the dry environments of the Tibetan plateau (Liang et al., 2012), Mediterranean mountains (García-Cervigón et al., 2018) or dry arctic tundra (Gamm et al., 2018). In the Western Italian Alps, by contrast,

Carrer et al. (2019) described a positive association between dwarf juniper growth and summer precipitation but did not report any significant effect of summer temperature on ring width.

Moreover, a negative effect of summer drought on RWI was only observed at QW over the full period considered (1960-2016). Accordingly, on west-facing slopes exposed to higher solar radiation and to earlier snowmelt (Carlson et al., 2013; Dobrowski, 2011), it is highly probable that individual *R. ferrugineum* plants may have experienced higher evaporative demand, especially in recent decades. Similar microsite differences were reported in the Central Norwegian Scandes (Bär et al., 2008), where extremely warm days were demonstrated to limit ring-width development on south-facing slopes, whereas shrubs located on ridges and north-facing slopes could still benefit from the higher temperatures. In addition, it seems plausible that the slightly thinner soils at QW could favor competition between roots and thereby exacerbate the sensitivity of individual plants to drought (Pichler and Oberhuber, 2007). Similarly, the potentially larger crowns of growing individuals in recent decades might have increased drought sensitivity. Evergreen shrubs and larger growth forms have, indeed, been demonstrated to be more sensitive to moisture availability than other functional groups (Corona-Lozada et al., 2019; Livenessperger et al., 2016). In any case, the limited sensitivity to drought observed at QN is consistent with numerous studies demonstrating that topography can buffer habitat and diversity loss in heterogeneous high mountain landscapes (Scherrer and Körner, 2011; Steinbauer et al., 2018) by providing topoclimatic microrefugia (Patsiou et al., 2014). We may thus hypothesize that shrub populations that are less exposed to solar radiation could be favored in the future (Bär et al., 2008).

We found no clear relationship between heat wave magnitude and shrub radial growth, which may be explained by the fact that extreme events occurred only four times during the period covered by the analysis. During these four years, *R. ferrugineum* formed thinner than average growth rings at QW and QN, except for summer 2003 during which growth was not unusual at QN. Isolating the effects of summer heat waves has proven to be difficult as negative effects of heat stress on mountain plant growth and productivity have only been observed in combination with water deficit (Corona-Lozada et al., 2019; Cremonese et al., 2017; De Boeck et al., 2016; Jolly et al., 2005). A higher correlation between shrub growth at QW and the heat wave index (as compared to QN) is in line with these results.

5 Conclusion

For our study site in the southern French Alps, we found that recent increases in summer temperatures, combined with more frequent and intense drought and heat waves, have led to a shift in climatic drivers controlling the growth of *R. ferrugineum*. Whereas radial growth was controlled mainly by growing season length between 1959 and 1988, during recent years growth has become more sensitive to drought, notably on west-facing slopes exposed to higher solar radiation and earlier snowmelt. The shift reported here still differs quite strongly from trends described in a majority of dendroecological studies for arctic and alpine environments documenting positive effects of increasing air temperature on shrub growth and productivity (Myers-Smith et al., 2015a). Accordingly, at least in the relatively dry context of the southern interior French Alps, our findings support the hypothesis of Ernakovich et al. (2014) who stated that by contrast to arctic ecosystems, the beneficial aspect on plant productivity of longer and warmer growing seasons may be locally outweighed by the detrimental effect of reduced soil water availability due to higher evaporative demands. This shift in climatic sensitivity may add further evidence to the warning signals outlined by Ernakovich et al. (2014) and their prediction of likely future changes in

plant community structures in alpine ecosystems. In addition, the limited drought sensitivity observed on the northern slope studied here tends to confirm that micro-topography could mitigate the impact of climate change by providing climate refugia (Patsiou et al., 2014), suggesting that shrub populations that are less exposed to solar radiation, could be favored in the future.

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Chapitre 4. Recent loss of shrub
sensitivity to growing season length
and temperature over the French
Alps

Les résultats présentés dans ce chapitre sont basés sur les séries dendrochronologiques utilisées dans le cadre des chapitres précédents. D'autres chronologies ont été édifiées pour couvrir des situations topoclimatiques représentatives des Alpes françaises : une pour le massif de Chartreuse (échantillonnage en 2016 par Christophe Corona, Erwan Roussel et moi-même), une additionnelle dans le massif du Queyras (que j'ai échantillonnée à l'été 2018), une dans le massif du Mont-Blanc, au pied de la dent de Loriaz (échantillonnage par Brad Z. Carlson, Christophe Corona, Jérôme Lopez-Saez et moi-même à l'été 2018). Brigitte Girard (PIAF, INRA) m'a grandement aidé pour réaliser les micro-sections. Les données météorologiques, provenant du modèle SAFRAN-Crocus de Météo-France, ont été extraites par Samuel Morin et Carlo Maria Carmagnola (CEN, Météo-France). De ces bases de données, j'ai extrait les séries météorologiques et nivologiques correspondant à chaque site échantillonné. J'ai fait les analyses dendrochronologiques, le choix et la réalisation des analyses statistiques. Cet article vise à être soumis prochainement à une revue scientifique.

Photographie de page précédente : Echantillonnage sur les versants de Loriaz, autour de 2200 m d'altitude.

Recent loss of shrub sensitivity to growing season length and temperature over the French Alps

Abstract

Contrary to the Arctic where a high sensitivity to temperature is evidenced by dendroecological studies and has been linked to shrub expansion and greening, comparable studies are lacking in mountainous regions. In the European Alps, where temperature increased almost twice as much as the global average over the last century and as a corollary, a significant decrease in snow cover is observed, the impacts of climate change on shrub radial growth have been poorly studied so far. The few existing dendroecological studies point out the prominent and consistent negative impact of winter precipitation for shrub growth over the last decades despite the persisting warming trend. Yet, due to the lack of highly-resolved micrometeorological series, the dendroecological studies held in the alpine belt did not account for the potential modulation/buffering of global warming impacts by mesotopography, nevertheless crucial in complex alpine environments. In order to fill this gap, we (1) assembled a network of eight sites where the dwarf shrub *Rhododendron ferrugineum* dominates the vegetation and which was designed to be representative of the contrasts in continentality, elevation and slope aspect across the French Alps, (2) measured the yearly radial increment on 119 individuals and (3) assessed the climate-growth associations using a mixed modeling approach that takes advantage of the hourly-resolved SAFRAN-Crocus meteorological dataset. This dataset takes into account the mesotopographic position of our study sites along elevational and aspect gradients within massifs in the French Alps. Our results confirm, in agreement with the vast majority of dendroecological studies conducted in Arctic and Alpine environments, that the amount of growing degree days during the snow-free period (SFGDDs) was a strong and consistent driver for *R. ferrugineum* growth across the studied gradients until the late 1980s. Since the 1990s, we document a marked loss of sensitivity of radial growth to SFGDDs. This non-linear relationship, modulated by moisture availability, is stronger in the driest sites where it leads to growth reduction. We assimilate this space-time variability of shrubs sensitivity to the “divergence” problem observed in tree-ring series from circumpolar and alpine regions.

Keywords

Dendroecology; dwarf shrubs; *Rhododendron ferrugineum*; Mixed modeling; drought; snow cover; global change; European Alps; divergence; topoclimate

1 Introduction

Mountainous and Arctic regions undergo a 1.5 times greater increase in temperature than the global average and, as a corollary, observations show a general decline in snow cover due to increasing melting (IPCC, 2019). In the Arctic, earlier snowmelt and higher temperatures during summer lead to intense

greening and increasing shrub productivity that drive climate feedbacks (Myers-Smith et al., 2015a) and modifies a wide range of ecosystem processes (Myers-Smith et al., 2011) by altering surface albedo, energy, water balance, or permafrost (Chapin, 2005; Liston et al., 2002; Sturm et al., 2001). Based on pan-Arctic shrub-ring networks, Ackerman et al. (2017), Gamm et al. (2018) and Myers-Smith et al. (2015a) however suggest that drought in moisture-limited sites could hinder the beneficial effect of rising temperatures above a certain threshold on shrub radial growth. Moisture limitation could hinder the beneficial effect of rising temperatures and advancing melt-out dates, even more markedly in temperate high mountains than in the Arctic (Ernakovich et al., 2014). Indeed, in alpine systems, advancing snow melt-out dates, summer droughts and heat waves has been shown to hamper the productivity and performances of alpine vegetation (Corona-Lozada et al., 2019; De Boeck et al., 2016; IPCC, 2019; Williams et al., 2015; Winkler et al., 2018; Francon et al., 2020ab, submitted).

In the European Alps, increasing vegetation productivity and denser shrub cover above treeline has been documented through remote sensing or diachronic comparison of phytosociological maps (Cannone et al., 2007; Carlson et al., 2017; Dullinger et al., 2003; Filippa et al., 2019) but cannot be unequivocally attributed to global warming. Dendroecological studies by creating long-term, annually resolved growth records, demonstrated the negative role of winter precipitation and subsequent delayed melt-out dates on the radial growth of shrubs as well as the positive effect of summer temperatures (Francon et al., 2017; Pellizzari et al., 2014). The only existing regional study pointed out a positive and stable effect of the growing season length on shrub growth in the Italian Alps (Carrer et al., 2019). However, in the Alps, the existing dendroecological studies do not account for the potential modulation of climate change impact by the topography. This is all the more detrimental that (1) the diversity of topoclimates observed in alpine environments (Bonet et al., 2010) is susceptible to impact the response of shrubs to global warming ; (2) strong moisture gradients induced by rough terrain (Scherrer and Körner, 2011) could potentially modulate the productivity and performances of alpine vegetation more markedly than in the Arctic (Ernakovich et al., 2014).

In this context, this paper aims at assessing the impacts of global warming on shrub productivity for a structuring dwarf shrub species in alpine heathlands, *Rhododendron ferrugineum* (L.), with a special emphasis on the potential modulation of global warming impacts by topoclimatic conditions. For this purpose, we (1) assembled annual growth records from a 8-site network designed to be representative of the contrasts in continentality, elevation and slope aspect across the French Alps; (2) used the SAFRAN-CROCUS dataset (Durand et al., 2009a, 2009b; Vionnet et al., 2012), a meteorological analysis system developed to provide hourly estimation of meteorological parameters and whose outputs, available for different slope aspects and per 300 m altitude steps within mountainous regions called "massifs", proved to satisfactorily describe the local snow cover variability and accumulation (Vionnet et al., 2012); (3) combined the bootstrap correlation functions typically used in dendroecological studies with a linear mixed model in order to quantify threshold effects and (4) shifts related to global warming in shrub-climate relationships in the French Alps.

2 Material and methods

2.1 Shrub-ring chronology development

R. ferrugineum was demonstrated to be a reliable model to study shrub response to long-term climate variability (Francon et al., 2017) due to (1) its wide distribution, from about 1600 to 2500 m asl across the European Alps (Ozenda, 1985), (2) high longevity as well as (3) clearly identifiable annual growth rings. We sampled *R. ferrugineum* individuals at eight sites across four massifs. Sites were chosen along a moisture gradient from the Chartreuse (total annual rainfall: 2045mm) to the Queyras (868mm) massifs (Fig. 1), the wettest and the driest of the 23 massifs delineated by Durand et al. (2009b) in the French Alps, respectively. The topographical and climatic characteristics of each massif are synthesized in figure 1 and table 1. At each site, the geological substrate is composed of metamorphic or plutonic acidic rocks excepted CHAM where fractured limestone bedrock may favor rapid water infiltration.

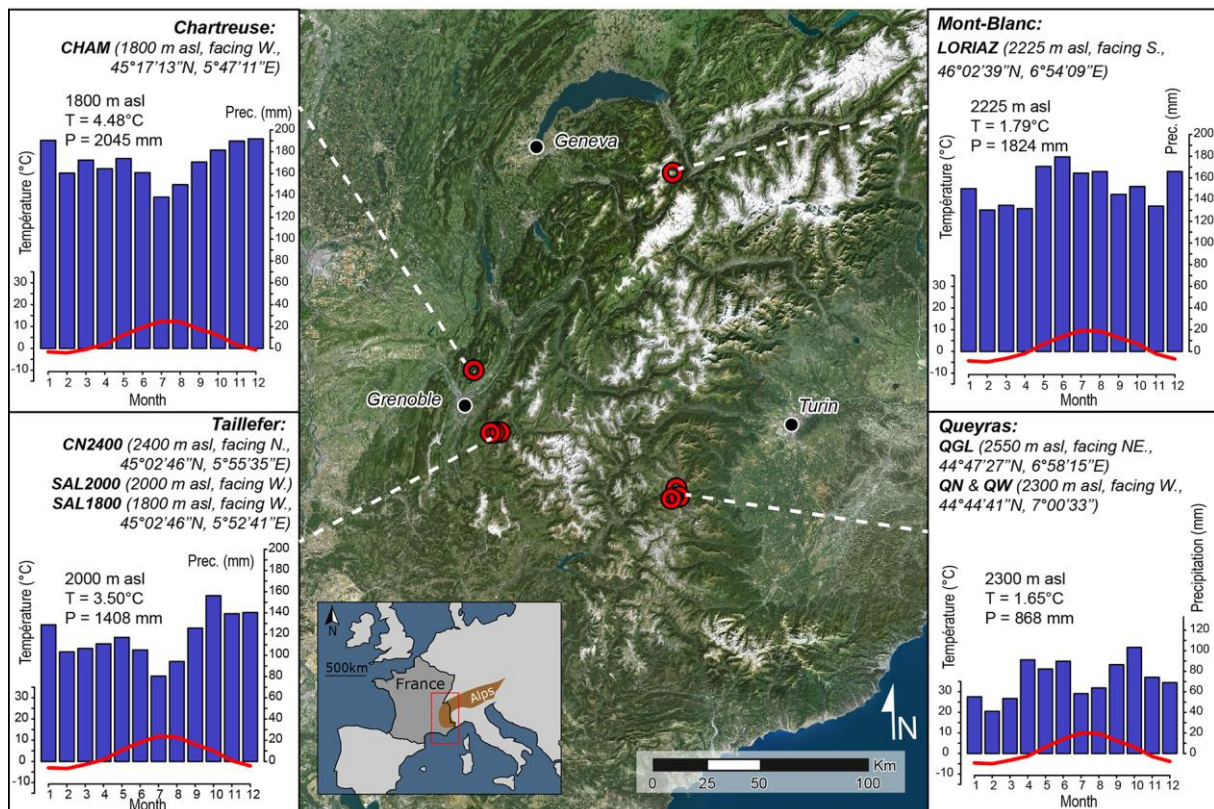


Figure 1: Characteristics of the *R. ferrugineum* 8-site network (CN2400, SAL2000, SAL1800, CHAM, QGL, QN, QW and LORIAZ) used in this study. Umbrothermal diagrams (Chartreuse, Oisans, Mont-Blanc and Queyras) are derived from the SAFRAN crocus model (Météo France, 1981–2010).

Table 1: Site and chronology characteristics: massif and sampling site names and their elevation, indice of continentality, aspect, chronology length, number of individuals included in the final chronology, signal strength (EPS: Expressed Population Signal and rbar: mean intercorrelation between individual series) and autocorrelation of order 1. The three last parameters refer to chronologies after detrending.

Massif	Site	Elev.	α	Asp.	Length	Nb.	EPS	rbar	AC
Taillefer	CN2400	2400	60.00	45°	1896-2016	14	0.82	0.28	0.01
	SAL2000	2000	54.8	315°	1821-2015	24	0.94	0.41	0.22
	SAL1800	1800	53.20	315°	1862-2016	11	0.86	0.32	0.14
Queyras	QGL	2550	71.50	30°	1940-2017	15	0.88	0.40	0.24
	QN	2350	69.50	30°	1906-2016	10	0.89	0.42	0.22
	QW	2350	68.70	270°	1918-2016	14	0.93	0.56	0.13
Chartreuse	CHAM	1800	41.40	270°	1900-2016	16	0.85	0.32	0.21
Mont-Blanc	LORIAZ	2225	50.70	135°	1905-2017	14	0.89	0.52	0.07

Excepted CN2400, where only isolated individuals were retrieved, *R. ferrugineum* individuals, with height ranging between 30 and 50 cm, were sampled in large heathlands or patches at each site. A minimum distance of four meters between each sampled individual was held to avoid sampling from the same individual (Escaravage et al., 1998). We sampled two to three sections from a single stem for each individual in order to apply the serial sectioning methods, consisting in repeated measures on the same stem to avoid missing ring as shrub produce often very narrow, wedging growth rings (Kolishchuk, 1990). On each section, a micro-section was cut, stained and mounted in laboratory using a microtome and safranin/astra blue dye to highlight ring boundaries (Schweingruber and Poschold, 2005).

Crossdating (i.e. the assignment of exact year of formation to each ring) from digitalized images of thin sections using Coorecorder and Cdendro softwares (CYBIS Elektronik & Data AB) was based on a three-step procedure relying on the visual synchronicity between (1) elementary ring width series measured within three radii of the same cross section, (2) mean ring width series for each section of the same individual, and finally (3) between individual chronologies at a given site. Visual crossdating was statistically checked with the COFECHA software (Holmes, 1994). In a subsequent step, we detrended each section chronology with a negative exponential function to eliminate non-climatic biological trends using the ARSTAN software (Cook, 1987). After detrending, for each cross-dated section and individual, ring-width indices (RWI) were averaged using a bi-weighted robust mean in order to reduce the influence of outliers and to develop mean detrended site chronologies (Cook and Peters, 1981). Finally, the eight detrended chronologies were compared within a correlation matrix to check for radial growth consistency between sites.

Descriptive statistics including standard deviation (SD), first-order autocorrelation (AC), mean inter-series correlation (rbar) and the Expressed Population Signal (EPS) were computed for each detrended site chronology using the ARSTAN software (Tab. 1). EPS quantifies the strength of the common climate signal in the tree-ring proxies (Wigley et al., 1984). We used the commonly applied quality threshold $EPS \geq 0.85$ to evaluate the reliability of our chronologies.

2.2 Extraction of meteorological series and topoclimatic characteristics for each site

Series of hourly temperature, precipitation totals and daily snow-cover height were extracted for each site from the SAFRAN-Crocus dataset over the period 1959-2017. The SAFRAN model combines *in-*

situ meteorological observations with synoptic-scale meteorological fields to provide continuous time series of meteorological variables at hourly resolution, for elevation steps of 300 m, different slope aspects and angles within massifs, i.e. horizontally climatologically homogeneous regions (Durand et al., 2009b). In combination with SAFRAN, the Crocus model provides snow data. Vegetation is represented in a simplified manner in the simulations, assuming grassy conditions to simulate typical snow conditions and underlying ground temperature for open areas (Durand et al., 2009a; Vionnet et al., 2012). Based on raw snow reanalyzes, we derived snow melt-out dates at our study sites. Melt-out dates were estimated when snow cover reaches the shrub canopy, located between 30 and 50 cm above the soil surface, depending on the population structure. From the melt-out dates until August 31st (considered as the last day of growth, based on multiple dendrometric series, not published), we summed above-zero daily mean temperature in order to obtain snow-free growing degree days (SFGDD). We also calculated monthly and seasonal temperature means and precipitation totals. Additionally, we extracted series of standardized precipitation-evapotranspiration indices (SPEI, Vicente-Serrano et al., 2010) computed over two-month periods to account for the potential impact of summer drought on radial growth. Finally, the topographical characteristics (elevation and slope aspect) and the Gams continentality Index (α , Gams, 1932) were used as additional variables to characterize each site. Northness index, ranging between -1 (South orientation) and 1 (North orientation), was computed at each site as the cosine of slope aspect. α was calculated following the equation:

$$\cot g(\alpha) = P/A$$

where P and A represent the mean annual precipitation sum (mm) and the elevation (m asl) at each site (Table 1). Elevation and slope aspect are known to affect temperature, light availability and soil conditions in mountainous sites (Bonet et al., 2010). On the other hand, continentality affects aridity and dryness (Driscoll and Fong, 1992).

2.3 Shrub radial growth / climate relationships

Climate-growth analyses were performed in two steps. First, bivariate correlation functions (BCFs) were computed between the detrended site chronologies and series of monthly (and summer) temperature, precipitation, SPEI, melt-out dates and SFGDD. This preliminary analysis was intended to determine the main drivers of radial growth at each site. BCFs were computed over the periods 1960-1988 and 1989-2017 to detect potential shifts in growth/climate relationships related to global warming. These periods of equal length cover almost 30 years, in accordance with the definition of a meteorological normal. Moreover, the second period reflects the marked warming observed since the end of the 1980s (Lo and Hsu, 2010; Reid et al., 2016). This regime shift had a particularly significant impact on the biophysical environment (Oberhuber et al., 2008). Subsequently, given the prominent and generalized impact of SFGDD on *R. ferrugineum* radial growth evidenced by BCFs, relationships between SFGDD and radial growth were further investigated using linear mixed models. The advantage of these model include (1) the analysis of shrub response at the individual level, thus maintaining information of finer-scale climate-growth interactions (Myers-Smith et al., 2015b); (2) the comparison of shrub responses in different topoclimatic situations accounting for potential interactions between variables, for example topography and climate (Myers-Smith et al., 2015b); (3) the use of raw ring measurements thus avoiding the detrending procedure that could remove meaningful ecological information from ring-width series

(Ackerman et al., 2018) and (4) the detection of possible non-linear relationships and potential threshold effects in growth /climate relationships, by introducing for example quadratic effects.

Linear mixed models were computed using the *nlme* package (Pinheiro and Bates, 2000). In order to achieve the required normality of residuals, mean ring width measurements at the section stage (hereafter referred as RW) were log-transformed and scaled. We considered sections nested within sites as random effects to take into account differences in individual shrub sections growth response to climate within each site. We used section mean ring widths instead of individual mean ring width because this is not possible to average the section series within individuals due to different biological trends. An autocorrelation structure (AR1, autoregressive process of order one) was additionally included in the model. Elevation, Gams continentality index and northness index (normalized and scaled), as well as cambial age and mean annual SFGDD were considered as fixed effects. Cambial age (in number of years) was introduced in the model to account for age-related trends in growth-ring series. A careful attention was paid to interactions between SFGDD and other fixed factors that could reveal potential modulation of the shrub responses by environmental factors. We also tested for second-order (nonlinear) relationships between SFGDD and radial growth as well as interactions with other environmental variables.

The predictive capacity of a single independent variable was determined by the absolute value of Student's t statistics for its linear or quadratic effect on RW. A conditional pseudo- R^2 (Nakagawa and Schielzeth, 2013) value was calculated with the *MuMIn* package (Barton, 2019). Backward elimination was used to select the most parsimonious model. The Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC), which imposes a stronger penalty for increasing model complexity, were used to compare resulting models using the *buildmer* R package. Finally, multicollinearity issues were checked based on the variance inflation factor (VIF) with a threshold at three (Zuur et al., 2010) using the *car* package available in R. In order to detect potential impacts of global warming on radial growth / climate relationships, three different models were implemented for the periods 1960-1988, 1989-2017 and 1960-2017.

3 Results

In total, eight detrended site chronologies (see Tab. 1 for their characteristics) and ring-width series of 225 sections sampled from 119 individuals were used for climate-growth analyses. Over the period 1960-1989, BCFs (see Fig. S2) computed between meteorological variables and detrended chronologies reveal strong (r values ranging between 0.39 and 0.75) and statistically significant correlations ($p < 0.05$) between RWI and SFGDD at all sites with the exception of CHAM ($r = 0.22$, $p = 0.24$, Fig. 2 and 3). SFGDD was the main climatic driver of radial growth at SAL1800, CN2400, LORIAZ, QGL QN. At SAL2000, comparable correlations ($r = 0.46$, $p < 0.05$) were computed between the shrub-ring chronology and SFGDD or summer temperature while at QW, the correlation with SFGDD ranks right after the correlation with February precipitation. More generally, winter precipitation also correlates negatively with RWI in a large majority of sites (excepted SAL1800 and SAL2000). Finally, mean late summer and early fall temperature in the previous year (Sept- Oct) positively correlated with RWI at SAL2000, CN2400, LORIAZ and QGL.

Over the period 1989–2017, climate-growth correlation profiles (Fig. S2) differ much more from site to site than over the previous period. SFGDD remains the most important driver of radial growth only at CN2400 ($r=0.42$, $p<0.05$) but correlations between SFGDD and radial growth decrease close to zero at CHAM, LORIAZ, QGL and SAL1800 and are even significantly negative at QW and QN. Moreover, significant negative correlations were found between shrub chronologies and August temperature at CHAM, QN, QGL and QW. At QW, the impact of drought on *R. ferrugineum* radial growth is also evidenced through significant correlations with SFGDD ($r=-0.29$, $p<0.05$) and summer SPEI ($r=-0.55$, $p<0.001$). By contrast, detrended ring width chronologies from SAL1800, SAL2000 and QGL are positively correlated with summer and early fall (Sept–Oct) temperatures. Finally, winter precipitations remain important drivers of radial growth at CN2400, LORIAZ, QGL and QN.

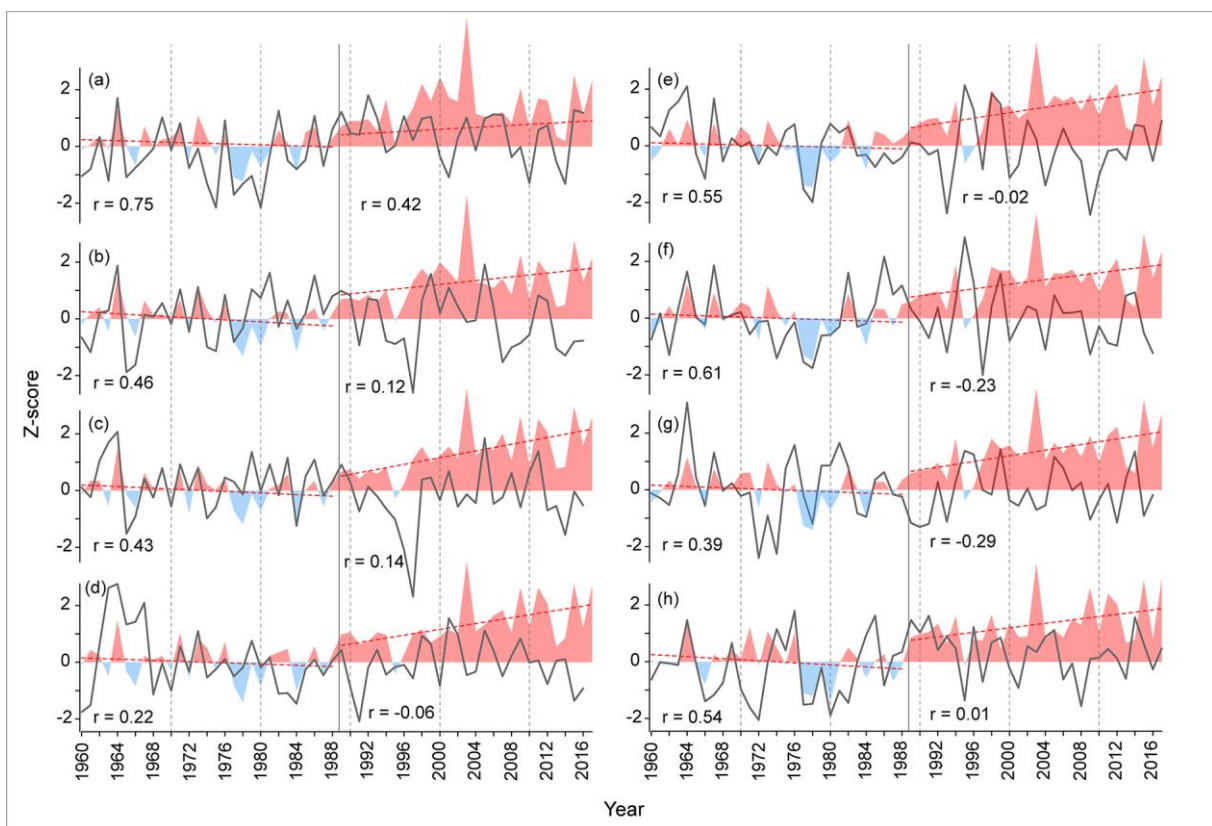


Figure 2: Annual snow-free growing degree-days (SFGDD, positive and negative anomalies in red and blue, respectively) and mean ring width indices (RWI, indicated with a black line) (1960–2017) at each sampled site: CN2400 (a), SAL2000 (b), SAL1800 (c), CHAM (d), QGL (e), QN (f), QW (g), and LORIAZ (h). SFGDD values were transformed into Z-scores with respect to their mean in the 1960–1988 reference period. Dashed red lines represent linear trends detected in SFGDD series for the time periods 1960–1988 and 1989–2017. Correlation coefficients between SFGDD and RWI are given for each period.

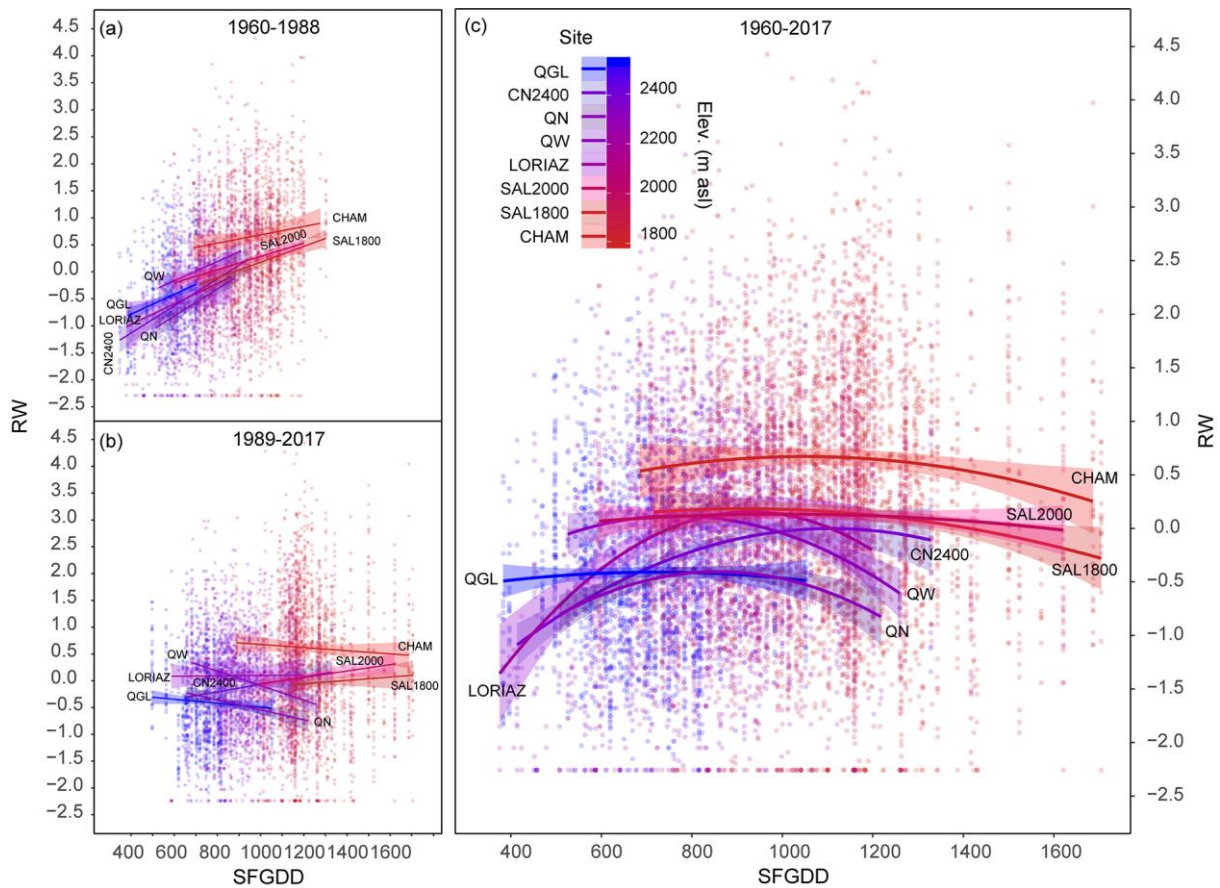


Figure 3: Relationships between snow-free growing degree days (SFGDD) and log-transformed scaled raw ring-width (RW) at each site for the 1960–1988 (a), 1989–2017 (b) and 1960–2017 periods. Regression lines with their confidence intervals of 0.95 are classified by color according to site elevation. Site names are indicated at the right or left of the regression lines.

The correlation matrices computed between site chronologies confirm this loss of consistency between both time periods (Fig. S3): mean intercorrelation thus decreased from 0.36 (stdev. 0.17) to 0.19 (stdev. 0.26) for the periods 1960-1988 and 1989-2017, respectively. In addition, while all chronologies, (excepted LORIAZ) were significantly and positively correlated among sites until 1988, the majority of correlation coefficients are low and insignificant over the period 1989-2017.

The mixed modeling analysis at the individual level, nested within sites, confirms the major impact of SFGDD accumulation on RW over the period 1960-2017 (Table 2). Conditional R^2 reveal that, regardless of the period, all models explain ~50% of the interannual growth variability (46%, 45% and 49% over the 1960-2017, 1960-1988 and 1989-2017 periods, respectively). Models computed over the periods 1960-1988 and 1960-2017 demonstrate that climatic variables explain a greater part of the interannual variability of *R. ferrugineum* growth than the null model ($\Delta AIC_{\text{null vs. model}} = 734.73$ and 704.004 , respectively). By contrast, since 1989, lower $\Delta AIC_{\text{null vs. model}}$ values (172.25) and smaller regression slopes reveal lower shrub sensitivity to climate. This loss of sensitivity since 1988 is confirmed by lower linear and quadratic effects of SFGDD on RW. In detail, the 1960-1988 model reveals a strong positive linear impact of SFGDD on radial growth (Fig. 3), only moderately modulated

by elevation (Fig. 4), with increasing sensitivity to SFGDD at increasing elevations. The model over the entire period and the 1989-2017 model indicate that the radial growth response to SFGDD is non-linear and depends on geographical position (slope aspect and continentality) (Table 2 and Fig. 4). According to the 1960-2017 model, climate sensitivity of shrub radial growth is less linear in drier sites than in moister sites. Indeed, in dryer alpine massifs, such as the Queyras, growth declines when SFGDD values exceeded 1000° (Fig. 4). For more humid regions, a similar growth decrease is modeled above 1550°. Regardless of other geographic variables, the model predicts that the slope aspect has no effect on shrub sensitivity to SFGDD below the 1000 GDD threshold (Fig. 4). Above this threshold, a growth decline is observed independently of the slope aspect but is greater on slopes with lower northness indices, i.e. more exposed to solar radiations. Elevation considered as independent variable or in interaction with SFGDD was not retained in the 1960-2017 and 1989-2017 models, contrary to the 1960-1988 model. Nevertheless, the models computed over the 1960-2017 and 1989-2017 periods highlight strong impacts of continentality, slope aspect on shrubs sensitivity to SFGDD. Moreover, in all models, conditional R^2 were about two times larger than marginal R^2 showing a strong variability within individuals nested in sites in their response to climate (the random effect of sites alone were much lower than the random effect of individuals nested in sites: standard-deviation of 0.48 for the random effect of individuals within sites vs. 0.072 for the random effect of sites alone).

Table 2: Fixed effect coefficients and t-values obtained for the parsimonious mixed models predicting *R. ferrugineum* ring width (mm, log-transformed) over the French Alps for the period 1960–2017, 1960–1988 and 1989–2017. Conditional R^2 , marginal R^2 and AIC differences between each model and a null-model are given for each model. All variables are scaled except stem age. * ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$) indicate the level of significance.**

Parameter	1960-2017		1960-1988		1989-2017	
	value	t-value	value	t-value	value	t-value
Intercept	0.602***	10.95	0.372***	6.24	0.552***	7.05
SFGDD	0.278***	21.94	0.420***	27.23	0.176***	8.67
(SFGDD) ²	-0.114***	-16.76			-0.065***	-5.75
Continentality	-0.148*	-2.95			-0.258**	-4.24
cos(Aspect)	-0.051	-1.06	-0.117	-2.31	-0.005	-0.08
Elevation			0.019	0.41		
SFGDD*Continentality	-0.190***	-11.69			-0.208***	-7.92
SFGDD*cos(Aspect)	0.108***	8.26			0.135***	7.39
SFGDD*Elevation			0.043**	2.71		
(SFGDD) ² *Continentality					-0.208***	-7.92
(SFGDD) ² *cos(Aspect)	0.056***	8.92				
(SFGDD) ² *Elevation						
Age	-0.016***	-18.14	-0.010***	-6.71	-0.013***	-10.53

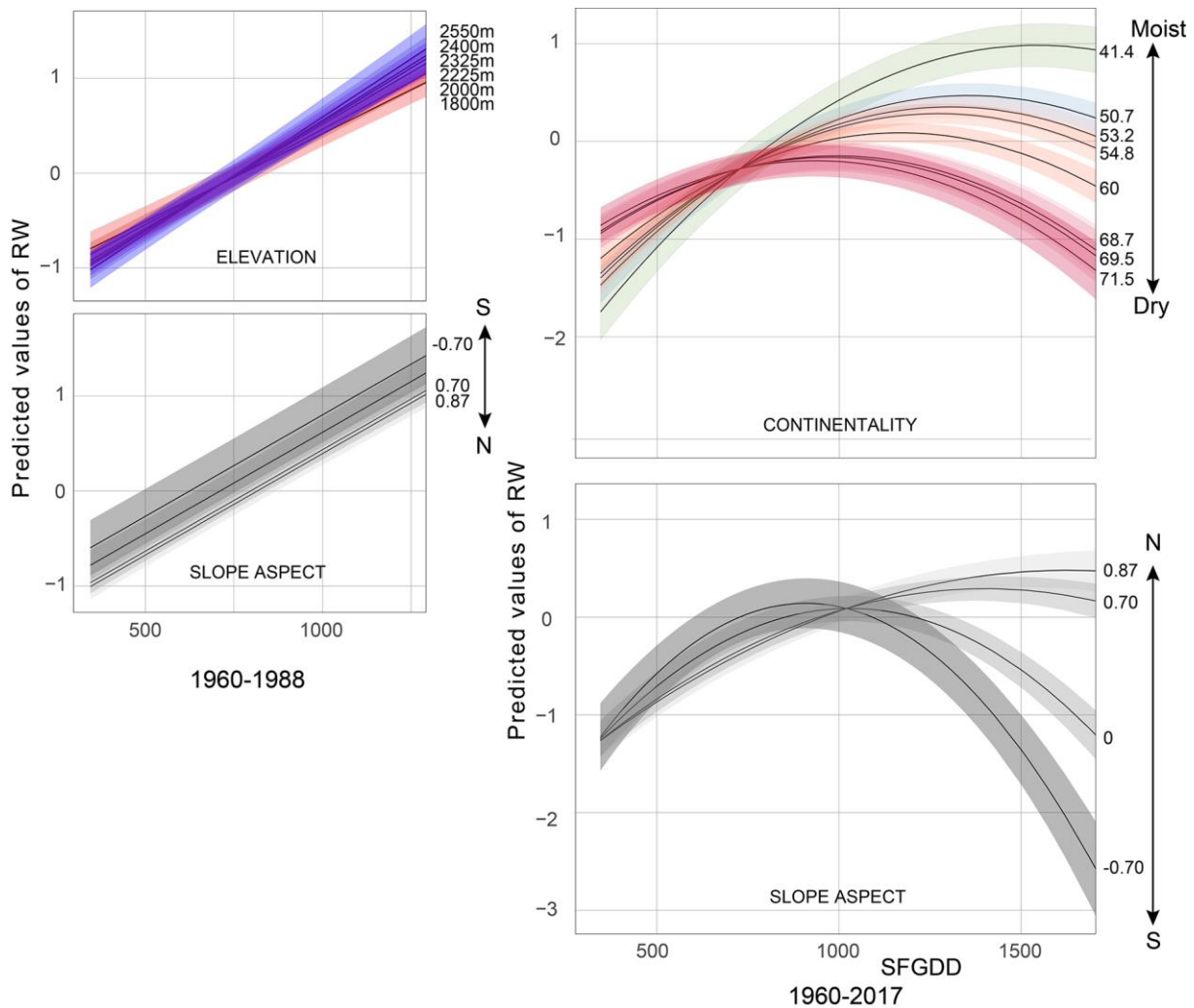


Figure 4: Linear mixed models of *R. ferrugineum* ring width (RW: log-transformed and scaled values) as a function of snow-free growing degree days (SFGDD). The graphs describe the interaction with elevation (upper left panel), continentality (upper right panel) and slope aspect (lower panels) for the subperiods 1960-1988 (Left panel) and 1989-2017 (Right panel). Ranges for elevation, northness and Gams continentality index are given on the right side of each panel.

4 Discussion

In this study, we studied the evolution of the climate sensitivity of the dwarf shrub *R. ferrugineum* across a network of sites in the French Alps reflecting the topoclimatic heterogeneity and continentality of the alpine environment. Our results show strong, highly significant and consistent relationships between SFGDD and shrub radial growth until 1988 for all eight sites of our network. They are consistent with the widely accepted fact that, in cold environments, temperature, and in particular growing degree days, are key drivers of plant growth (Hoch, 2015; Körner, 2003; Wipf, 2010). These results are also in line with the wide majority of dendroecological studies conducted in Arctic environments that identified summer temperatures as the main driver of shrub growth (Blok et al., 2011; Jørgensen et al., 2015; Myers-Smith et al., 2015a). This sensitivity to temperature was found to be consistent over contrasted topography or landscape in most studies (Ackerman et al., 2018; Bär et al., 2008). Similarly, in the Alps, dendroecological studies have demonstrated the positive effect of summer temperatures and the negative

effect of snowpack duration on shrub radial growth at the upper elevational limit of shrubs (Francon et al., 2017; Pellizzari et al., 2014).

Nevertheless, no radial growth release was observed as a response to the increasing number of growing degree-days observed in our meteorological series after 1989. Our analyses rather suggest a divergence between increasing SFGDD and shrub radial growth indicative of non-linear relationships between both variables. In other words, in continuity with the smaller scale studies carried out in the Taillefer and Queyras massif (Francon et al., 2020a,b, submitted) which show that, above a certain threshold, whose value is modulated by continentality and aspect, a loss of sensitivity of shrub growth to SFGDD is observed in all sites. Here, we attributed this non-linear response to a strong increase in the length of the growing season which makes shrubs (i) less constrained by the availability of energy to complete their life cycle (Francon et al., 2020a, submitted), but also (ii) the compensation of the beneficial effect of rising temperatures on growth by the negative effects of the resulting reduced soil water availability that strongly depends on the shrubs position along moisture gradients (Francon et al., 2020b, submitted). Such non-linearity is not observed by Carrer et al. (2019) who report, despite the persistent and significant warming trend, a consistent and negative role of winter precipitation on *Juniperus communis* growth across a network of seven sites covering the Italian Alps. By contrast, a similar loss of sensitivity to temperature, observed since the 1990s on *Betula nana* and *Salix glauca* from Western Greenland (Gamm et al., 2018) and on *B. nana* and *Empetrum hermaphroditum* in the central Norwegian Scandes (Weijers et al., 2018), was in both case attributed to global warming through increasing soil moisture limitation or more frequent late frost events. The loss of sensitivity to climate evident in our study also echoes the “divergence problem” reported in trees growing at circumpolar northern latitudes (Briffa et al., 1998; D’Arrigo et al., 2008; Driscoll, 2005) and high-elevation sites (Büntgen et al., 2008). This body of literature suggests complex and nonlinear growth responses of trees to a changing climate, thereby leading to a decrease in year-to-year sensitivity of tree growth in previously temperature-limited sites (D’Arrigo et al., 2004; Wilmking, 2005). Potential causes for this divergence include warming-induced thresholds of tree growth (D’Arrigo et al., 2004) or increasing drought stress (Büntgen et al., 2006).

In our study, lower correlations between the chronologies of our eight site and the greater heterogeneity of BCF profiles since 1989 suggest that strong site effects modulate the response to climate over the last decades. We believe that the recent loss of sensitivity and the non-linearity of the response to SFGDD are probably related, as mentioned for trees (Büntgen et al., 2008; Leonelli et al., 2009), to topoclimate-related moisture limitations. This topoclimatic effect is confirmed by our mixed modeling approach which demonstrates that the non-linearity is due to continentality at the regional scale and on slope aspect at the meso-scale. Both environmental variables directly interact with soil moisture (Gracia et al., 2007). Shrubs growing at sites with higher Gams angles (α) and lower northness indices are the most negatively affected by increasing SFGDD in line with the moisture limitation theory (Ackerman et al., 2017; Myers-Smith et al., 2015a). Based on dendroecological Arctic studies, Myers-Smith et al. (2015a) hypothesize that the non-linearity of shrub growth-temperature relationships and the crucial role of topography, soil properties and snow-related moisture availability modulate global warming impacts. In other words, shrubs, like trees (Wilmking, 2005), appear to have become more sensitive to moisture stress but this evolution greatly depends on microsites. We hypothesize that the absence of a comparable topographical effect in the Italian Alps might be explained by (1) the choice of a less drought-sensitive

species as a model dwarf shrub species (*J. communis*) and/or (2) the absence of a strong topoclimatic heterogeneity in the site network. Finally, based on raw data at the individual level, the mixed modeling approach reveals that growth differences between sites are mainly driven by continentality. Higher growth and larger rings are indeed observed in the wetter westernmost site of our network. The limited impact of elevation, rather surprising at first, is probably due to the continentality gradient as moisture conditions could strongly differ within the same altitudinal band from the western to the easternmost site. But the significant correlation between the two variables (continentality and elevation) makes the detected absence of a significant effect of elevation uncertain.

Finally, the mixed modeling approach shows a strong heterogeneity among individual responses to topoclimate as highlighted by the high proportion (about 50%) of the variation of ring-width which is not explained by the mesotopographic and climatic variables of interest (fixed effects). This part of the variance explained by random effects can be used to quantify the inter-individual variances of intercept (Avanzi et al., 2019). Here, a high proportion of the variation of ring-width is not explained by the mesotopographic and climatic variables of interest. This could be attributed to variables that we have not quantified, such as microtopography at the individual level, competition, disturbance or genetic/phenotypic variability.

5 Conclusion

The analysis presented here relies upon a pool of 10065 growth rings measured from 225 sections of 119 individuals sampled in 8 sites with different climatic and topographic characteristics across the French Alps. To assess the evolution of radial growth/climate relationships for the dwarf shrub *R. ferrugineum* in a warming climate, we coupled classical bootstrap correlation functions with more innovative linear mixed models within a common dendroecological analysis computed over two periods of equal length, before and after the climate regime shift that occurred in the late 1980s. The linear mixed models reveal a strong and very consistent sensitivity of *R. ferrugineum* to SFGDD that vanished after the late 1980s. This evolution, comparable to the divergence problem observed in tree-ring series at high-latitude and high-elevation sites, is indicative of strong non-linear interactions between temperature and shrub growth (D'Arrigo et al., 2004). In this paper, we show that the threshold value since which SFGDD has a negative effect on growth is highly variable and depends on continentality which is driven by geographical position within the Alps, and on slope aspect, that determines solar radiation. According to our data, SFGDD greater than 900° in the inner Alps on a west-facing slope, and than 1700° on a north-facing slope in the outer Alps, have negative effects on growth.

As temperatures continue to rise and snowpack duration in spring continues to decrease in the European Alps due to global change, we expect that the threshold we have defined will be exceeded more frequently in the future. Therefore, in light of our results, this could lead to a substantial decrease in radial growth over the next few decades at the driest sites. On the contrary, dwarf shrubs growing on the wettest and coldest slopes could be favored. However, much of the inter-individual variation in the response of shrubs to climate remains unexplained by the models we built, suggesting that mesotopography alone cannot explain all of the growth variability, and that even finer-scale mechanisms are involved. We believe that in order to better characterize the sensitivity of alpine shrubs to climate,

future studies should focus on the characterization of microsites to further our understanding of the sensitivity of shrubs to climate in complex alpine environments.

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Supplementary material

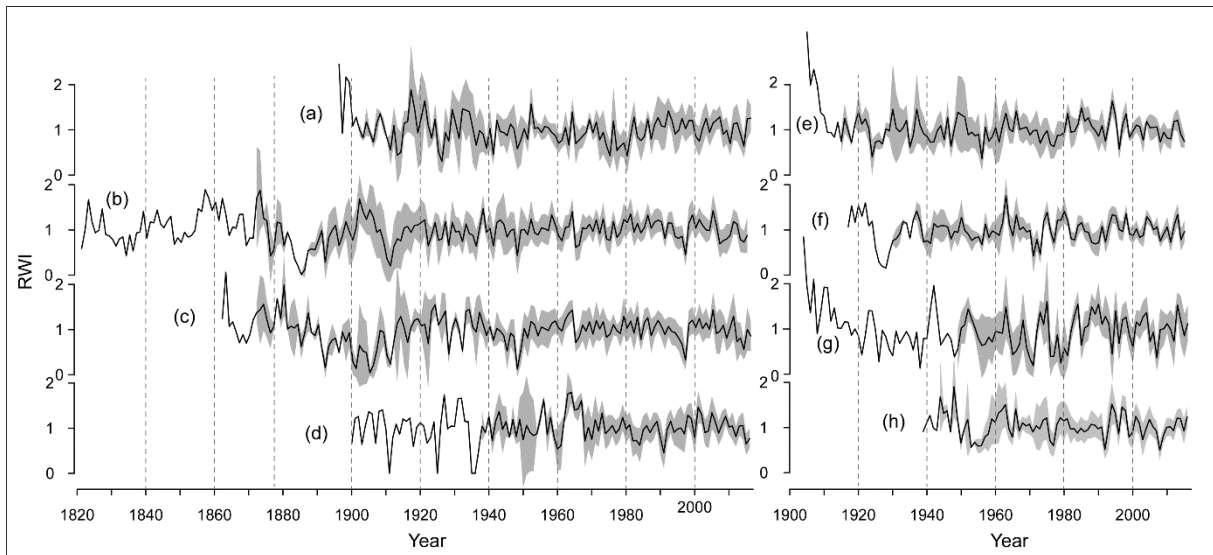


Figure S1: Detrended *R. ferrugineum* ring width (RWI) chronologies from CN2400 (a), SAL2000 (b), SAL1800 (c), CHAM (d), QGL (e), QN (f), QW (g) and LORIAZ (h) and their confidence intervals (± 1 SD; grey areas).

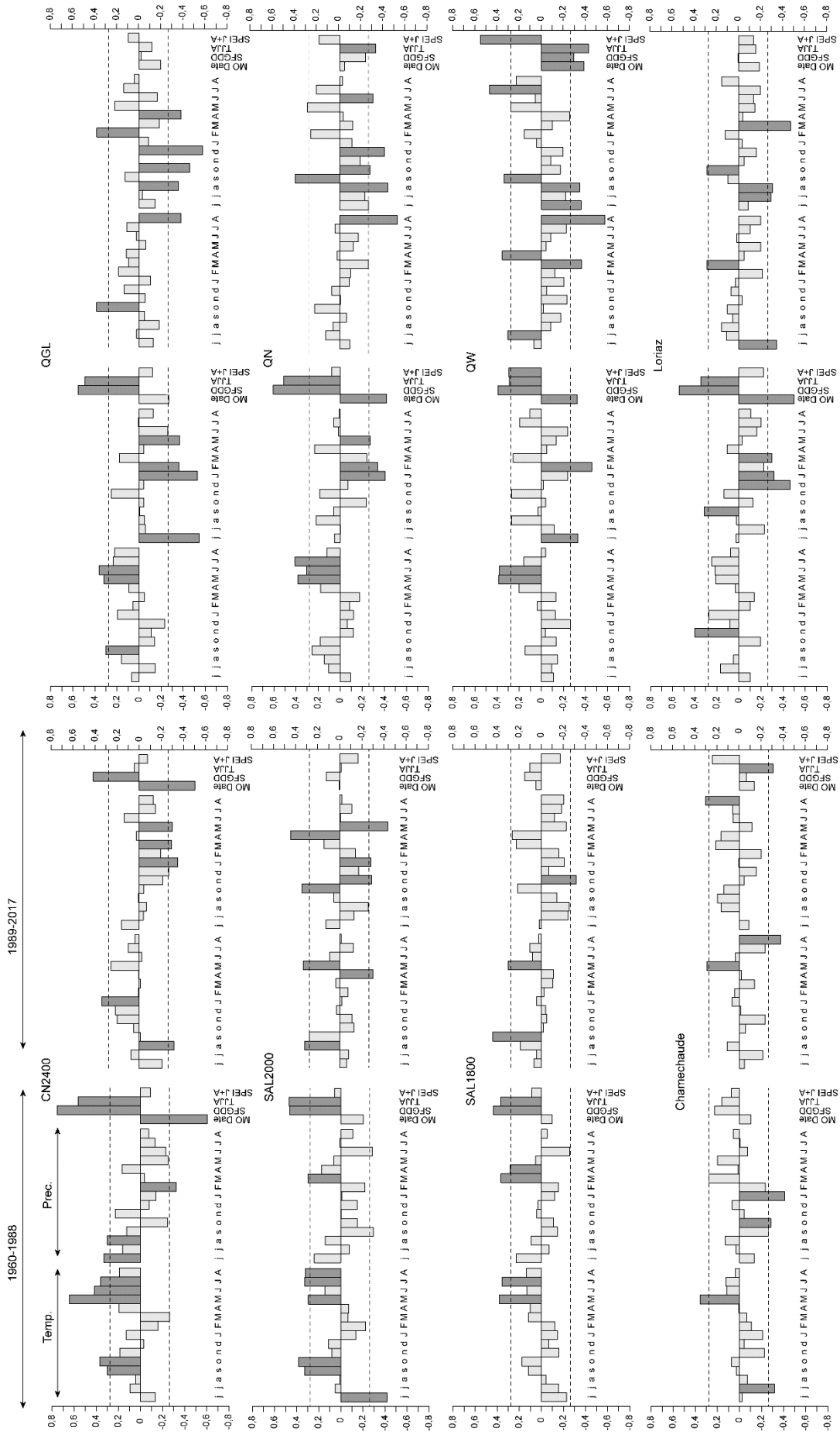


Figure S2: Bivariate correlations functions (BCFs) computed between *R. ferrugineum* chronologies and monthly precipitation sums, mean temperatures, snow melt-out date (Melt-out), Snow-Free Growing Degree Days (SFGDD), summer temperature (TJJA) and July-August Standardized Precipitation-Evapotranspiration Index (SPEI J+A) for the time periods 1960–1988 and 1989–2017. Months of the year preceding (N-1) ring formation (N) are written with lowercase letters; months of the current (N) year are written with capital letters.

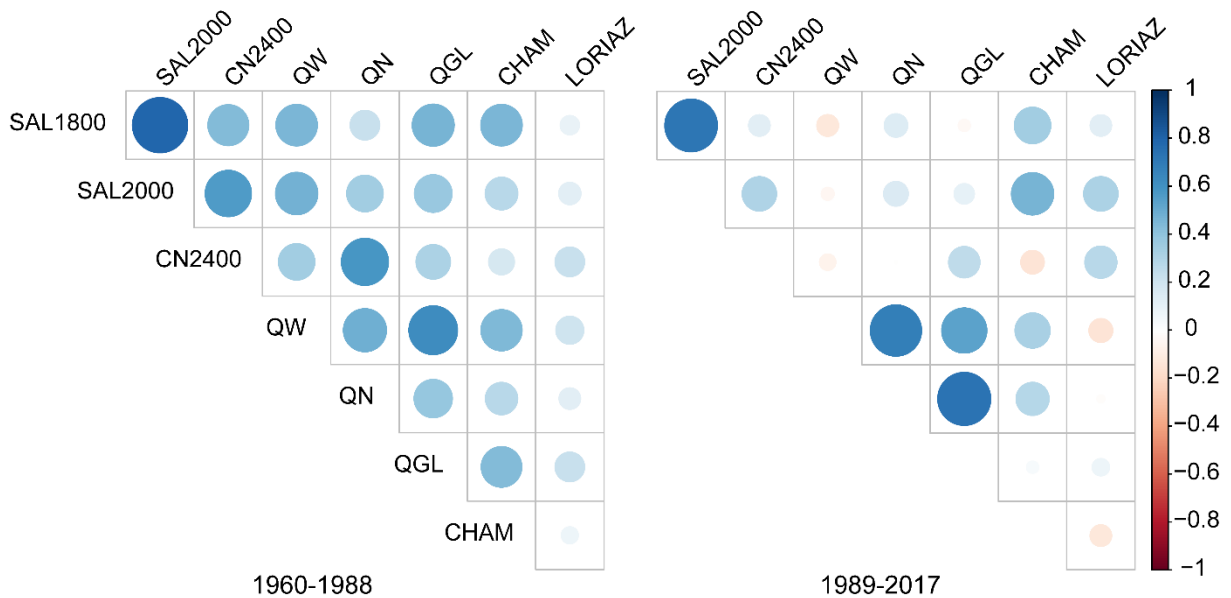


Figure S3: Correlation matrices between detrended *R. ferrugineum* site chronologies for the periods 1960–1988 (left panel) and 1989–2017 (right panel). Color intensity and the size of the circle are proportional to the correlation coefficients (see color-scale on the right of the figure).



Conclusion et perspectives

Photographie de page précédente : Le lac Fourchu, vu depuis la combe nord du Taillefer.

Sur la base des verrous scientifiques identifiés dans le chapitre introductif, l'objectif principal de cette thèse est de mettre en évidence les impacts du réchauffement climatique récent sur une espèce de ligneux bas, *Rhododendron ferrugineum* L., caractéristique des étages supraforestiers alpins. La dendrochronologie a été choisie pour atteindre cet objectif en raison du caractère intégrateur des cernes de croissance qui permettent de reconstituer l'évolution des relations entre la croissance radiale et le climat sur plusieurs décennies. D'un point de vue méthodologique, la mise en œuvre de cette approche a nécessité l'utilisation d'outils statistiques, empruntés à l'écologie *stricto sensu*, permettant de prendre en compte la complexité topo-climatique du milieu alpin. A l'interface entre ces deux disciplines, la démarche adoptée ici n'en reste pas moins géographique par son caractère interdisciplinaire mais surtout le choix assumé, malgré la complexité inhérente à cette approche, d'un échantillonnage en conditions non-contrôlées, le long de gradients topo-climatiques et dans des massifs caractérisés par des niveaux de continentalité représentatifs des Alpes françaises. Les deux premières parties de ce chapitre synthétisent ainsi les résultats obtenus et les limites de ce travail. La troisième propose des perspectives de recherche pour une étude intégrée, de la cellule au paysage, du verdissement en milieu alpin.

1 Synthèse des résultats obtenus

La réalisation d'une thèse sous forme d'articles scientifiques ne permet pas d'exposer les résultats sous la forme d'un ensemble homogène, mais nécessite un formatage des résultats en adéquation avec les exigences des revues. Cette première partie synthétise les résultats obtenus dans les chapitres 1 (sur le potentiel dendroécologique de *R. ferrugineum*) puis 2-3-4 (sur la réponse de *R. ferrugineum* aux fluctuations climatiques) de ce travail mais présente également un certain nombre de résultats et de réflexions qui n'ont pas pu être inclus dans les différents manuscrits.

1.1 Evaluation du potentiel dendroécologique de *Rhododendron ferrugineum* (chapitre 1)

Le premier chapitre de cette thèse nous a permis de mettre en évidence le potentiel dendroécologique de *Rhododendron ferrugineum*. Nous avons ainsi pu développer la première chronologie de référence pour cette espèce pour une population située à 2000 m d'altitude dans le massif du Taillefer. Cette chronologie couvre la période 1821-2015 confirmant ainsi la longévité de l'espèce, entrevue dans la littérature, et le caractère annuel des cernes de croissance. Cette chronologie a permis, au moyen de corrélations partielles, avec des données climatiques de résolutions spatiale et temporelle limitées, de déterminer les facteurs conditionnant la croissance radiale de *R. ferrugineum* et de démontrer que ceux-ci diffèrent des populations d'arbres voisines. Ainsi, alors que la chronologie de largeur de cernes de *P. abies* est principalement corrélée aux températures estivales, celle de *R. ferrugineum* est, de surcroît, conditionnée par les températures automnales et les précipitations hivernales. L'analyse des années caractérisées par des cernes étroits permet aussi d'entrevoir les effets négatifs des dates de déneigement trop précoces du fait des événements de gel tardifs, préfigurant ainsi la mise en évidence dans la suite de la thèse de la non-linéarité des relations cerne-climat.

A l'issue de ce premier chapitre, basé sur des données climatiques de faible résolution et sur des méthodes statistiques simples, nous discutons un certain nombre d'hypothèses. La question majeure qui subsiste porte sur le rôle des températures du mois de mai et des précipitations hivernales sur la longueur de la saison végétative. Les articles/chapitres suivants vont chercher à tester ces différentes hypothèses.

Les observations de terrain et une analyse exhaustive de la littérature relative à l'écologie de *R. ferrugineum* (Larcher and Wagner, 2004; Schlüssel et al., 2000) nous ont également permis de confirmer la pertinence de notre choix d'espèce. En effet, de la base de l'étage subalpin à l'étage alpin, la morphologie et l'architecture des individus changent progressivement, avec des individus de plus en plus prostrés à haute altitude. Cette capacité, très « alpine » à se développer à proximité du sol lorsque les conditions deviennent particulièrement contraignantes (en comparaison avec des arbustes plus grands, l'aulne vert par exemple, qui reste érigé), explique la sensibilité de *R. ferrugineum* aux conditions microclimatiques et notamment à la variabilité de l'enneigement. Cette sensibilité est confirmée par les micro-habitats privilégiés par cette espèce, qu'on retrouve préférentiellement en position abritée en limite altitudinale supérieure (dans de petites dépressions, par exemple, ou à l'abri d'un rocher) pour bénéficier de la protection du manteau neigeux jusqu'à la fin de l'hiver (Larcher and Wagner, 2004). Sur ce point, elle contraste avec des espèces à plus large amplitude écologique telles que le genévrier nain que l'on retrouve en positions topographiques beaucoup plus diverses (Carrer et al., 2019). Comparé au genévrier nain en particulier, cette niche écologique restreinte pourrait être considérée comme problématique puisque les contraintes microclimatiques supplantent les forçages climatiques régionaux. Nous considérons au contraire, que la sensibilité du rhododendron à la sécheresse et au gel, en lien avec la position microtopographique et son influence sur la variabilité du manteau neigeux et sur l'humidité, font de cette espèce un excellent indicateur dendroécologique à la différence du genévrier nain plus approprié aux études dendroclimatologiques ayant pour objectif la reconstruction de la variabilité climatique passée (Pellizzari et al., 2014).

1.2 Réponses du rhododendron aux fluctuations du climat dans les Alpes françaises : non-linéarité et effets de seuil (chapitres 2, 3 et 4)

Les conclusions du chapitre 1 ont conditionné l'échantillonnage des populations de *R. ferrugineum*. A petite échelle, les massifs montagneux ont été choisis pour représenter la diversité des situations climatiques, en termes de continentalité, existantes dans les Alpes françaises. Depuis le Queyras au sud et dans les Alpes internes, aux massifs plus humides du Mont-Blanc et de la Chartreuse au nord et à l'ouest, en passant par le massif du Taillefer en situation intermédiaire, les contrastes de totaux pluviométriques sont les plus forts des Alpes françaises. Plus localement, les sites au sein des massifs ont été choisis pour couvrir de forts gradients topographiques. Les deux placettes échantillonnées dans le Taillefer à 1800 et à 2400 m d'altitude, en complément de celle échantillonnée à 2000 m dans le cadre du chapitre 1 ainsi que les trois placettes échantillonnées dans le Queyras en exposition nord et ouest visaient à mettre en évidence le rôle du gradient altitudinal et du topoclimat sur la croissance radiale. L'ensemble des chronologies de largeur de cernes édifiées sont visualisables à la fin de ce manuscrit (figures S1 à S8). Plus généralement, et sur la base des résultats de notre premier article, nous souhaitons montrer l'effet de la date de déneigement le long de différents gradients (voir figure complémentaire S9, qui présente des indices de croissance radiale en fonction de la date de déneigement à différentes altitudes dans le massif du Taillefer). Notre hypothèse sous-jacente était que la date de déneigement contrôlait la croissance radiale en conditionnant la quantité d'énergie reçue pendant la saison végétative (SFGDD). Dans le massif du Queyras, l'échantillonnage nous a également permis d'aborder les questions de sensibilité à la sécheresse que nous ne pensions initialement pas observer en milieu alpin. Dans le massif du Taillefer, la comparaison des modèles d'équations structurelles pour les trois placettes échelonnées le long du gradient altitudinal démontre que la somme des degrés-jours supérieurs à 0°C pendant la période déneigée (SFGDD) et, par extension, les dates de déneigement ont une influence maximale sur la croissance radiale à 2400m d'altitude. En revanche, à 1800 et 2000 m d'altitude, les dates de déneigement contraignent peu les SFGDD qui ne limitent que partiellement la productivité. Dans le Queyras, l'impact des SFGDD sur la croissance est plus forte en versant nord qu'en versant ouest où la sécheresse estivale est le principal facteur limitant.

Dans le chapitre 4, à la différence de la grande majorité des études dendroécologiques, l'analyse des relations cernes/climat est réalisée à l'échelle individuelle et non sur des moyennes par populations. Pour cela, les séries de largeurs de cerne de 119 individus prélevés sur 8 sites, en situations topoclimatiques contrastées, ont été utilisées. Les modèles linéaires mixtes démontrent une très forte non-linéarité dans la relation entre les SFGDD et la croissance radiale. Ils permettent également de détecter des seuils, variables selon les populations en-dessus desquels les températures et les dates de déneigement ont un impact négatif sur la croissance. Nous faisons l'hypothèse que la sécheresse édaphique (déficit en eau du sol), exacerbée par les températures élevées et par la fonte précoce, explique cette non-linéarité. Cette hypothèse est partiellement validée par les comparaisons réalisées en situation topoclimatique contrastée qui montrent que les seuils sont fortement modulés par la continentalité et l'orientation du versant et que le seuil minimal (900 degrés-jour) est observé pour les populations du Queyras localisées sur un versant adret. Au contraire, dans le massif de la Chartreuse, le plus humide massif échantillonné sur versant ouest, la valeur de ce seuil se situe aux alentours de 1600 degrés-jour.

1.3 Impacts du réchauffement climatique sur la croissance de *R. ferrugineum* (chapitres 2, 3 et 4)

Afin de mettre en évidence les effets potentiels du réchauffement climatique sur la croissance radiale de *R. ferrugineum*, les analyses climatiques ont été systématiquement réalisées pour les périodes 1959-1988 et 1989-2018. Ces périodes, de durées égales, couvrent chacune 30 années, conformément à la définition d'une normale météorologique. De plus la seconde période coïncide avec le réchauffement marqué, observé depuis la fin des années 1980, dont les conséquences sur le milieu biophysique ont été particulièrement importantes (North, 2013; Oberhuber et al., 2008). Avant 1989, des relations linéaires sont observées entre la croissance de *R. ferrugineum* et les degrés-jours sur la totalité des sites étudiés. Les corrélations sont très significatives ($p < 0.05$) et excèdent $r = 0.39$ (maximum de $r = 0.75$). On observe un fonctionnement que je serais tenté d'appeler « de référence » car la croissance est classiquement, très fortement régie par les SFGDD, quelle que soit la situation topoclimatique (chapitre 4). La matrice de corrélation calculée entre les différents sites confirme la cohérence du signal climatique. Une rupture est observée dès le début des années 1990. Elle se caractérise par la baisse des coefficients de corrélations entre la croissance radiale et les SFGDD (coefficients de corrélation variant entre -0.32 et 0.42 selon les sites) et traduit une baisse de la sensibilité des arbustes aux températures. En comparaison avec la période 1960-1988, la croissance radiale ne suit plus l'élévation des SFGDD, mettant en évidence une déconnection entre les deux séries depuis le début des années 1990. Cette rupture, liée au dépassement de plus en plus fréquent des seuils de degrés-jours décrits dans le chapitre 4, est attribuée au réchauffement climatique. La matrice de corrélation inter-sites, beaucoup plus hétérogène, confirme que la croissance des individus devient plus contrainte par la topographie que par le climat régional (en particulier par les températures moyennes estivales, fortement corrélées à travers les Alpes). Cette tendance est en adéquation avec la théorie du micro-refuge (*micro-refugia*) qui postule que certaines espèces alpines, situées dans des micro-habitats favorables, seront moins touchées par le réchauffement du climat (Kulonen et al., 2018; Winkler et al., 2018).

Trois hypothèses sont avancées et discutées dans les chapitres 2, 3 et 4 pour expliquer les raisons de cette évolution et de la perte de sensibilité aux SFGDD.

- (1) D'abord, la quantité de degrés-jours reçue chaque année est suffisante pour que les individus puissent achever leur croissance et leur cycle phénologique (chapitre 2). En complément, on peut ajouter le fait que les espèces alpines adoptent une stratégie habituellement plus conservatrice (Körner, 2003; Totland and Alatalo, 2002), privilégiant un équilibre dans l'allocation du carbone au sein des parties végétatives afin de maintenir une taille réduite.
- (2) Ensuite, les degrés-jours ne sont plus systématiquement le facteur limitant principal ; en particulier la disponibilité en eau, principalement contrôlée par la topographie, contrôle la croissance en particulier lors des années chaudes (chapitre 3).
- (3) Enfin, les événements extrêmes, tels que les gels de printemps, les canicules ou les sécheresses intenses (chapitres 2 et 3) contrebalancent les effets positifs de la hausse des températures sur la croissance des ligneux bas.

Nous postulons que cette perte de sensibilité des ligneux bas aux SFGDD et cette déconnection entre les séries dendrochronologiques et climatiques est assimilable au phénomène de divergence mis en évidence dans les séries dendrochronologiques des arbres des régions froides (Büntgen et al., 2008; D'Arrigo et al., 2008).

Ainsi, dans le Taillefer, à 1800 m d'altitude, les dates de déneigement sont de plus en plus précoces et le manteau neigeux peut disparaître dès avril. Les événements de gels tardifs sont de plus en plus fréquents (chapitre 2, figure 1). Le cerne de 1997, extrêmement fin sur tous les individus situés 1800m et à 2000m d'altitude, n'est pas atypique à 2400 m. Les réanalyses SAFRAN-Crocus, montrent que les *R. ferrugineum* situés à basse altitude ont été exposés pendant plusieurs jours d'avril 1997 à des cycles gel-dégel intenses alors que les individus situés à plus haute altitude étaient protégés par le manteau neigeux. De la même manière, dans le Queyras, la sensibilité accrue des ligneux bas à la sécheresse (chapitre 3) est exacerbée par les canicules de plus en plus fréquentes, en particulier en exposition ouest. Ces événements extrêmement froids (cycles gel-dégel) ou chauds (canicule) en accroissant les sécheresses hivernale ou estivale, peuvent induire la rupture de continuité hydraulique de certains vaisseaux, des processus de cavitation, et limiter la croissance radiale des individus (Charrier et al., 2015; Mayr et al., 2010). De plus, les dommages, causés par le gel (Charrier et al., 2015), l'irradiation (Neuner et al., 1999) ou les fortes températures sur les parties ligneuses ou sur les cellules vivantes (Buchner and Neuner, 2003) illustrent de manière très claire les non-linéarités induites par le réchauffement climatique dans les relations cerne/climat.

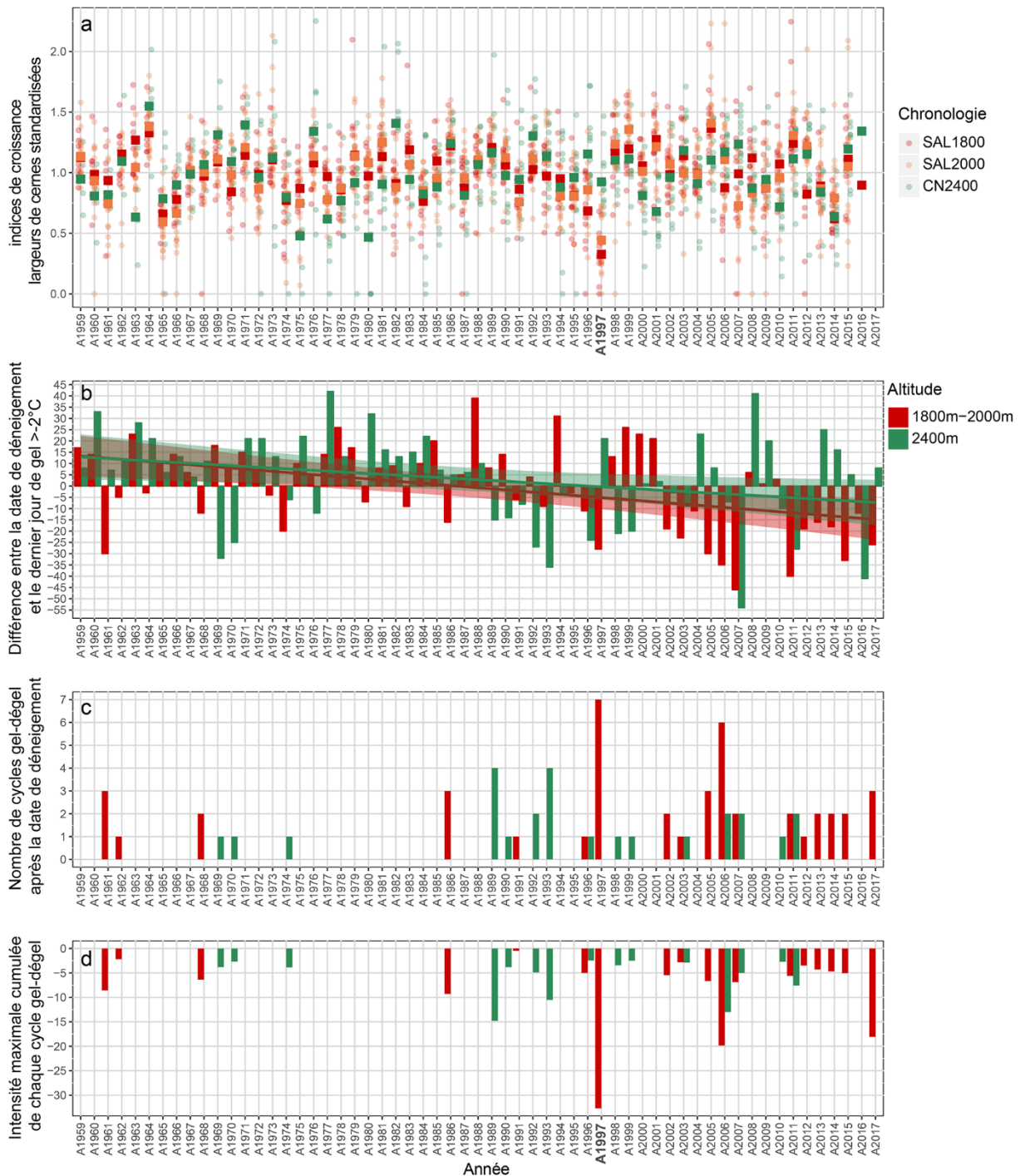


Figure 1: De haut en bas : indices de croissance radiale (correspondant aux largeurs de cerne standardisées et moyennées par population échantillonnées le long du gradient altitudinal dans le Taillefer : SAL1800 à 1800 m d'altitude, SAL2000 à 2000 m, CN2400 à 2400 m) (a) ; indice d'exposition au gel obtenu en calculant la différence entre la date de déneigement et la date du dernier gel supérieur à -2°C pour deux étages (1800-2000 m et autour de 2400 m). Cela permet de voir les tendances d'exposition au gel des ligneux bas depuis 1959 : des valeurs négatives signifient que les ligneux bas ont été exposés à des événements de gel. La tendance depuis 1959 est vers une exposition de plus en plus fréquente des plantes, en particulier à basse altitude dans le massif du Taillefer où le dernier gel se produit en moyenne 15 jours après la date de déneigement (b) ; nombre de cycles gel/dégel (c) ; intensité cumulée des cycles (d). On remarque le cerne caractéristique de 1997, étroit à basse altitude, mis en évidence dans le chapitre 2. 1997 est également l'année au cours de laquelle les gels ont été les plus intenses au cours de la période 1960-2017.

1.4 Nouvelles approches statistiques pour une détection affinée du signal climatique dans les cernes de croissance des ligneux bas (chapitres 2, 3 et 4)

Les réanalyses météorologiques issues du modèle SAFRAN-Crocus (Durand et al., 2009b, 2009a) fournies par le Centre d'Etude de la Neige (CEN) ont été décisives pour la réalisation de cette thèse. De résolution horaire et fournies par massif, par tranche d'altitude et pour des expositions et des niveaux de déclivité de versant différents, ces données à haute résolution spatio-temporelle, permettent de reconstituer finement l'évolution de l'enneigement, des températures et des précipitations (Brun et al., 2012). Elles ont permis d'exploiter au mieux l'échantillonnage réalisé dans les différents massifs et le long des différents gradients. Elles ont aussi permis d'analyser les relations cernes/climat avec une précision inégalée. Cependant, compte-tenu des résolutions très différentes des séries dendrochronologiques (annuelle) et météorologiques (horaire) et de la multiplicité des paramètres fournis par SAFRAN-Crocus, souvent fortement corrélés, nous avons été amenés à développer des outils statistiques alternatifs à ceux traditionnellement utilisés en dendroécologie.

Dans le dernier chapitre, des modèles linéaires mixtes (LMM : *Linear Mixt Model*) ont été utilisés pour quantifier la réponse individuelle des ligneux bas aux degrés-jours, et mettre en évidence la modulation par la topographie. Ce type de modèle a déjà été utilisé en dendroécologie sur les arbres (e.g. Galván et al., 2014; Primicia et al., 2015; Speed et al., 2011) ou sur les arbustes (voir tableau 3 en introduction). Ces modèles sont particulièrement adaptés à la problématique de cette thèse car ils permettent de dissocier l'influence d'effets fixes (les variables climatiques, la topographie et leurs interactions, dans notre cas) et d'effets aléatoires (les variations de croissance annuelles inter-individuelles et inter-sites) (Bolker et al., 2009; Harrison et al., 2018). Leur utilisation permet également de s'affranchir des problèmes liés à la standardisation des données dendrochronologiques (voir introduction) puisque la tendance d'âge ou l'autocorrélation temporelle sont prises en compte dans le modèle. Les séries sont considérées individuellement et ne sont pas moyennées par population ce qui limite la perte d'information inhérente à la conversion des largeurs de cernes en indices (Avanzi et al., 2019). Enfin, les modèles linéaires mixtes, à la différence des fonctions de corrélation ou de réponse, permettent de tester les non-linéarités potentielles dans les relations cerne-climat.

L'utilisation de modèles d'équations structurelles (SEM : *Structural Equation Model*) dans les chapitres 2-4 est plus originale. Les SEMs fonctionnent sur la base d'hypothèses définies *a priori*. Dans les chapitres 2 et 3, nous les avons utilisés pour mettre évidence l'influence du manteau neigeux sur les degrés-jours, puis sur les ligneux bas. Ils sont particulièrement adaptés à notre problématique car ils permettent de cerner l'influence des paramètres climatiques définis comme limitants mais également leur colinéarité et leurs effets directs ou indirects. Ce type de modélisation repose sur un réseau de régressions multiples et partielles et s'est révélé bien adapté aux données complexes extraites de SAFRAN-Crocus. A la différence des régressions (simples/multiples, partielles, avec sélection des variables de type *stepwise* très communes dans la littérature (Fritts and Xiangding, 1986; Meko et al., 2011), les SEMs n'ont été que rarement utilisés en dendroécologie (à l'exception de Brien et al., 2010; Madrigal-González et al., 2017, 2018) et leurs apports n'ont été que très peu discutés dans la littérature.

2 Limites

Malgré les avancées significatives des connaissances sur la réponse des ligneux bas alpins au réchauffement du climat permises grâce (1) au développement d'un réseau de chronologies, (2) l'utilisation de données météorologiques à haute résolution et (3) le développement de méthodes statistiques, plusieurs limites et incertitudes demeurent à l'issue de cette thèse. Celles-ci concernent : (1) le réseau de chronologies, à densifier ; (2) l'analyse dendroécologique, limitée à l'analyse entre largeurs de cernes et climat, qui aurait pu être approfondie par le biais d'indicateurs anatomiques tels que, par exemple, la variabilité intra/interannuelle de tailles de vaisseaux ; (3) des aspects méthodologiques, liés à l'extraction du signal climatique des séries dendrochronologiques au sein des individus ; (4) la connaissance limitée des processus écophysologiques régissant les relations cerne/climat. Enfin, même si cela ne constitue pas véritablement une limite à ce travail car ne répondant pas aux objectifs fixés en introduction, l'étude des liens entre la croissance radiale, les dynamiques arbustives, et le phénomène de verdissement observés dans les Alpes françaises reste un enjeu de recherche important et encore insuffisamment exploré.

2.1 Un réseau de chronologies unique mais encore limité

Dans les bases de données internationales, de multiples séries dendrochronologiques existent pour les arbres dans les Alpes ou les ligneux bas des hautes latitudes. Comme nous l'avons souligné dans le chapitre introductif, aucune chronologie n'était disponible pour les arbustes alpins dans les Alpes françaises. Le développement de chronologies pour les ligneux bas est beaucoup plus complexe et requiert beaucoup plus de temps que pour les arbres. Le jeu de données acquis au cours de cette thèse est donc unique (8 chronologies dans 4 massifs) et a été conçu pour représenter au mieux la variabilité topoclimatique des Alpes françaises. Il n'en reste pas moins très limité. Cette lacune est d'autant plus préjudiciable que nos résultats démontrent une forte variabilité de la réponse au climat, tant au niveau individuel qu'au niveau spatial. Ils confirment ainsi les études récentes réalisées en Arctique (Ackerman et al., 2017; Ropars and Boudreau, 2012) et donc la nécessité de prélever dans des situations topographiques contrastées. Pour cela, il est bien entendu possible et souhaitable de densifier le réseau dendrochronologique mis en place. Cependant, compte-tenu de la complexité du protocole d'élaboration des chronologies, il nous semble préférable, au préalable de futures campagnes de prélèvements, d'axer les recherches futures sur l'élaboration de modèles mécanistes de croissance, afin de préciser le protocole d'échantillonnage.

2.2 Absence d'analyse anatomique des cernes de croissance

Notre étude, a été limitée, en raison des contraintes de temps, au développement de chronologies de largeurs de cernes. Les indicateurs micro-anatomiques inter et intra-annuels, de plus en plus utilisés en dendrochronologie grâce au développement de méthodes quantitative et automatisées (von Arx and Carrer, 2014; Fonti et al., 2010), auraient probablement permis d'améliorer la compréhension des relations cernes/climat à l'échelle infra-annuelle. Encore peu utilisés chez les arbustes, la taille et la densité des vaisseaux (Eilmann et al., 2009), la proportion de cellules de parenchymes par rapport aux tissus de soutien et de conduction hydraulique (Anadon-Rosell et al., 2018), les cernes de gel (Hantemirov et al., 2000) ou l'épaisseur des parois cellulaires (Lehejček et al., 2017), pourraient

constituer des indicateurs robustes pour quantifier la réponse écologique aux stress occasionnés par les sécheresses hivernale ou estivale (voir par exemple Fonti et al., 2010, 2013). La finesse des cernes de croissance de ligneux bas ne constitue pas un écueil : la possibilité de travailler sur l'intégralité de la section de bois permet de compenser ce problème par la quantification de l'anatomie sur la totalité de la surface du cerne. Cependant, une grande force de calcul est nécessaire afin de quantifier la taille de milliers de cellules sur des images extrêmement définies, et beaucoup d'attention doit être portée à la détection et au tracé des limites entre les cernes de croissance, rendant cette tâche plus fastidieuse pour les arbustes que pour les arbres.

2.3 Limites liées à l'extraction du signal au sein des individus et à la standardisation des données

La troisième limite concerne le choix de la méthode de mesure des cernes de croissance, qui a un impact sur l'approximation du signal climatique extrait et sur le choix de la méthode de standardisation des séries mesurées permettant d'extraire le signal écologique et climatique recherché et d'éliminer le « bruit » que constitue la tendance d'âge ou les perturbations stationnelles d'origine non-climatiques. En effet, il a été démontré qu'au sein d'un même arbuste, le signal peut changer depuis la base jusqu'aux tiges les plus hautes (Ropars et al., 2017) ou au niveau d'une même section transversale (Buras and Wilmking, 2014), démontrant également des stratégies complexes d'allocation du carbone au sein des tiges. La méthode de « *serial sectioning* » adoptée ici, permettant en premier lieu de détecter les cernes manquants le plus souvent à la base de la tige en prélevant des sections à différentes hauteurs, a permis de remédier à cet éventuel problème. Cependant, je n'ai pas cherché à isoler les signaux climatiques à différentes hauteurs de la tige et/ou par rapport au sol afin de vérifier s'il y a ou non une évolution du signal climatique le long de la tige, et si oui, de la quantifier. De plus, la standardisation des séries dendrochronologiques, destinée à éliminer les signaux parasites d'origine non-climatique, peut faire disparaître des informations écologiques ou climatiques intéressantes (Avanzi et al., 2019). Plusieurs solutions peuvent être envisagées afin d'améliorer la mesure des cernes et la standardisation : (1) comparer les signaux climatiques dans nos chronologies de largeurs de cernes standardisées et ceux de chronologies de surface de cernes qui ne nécessitent aucune standardisation puisqu'elles sont exemptes de tendance d'âge (Bär et al., 2006) ; (2) analyser l'évolution du signal climatique le long des tiges, en prélevant des sections dont l'exposition au gel ou au rayonnement solaire varie en fonction de leur hauteur par rapport au sol, et donc précisément localisées par rapport à la surface du sol ; (3) tester l'impact de différents types de standardisation afin de proposer la plus adaptée à l'extraction d'un signal climatique optimal pour les ligneux bas.

2.4 Limites de l'approche dendroécologique : corrélations et causalités

L'ensemble des méthodes statistiques utilisées repose sur le calcul de corrélations entre les chronologies de largeurs de cernes et les co-variables météorologiques. Le cerne de croissance annuel est assimilé à un système « boîte noire » dont on ne considère pas le fonctionnement mais simplement la résultante, i.e. la largeur. Celui-ci intègre ainsi une multitude de signaux, climatiques ou non, résultant de conditions moyennes ou extrêmes, que seule une approche de type mécaniste pourrait permettre de dissocier convenablement. Trois exemples illustrent ces limitations :

(1) il est difficile d'expliquer les corrélations positives, statistiquement significatives, calculées entre les séries de largeurs de cerne et les précipitations des mois de mars et d'avril sur plusieurs sites de basse altitude. Il existe probablement un lien entre ces précipitations, le manteau neigeux et la croissance mais celui-ci n'est pas évoqué dans la littérature.

(2) la relation positive détectée entre la croissance et les températures automnales de l'année précédente est attribuée (1) à l'effet négatif des événements de gels (fréquents à cette période en cas de température froide, et auxquels les plantes basses sont exposées du fait de l'absence de manteau neigeux), susceptibles d'affecter la croissance de manière directe (dommages cellulaires) ou indirecte (effets sur les micro-organismes du sol) ou (2) à la constitution de réserves sous forme de glucides non-structuraux, disponibles dans les parties végétatives de la plante pour la croissance de l'année suivante (Hoch, 2015; Martínez-Vilalta et al., 2016). L'approche dendroécologique ne nous permet pas de trancher entre ces hypothèses.

(3) Enfin, et malgré la pertinence des relations calculées entre degrés-jours et productivité, on peut s'interroger sur l'influence directe de la date de déneigement sur la croissance en raison de son impact sur l'activité microbienne des sols et donc sur les ressources nutritives du sols (Brooks and Williams, 1999). En effet, l'avancement des dates de déneigement influence directement l'activité microbienne, active pendant l'hiver mais perturbée par les cycles gels-dégels. Donc une saison enneigée plus courte implique moins de nutriments disponibles pour la croissance et une désynchronisation entre le pic de nutriment dans le sol et le début de la croissance des ligneux bas, qui a lieu plus tard dans la saison (Ernakovich et al., 2014)

2.5 Croissance radiale, verdissement et dynamiques arbustives

Peut-on penser qu'il existe un lien entre les variations interannuelles de largeur de cerne et la tendance au verdissement mise en évidence à l'échelle de certains massifs des Alpes françaises et italiennes depuis les années 1980 (Carlson et al., 2017; Filippa et al., 2019) ? Plusieurs études ont tenté de répondre à cette question, en comparant les séries dendrochronologiques et les séries de productivité obtenues par télédétection (NDVI, *Normalised Difference Vegetation Index*, construit à partir des canaux rouge et proche infra-rouge et permettant de suivre la biomasse et l'activité photosynthétique des plantes). Leurs résultats sont contrastés : Forbes et al. (2010), Ropars et al., (2015) et Weijers et al., (2018) démontrent des liens significatifs entre la croissance radiale et les indices annuels de productivité. Il semblerait cependant, une fois la lande établie, qu'un découplage entre les deux variables soit observé (Ropars et al., 2015). Angers-Blondin, (2019), au contraire des auteurs précédents, ne démontre aucun lien entre croissance radiale et NDVI.

Ces divergences questionnent la capacité du cerne à refléter la productivité de l'individu sur lequel il est mesuré, la séquestration du carbone et donc l'utilisation de la croissance radiale comme bioindicateur de la productivité de certaines communautés alpines. Toutefois, étonnamment peu d'attention n'a encore été portée sur les relations entre la croissance secondaire (ou radiale) et la croissance primaire (élongation des rameaux). Selon Au et Tardif (2007), cette relation entre croissance radiale et productivité pourrait être mise en évidence au moyen d'équations allométriques entre la croissance radiale, la croissance apicale, la taille ou la biomasse de l'individu échantillonné. Pourtant, selon Shaver (1986), la contribution de la croissance secondaire à la production primaire nette des

communautés végétales est importante. Les études existantes se sont cependant heurtées à des difficultés pour monter des relations allométriques au sein des individus car les stratégies d'allocation de l'énergie au sein d'un même individu sont complexes et mal connues (Buras and Wilmking, 2014; Sadras and Denison, 2009), en particulier en contexte extrême (très hautes latitudes et très hautes altitudes, cf. Angers-Blondin (2019)).

Dans le cadre de cette thèse, les courbes splines qui permettent de faire apparaître les fluctuations moyennes fréquences dans les chronologies de largeur de cerne une fois que la tendance d'âge ait été supprimée par une courbe exponentielle négative, ne montrent pas de tendance significative au cours des dernières décennies (à l'exception de CN2400, qui montre une augmentation de la croissance radiale suite à l'augmentation des SFGDD à la fin des années 1980, voir figure S3 à la fin de ce manuscrit). Ce résultat suggère une absence de relation entre NDVI (en hausse dans les Alpes selon Carlson et al., 2017) et la croissance radiale de *R. ferrugineum*. On peut également penser que l'absence de tendance récente (également en lien avec l'augmentation du stress climatique) est liée (1) à un décalage dans la réponse des écosystèmes au changement climatique (Ash et al., 2017; Danby and Hik, 2007) ou (2) à des interactions positives au sein et/ou entre les clones de *R. ferrugineum*, qui augmenterait leur résilience.

En ce qui concerne les dynamiques arbustives, les études alpines concernent majoritairement l'expansion de grands arbustes (Anthelme et al., 2007; Dullinger et al., 2003) et sont liées à des dynamiques de reconquête de prairies subalpines suite à la déprise agro-pastorale. Les dynamiques des ligneux bas prostrés de l'étage alpin, potentiellement sensibles au réchauffement climatique (Cannone et al., 2007) même si les impacts des héritages anthropiques ne peuvent être exclus (Tinner and Theurillat, 2003; Valsecchi et al., 2010), n'ont été que peu étudiées. Il est peu probable qu'il existe un lien entre croissance radiale et expansion des ligneux bas. En revanche, la dendrochronologie pourrait être utilisée pour retracer les phases de colonisation arbustive (Büntgen, 2019; Büntgen et al., 2015). En effet, la datation des tiges peut servir à retracer les phases de colonisation et d'expansion arbustive. Un échantillonnage aléatoire des tiges sur plusieurs placettes est conseillé, et la datation de la base par comptage des cernes de croissance peut permettre de manière assez rapide de reconstruire les phases de germination (les recrutements) et donc les phases d'expansion, dans le temps et dans l'espace, des ligneux bas prélevés (Büntgen, 2019; Büntgen et al., 2015).

3 De la cellule au paysage : proposition d'un cadre méthodologique pluridisciplinaire pour l'étude des impacts du réchauffement climatique sur les dynamiques arbustives en milieu alpin

Cette thèse a permis de mettre en évidence le potentiel mais également les limites de l'approche dendroécologique pour la compréhension de la sensibilité au changement climatique des ligneux bas en haute montagne alpine. Il reste cependant un long chemin à parcourir dans la compréhension des

mécanismes biologiques et physiologiques derrière les phénomènes que la dendroécologie met en évidence par l'approche statistique : non-linéarité des relations cerne/climat, effets de seuil, sensibilité aux événements extrêmes. Mais le potentiel de la croissance radiale comme trait caractérisant la productivité des individus, voire des landes ou des communautés associées aux ligneux bas, reste méconnu est nécessite d'être précisé, afin de pouvoir faire le lien entre les résultats dendroécologiques et les données de productivité obtenues par télédétection. En ce sens, nous plaçons **pour une étude multi-échelle (cellulaire à paysagère) et intégrée (écophysiologie – dendroécologie – télédétection) de la sensibilité de la végétation arbustive au changement climatique, des dynamiques, et des processus associés (de la division cellulaire au sein du cambium au verdissement à l'échelle paysagère).**

L'expérience acquise et les réflexions menées au cours de ce travail nous permettent de proposer, en perspectives, un cadre méthodologique pluridisciplinaire, qui permettrait d'affiner les connaissances concernant les **impacts du changement climatique sur les dynamiques de croissance arbustive en contexte alpin**. Celui-ci est issu de multiples discussions collectives ayant eu lieu dans le cadre des projets SHRUB, CRYOSHRUB (financés par l'OHM Vicdessos, Labex DRIIHM 2017-2018), SNOWSHRUB (financé par CNRS EC2CO 2018-2019) et ACOUFOLLOW (soumis à l'ANR franco-autrichienne en 2020) auxquels j'ai participé et qui visaient à mettre en évidence les liens entre croissance radiale et dynamiques de la cryosphère dans les Alpes et les Pyrénées. Afin d'atteindre l'objectif fixé, le projet se déclinera en trois tâches : le suivi écophysiologique et microclimatique (T1), l'analyse dendroécologique et micro-anatomique (T2) et l'analyse allométrique couplée à la télédétection (T3). Une tâche préalable (T0) sera dédiée à la sélection de la placette et des espèces étudiées, cruciales pour la réalisation du projet.

3.1 T0 – Choix des espèces, de la placette et extraction des variables climatiques

Afin d'accroître la robustesse des résultats, deux espèces arbustives seront sélectionnées. Compte-tenu du travail réalisé au cours de cette thèse et de la littérature existant dans les Alpes, notre choix se portera sur *R. ferrugineum* et *J. communis*. Le genévrier commun est de taille comparable au rhododendron et il est suffisamment longévif pour permettre une analyse dendroécologique (Carrer et al., 2019). De plus, on les trouve assez souvent en association au sein de la même communauté végétale.

Le choix des placettes étudiées est également primordial. Idéalement, il serait préférable de pouvoir répliquer le protocole exposé ici sur plusieurs sites, par exemple le long d'un gradient mésotopographique (altitudinal, et/ou d'orientation de versant). Toutefois, la placette idéale serait localisée en limite supérieure de la lande arbustive, dans un site où la topographie est suffisamment contrastée pour permettre la prise en compte de gradients d'humidité et d'enneigement et où le pastoralisme est très limité. Elle correspondra à un pixel Landsat (30mx30m). Sur cette placette, la microtopographie sera caractérisée au moyen d'un modèle numérique de terrain (MNT) à haute résolution obtenu par photogrammétrie multi-image (Nouwakpo et al., 2016). Les séries d'épaisseur du manteau neigeux, de températures de l'air et du sol et de précipitations liquides et solides, seront extraites des réanalyses SAFRAN-Crocus de Météo-France. Ces données seront utilisées pour construire des indices annuels de risque de canicule et de gel. Pour cela, nous utiliserons le modèle conceptuel développé par Bréda and Peiffer (2014) qui prend en compte l'intensité de l'aléa (détecté dans les

données SAFRAN-Crocus, par exemple l'intensité des événements de gels printaniers), la vulnérabilité (en lien avec la phénologie, et l'écophysiologie des espèces prélevées, connues grâce à la bibliographie, cf. Buchner and Neuner (2003); Larcher and Wagner (2004); Schlüssel et al. (2000)) et le degré d'exposition (présence de manteau neigeux ou pas, sol gelé ou sec). L'indice de risque dépend de la synchronicité entre l'aléa, la vulnérabilité et l'exposition (Fig. 4).

3.2 T1 – Impacts des événements extrêmes sur les processus écophysiologiques et la croissance radiale

L'impact des événements extrêmes sur la croissance radiale sera quantifié au moyen d'un suivi microdendrométrique et microclimatique.

- (1) D'abord, d'un suivi microdendrométrique réalisé sur plusieurs individus disposés selon un gradient topographique à l'origine de stress croissants (lié à la sécheresse édaphique ou à l'enneigement). Les microdendromètres mesurent la variation du diamètre de la tige instrumentée : l'augmentation radiale irréversible reflétant la croissance, d'une part ; les rythmes réversibles, généralement nycthéméraux, liés à la déshydratation diurne et à la réhydratation nocturne, d'autre part. Ils permettent également de quantifier les dommages cellulaires liés au gel identifiables par de fortes contractions ou un stress hydrique détectable par le biais de la déshydratation progressive de la tige (Daudet, 2004). Le suivi microdendrométrique sera réalisé sur trois années puis les sections équipées seront prélevées afin de quantifier la variation des traits anatomiques (taille de vaisseaux, parois cellulaires endommagées, largeur de cerne) selon le gradient d'exposition au stress. Pour pallier l'absence potentielle d'événements de gel, le déneigement pourra être avancé en utilisant soit un obstacle (*snowfence*) pour limiter l'accumulation de la neige, soit en déneigeant manuellement certains individus (Addis and Bret-Harte, 2019; Neuner et al., 1999; Wipf and Rixen, 2010).
- (2) Ensuite, d'un suivi microclimatique permettant de quantifier précisément les gradients de stress liés au gel ou à la sécheresse. Dans cet optique, la température de l'air sera mesurée à différentes hauteurs entre 0 et 150 cm ; celle du sol, à des profondeurs comprises entre 0 et -50 cm. Ces données thermiques permettront également de reconstituer finement l'évolution du manteau neigeux. Des capteurs d'humidité du sol et NDVI seront utilisés pour quantifier la sécheresse édaphique et la phénologie au niveau de plusieurs individus choisis dans des situations topographiques contrastées.

La figure 2 (extraite de Francon et al. (2018), poster, en annexe), démontre la faisabilité et les enseignements potentiels de ce suivi horaire. Le suivi microdendrométrique permet de suivre la croissance après la date de déneigement, et donc, par exemple, de quantifier le nombre de degrés-jour atteint au moment de l'initiation cambiale, ou au dernier jour de croissance (Fig. 2a). La microdendrométrie permet également de suivre le fonctionnement hydraulique de l'individu soumis à des cycles gel/dégel ou à une évapotranspiration intense. Contractions dues à la déshydratation ou à la prise en glace du xylème et réversibilité des processus peuvent ainsi être suivies (Améglio et al., 2002).

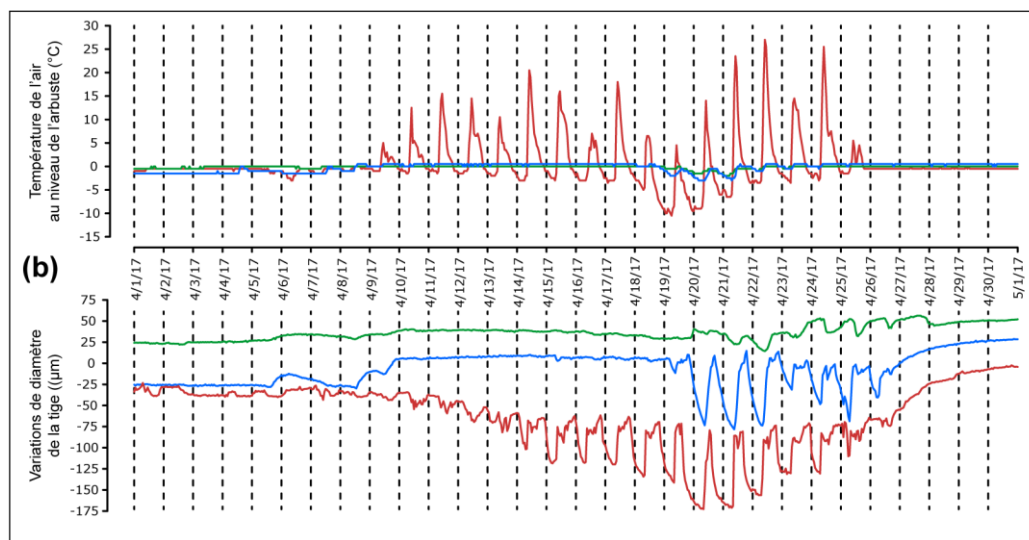
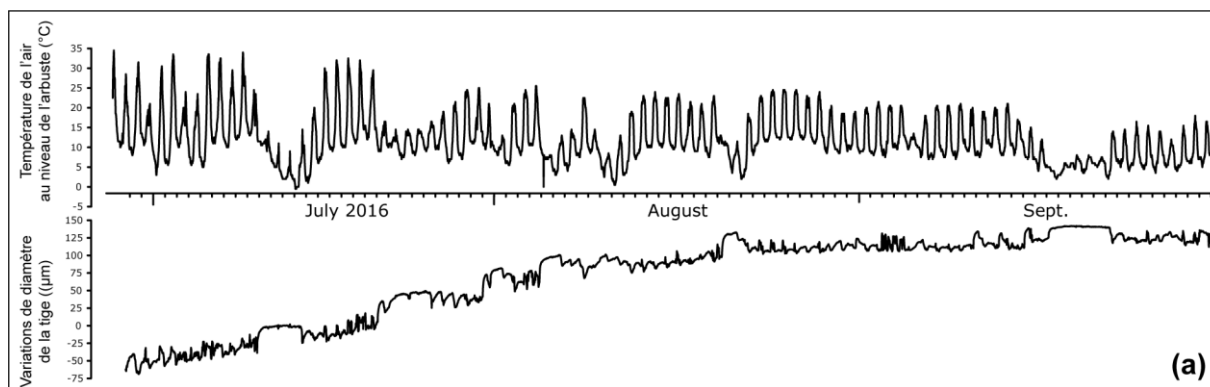


Figure 2 : Variations des températures au niveau du sol et du diamètre des tiges d'un individu de *R. ferrugineum* situés à 1800 m (été 2016) (a), et de trois individus situés 2500 m d'altitude (courbes vertes, bleues et rouges, avril 2017) (b). Ces courbes illustrent le potentiel du suivi microdendrométrique pour l'analyse de la croissance radiale estivale (a). Elles montrent notamment les variations journalières des diamètres liées aux cycles de déshydratation/réhydratation du xylème et l'arrêt de la croissance radiale à la fin du mois d'août (a). A 2500 m (b), des températures très douces en avril ont conduit à un déneigement très avancé, début-avril, suivi par des chutes de neiges le 27 avril. Toutefois, on observe que les conditions microclimatiques varient fortement malgré la proximité des individus équipés, distants d'une dizaine de mètres, montrant l'impact de la microtopographie sur les dates de déneigement : l'individu 1 (courbe verte) est maintenu sous la neige durant presque tout le mois d'avril (la courbe des températures est maintenue à la température de la neige, sauf autour du 21 avril) alors que l'individu 3 (courbe rouge) subit plusieurs cycles gels/dégels très intenses montrant qu'il est exposé à l'air. L'amplitude des contractions du xylème, en lien avec la prise en glace des vaisseaux, est très importante au niveau de l'individu 3. L'individu 1, au contraire ne subit pas de contractions liées au gel mais au contraire, de légères contractions pendant le jour, dues à la transpiration entre le 21 et le 27 avril. Il est probable que cet individu reste protégé au niveau de la tige (pas de gel du xylème), mais que les feuilles les plus hautes soient exposées au rayonnement solaire. L'individu 2 (le bleu) est en situation intermédiaire. Ces différences sont essentiellement conditionnées par la microtopographie.

3.3 T2 – Analyse dendroécologique et micro-anatomique

Dans cette deuxième tâche, une analyse dendroécologique comparable à celle utilisée dans le cadre de cette thèse sera mise en œuvre. Le protocole sera cependant adapté pour prendre en compte les limites évoquées précédemment :

- (1) afin de vérifier l'hypothèse de l'existence d'un gradient d'exposition aux effets du gel ou des canicules le long des tiges, chaque section sera prélevée et précisément localisée (position au niveau de l'individu et dans la placette) ;
- (2) après l'interdatation, un modèle linéaire mixte (cf. chap. 4) sera utilisé pour quantifier l'impact des fluctuations climatiques sur la largeur des cernes ou de différents traits anatomiques. La microtopographie et les gradients d'exposition au gel, les variables climatiques et les indices de risques (cf. tâche T0, paragraphe 3.1) seront pris en compte comme effets fixes dans le modèle. Les traits micro-anatomiques (taille des vaisseaux, indice de groupement des vaisseaux, cernes clairs, caractéristiques des rayons ligneux) seront choisis, en concertation avec des écophysiologistes, en raison de leur sensibilité à la sécheresse estivale ou hivernale (Anadon-Rosell et al., 2018; Nielsen et al., 2017, fig. 3) ;
- (3) en complément, des chronologies de cernes de gels, identifiables par un arrangement chaotique des trachéides ou des irrégularités dans le xylème, seront élaborées pour chaque espèce afin de mettre en évidence rétrospectivement les impacts des gels passés (Fig. 3).

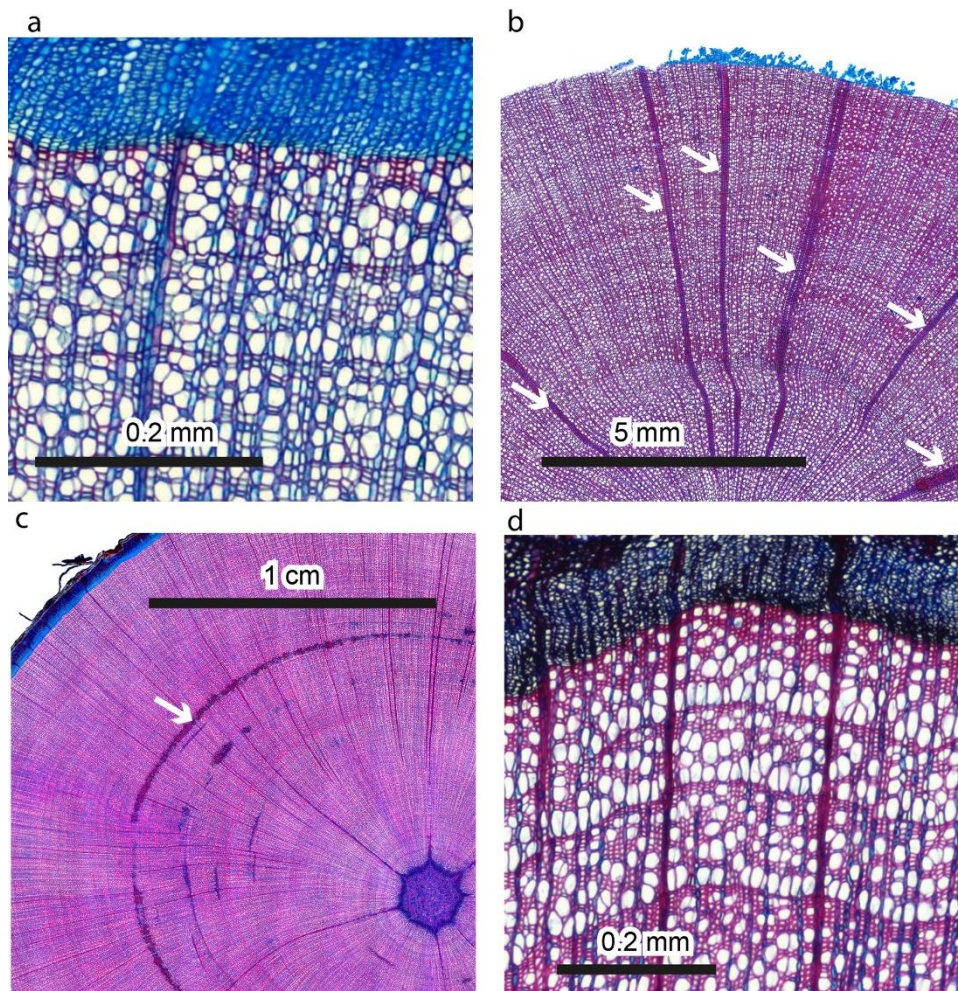


Figure 3: Aperçu de traits micro-anatomiques identifiables et pouvant être datés sur des microsections de *R. ferrugineum* réalisées dans le cadre de cette thèse. Portion de xylème de *R. ferrugineum* caractérisé par un bois à pore diffus dans lequel les cernes présentent des vaisseaux de taille et de répartition relativement uniformes (a) ; rayons ligneux (indiqués par les flèches)

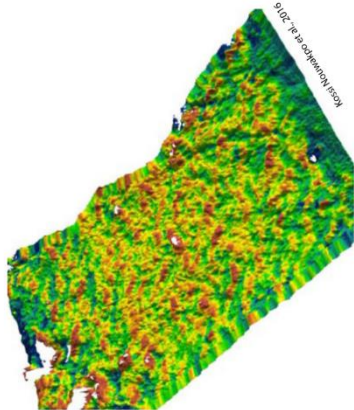
transversaux composés de cellules de parenchyme (b) ; cerne de gel identifiable à sa couleur sombre sur une grande partie de la circonférence de la section (indiqué par la flèche) (c) ; bois à zones semi-poreuses (bois dans lequel le bois initial est marqué par une zone comportant de gros vaisseaux) sur les cernes périphériques d'une section : les changements de types de bois sont rares et pourraient être liés à des changements écologiques (d).

3.4 T3 – Comparaison de la croissance radiale, de la productivité annuelle à l'échelle de l'individu et celle de la communauté

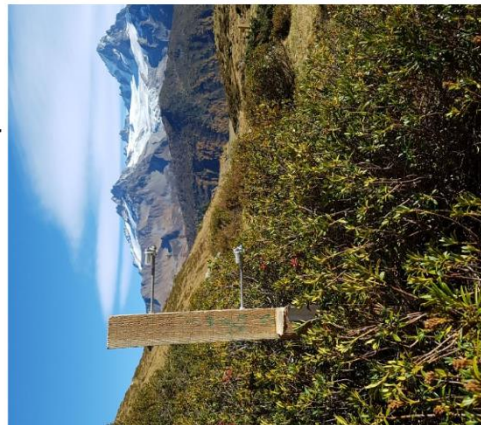
L'objectif de cette tâche est de comparer les fluctuations interannuelles de largeurs de cernes (cf. T2, paragraphe 3.3) avec les fluctuations de productivité à l'échelle individuelle (production de biomasse, croissance apicale...) puis à l'échelle de la placette. La relation entre croissance radiale et productivité annuelle sur un individu s'obtient par des équations allométriques, les fluctuations de productivité de l'ensemble de la communauté végétale à l'échelle de la placette s'obtiennent par télédétection.

Certaines tiges (une dizaine) des individus échantillonnés en T2 (cf. paragraphe 3.3) seront prélevées intégralement et plusieurs traits seront mesurés (largeur moyenne des cernes de croissance sur plusieurs sections, longueur de la tige, surface foliaire spécifique et biomasse totale, notamment). Ces derniers seront utilisés pour caractériser la croissance en hauteur et la productivité. Avant prélèvement, des méthodes de photogrammétrie multi-image permettant de décrire l'architecture des arbustes seront utilisées pour quantifier la biomasse (Cunliffe et al., 2016). Le *continuum* croissance radiale - croissance en hauteur - productivité de l'arbuste sera modélisé au moyen d'équations allométriques. On peut faire l'hypothèse d'une forte dépendance entre la croissance radiale et la biomasse de la tige. En complément, des relations allométriques seront testées entre les diamètres des vaisseaux et la longueur de la tige (Carrer et al., 2015). De telles relations ont déjà été proposées pour les arbustes (Ackerman et al., 2018) mais elles sont souvent complexes car elles dépendent des stratégies d'allocation du carbone dans la plante. Les déconnexions entre la croissance radiale moyenne et la longueur de la tige ou la taille de l'individu sont fréquentes (Angers-Blondin, 2019), mais la croissance radiale moyenne n'a que rarement été mesurée sur un grand nombre de sections d'une même tige.

A l'échelle de la placette, les variations interannuelles de productivité seront estimées par télédétection en utilisant le NDVI extrait des séries d'images Landsat. Certaines études ont déjà pu mettre en évidence des relations fortes entre NDVI et les séries de largeurs de cerne (Forbes et al., 2010; Ropars et al., 2015). Les séries n'ont cependant jamais été comparées pour un pixel Landsat centré sur la placette échantillonnée. Une relation significative permettrait de démontrer que la croissance radiale est un bioindicateur robuste pour reconstruire la productivité et l'éventuel verdissement des communautés arbustives étudiées. Une divergence potentielle pourrait être attribuée à une allocation du carbone plus complexe au sein de différentes parties des végétaux ou à du bruit au sein du signal NDVI engendré par la présence d'autres espèces sur la placette.



Caractérisation fine de la microtopographie



Suivi microclimatique

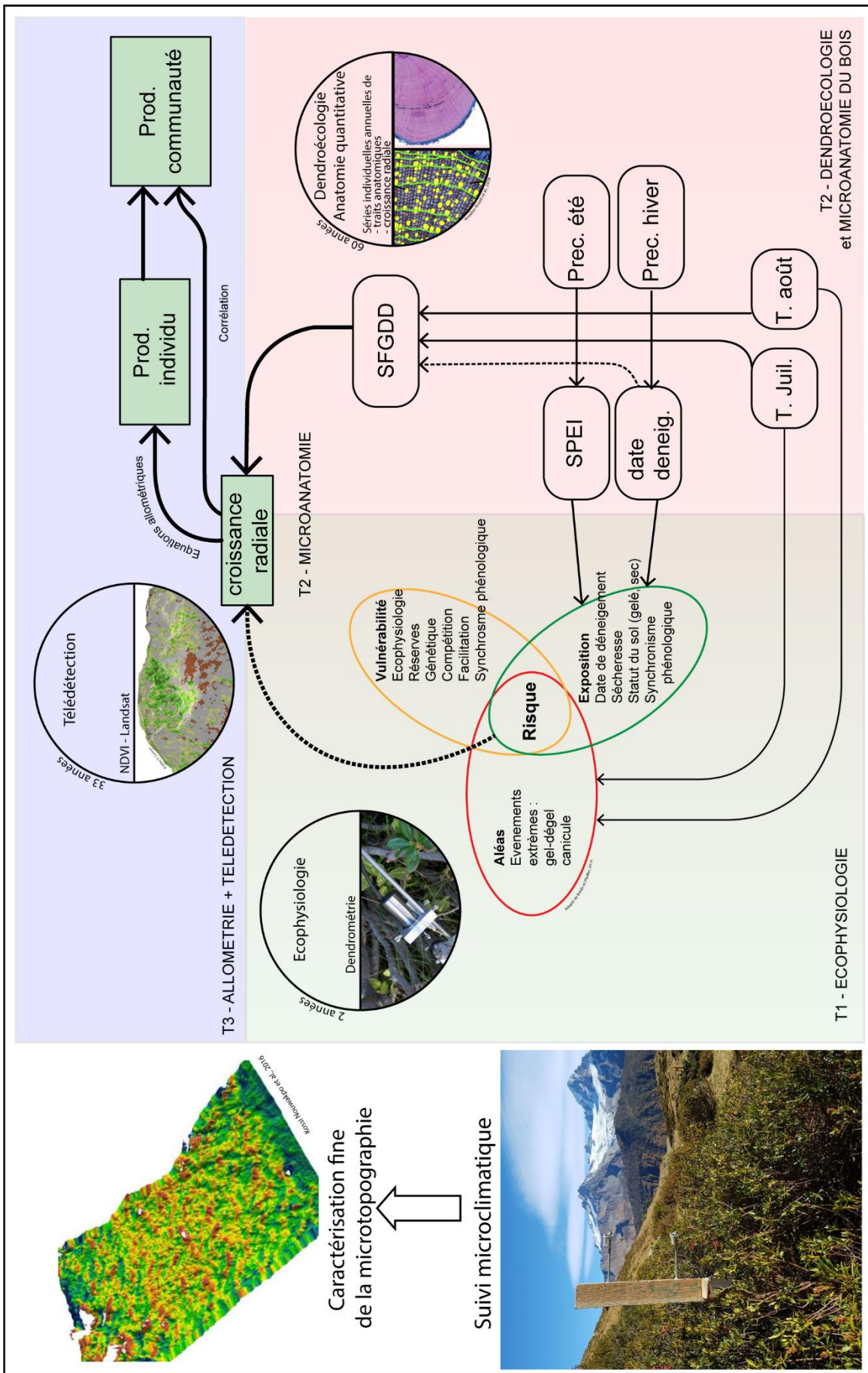


Figure 4 : Schéma synoptique des différentes tâches. Les flèches pleines représentent un impact positif, les flèches en pointillé, un impact négatif. « Prod. » = productivité ; « T. » = température ; « SFGDD » = Snow-Free Growing Degree Days : le nombre de degrés-jours supérieurs à 0°C comptabilisés à partir de la date de déneigement ; « NDVI » = Normalized Difference Vegetation Index : Indice de végétation par différence normalisé.



Microdendromètre installé dans les Pyrénées sur une tige de rhododendron. La tige a été coupée de manière à faire des analyses anatomiques

4 Conclusion générale

Les atouts de cette thèse résident dans la diversité des approches mises en œuvre, dendrochronologie et écologie, et dans son aspect géographique. Elle a ainsi permis de confirmer le lien entre le climat et la croissance radiale de *R. ferrugineum*, un ligneux bas répandu et dominant des landes autour et au-dessus de la limite supérieure de la forêt dans les Alpes, mais également la complexité des relations induites par la variabilité topoclimatique alpine. Ainsi, la quantité de degrés-jours reçus durant la période végétative, conditionnée par la date de déneigement, est le principal facteur limitant pour la croissance du ligneux bas, localement modulé par la sécheresse ou les événements extrêmes tels que le gel précoce de 1997 dans le Taillefer. Cette étude a également permis de mettre en évidence des non-linéarités dans les relations cerne/climat et de déterminer des seuils au-dessus desquels l'effet positif des degrés-jours s'inverse. Ces seuils, fréquemment évoqués dans la littérature (Ernakovich et al., 2014; Myers-Smith et al. 2015a), avaient rarement été quantifiés jusqu'alors, en particulier en situation topographique et géographique variée. Ici, les sites échantillonnés se veulent aussi représentatifs des Alpes françaises que possible. La mise en évidence du principal facteur limitant la croissance de *R. ferrugineum* et la quantification des seuils a été réalisable grâce à l'utilisation de modèles statistiques, empruntés à l'écologie, qui permettent de simuler les interactions entre les variables climatiques (modèles d'équations structurelles) et de considérer chaque individu indépendamment de la chronologie de référence (modèles linéaires mixtes). Nos résultats montrent également que le réchauffement climatique a induit des modifications très importantes des relations cernes/climat. La perte de sensibilité des ligneux bas à la température durant la période végétative, depuis le début des années 1990, est similaire au phénomène de divergence observé sur les arbres des forêts boréales (D'Arrigo et al., 2008). Dans les sites les plus secs, nous avons pu démontrer que la croissance était de plus en plus fortement régulée par l'intensité des sécheresses et par les températures de fin d'été. Dans les autres sites, cette évolution est plus diffuse et il est difficile de détecter l'apparition d'un nouveau facteur de contrôle prédominant, expliquant la baisse de sensibilité aux températures estivales. Nous soupçonnons un impact croissant des gels de printemps favorisés par l'avancement des dates de déneigement mais cette hypothèse reste difficile à valider au moyen de l'approche dendroécologique. En effet, le caractère intégrateur des cernes de croissance (effet « boîte noire ») ne permet pas de mettre en évidence l'effet de ces événements extrêmes, dont la durée est très limitée (quelques heures à quelques jours), mais qui peuvent impacter durablement la croissance. Pour cette raison, nous proposons en perspective de ce travail, un cadre méthodologique pluridisciplinaire (écophysiologie, dendroécologie et télédétection) qui permettra de mieux comprendre les effets du réchauffement climatique, en particulier des événements extrêmes, sur les dynamiques de croissance des landes arbustives, de l'échelle de la cellule à celle de la communauté.

De manière générale, cette thèse répond au manque initial de connaissance en dendroécologie alpine et représente une avancée significative dans la compréhension des relations complexes entre la croissance des ligneux bas et le climat en milieu montagnard. Elle a permis de mettre en évidence des impacts du changement climatique sur la végétation alpine qui ne sont pas observables à l'échelle du paysage mais clairement intégrés dans les séries dendrochronologiques. Les fluctuations de la croissance radiale de *Rhododendron ferrugineum* peuvent à ce titre être considérées comme des indicateurs écologiques particulièrement sensibles, et des archives naturelles précieuses, des impacts du changement climatique que nous vivons aujourd'hui et dont nous avons, collectivement, la responsabilité.

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Figures complémentaires

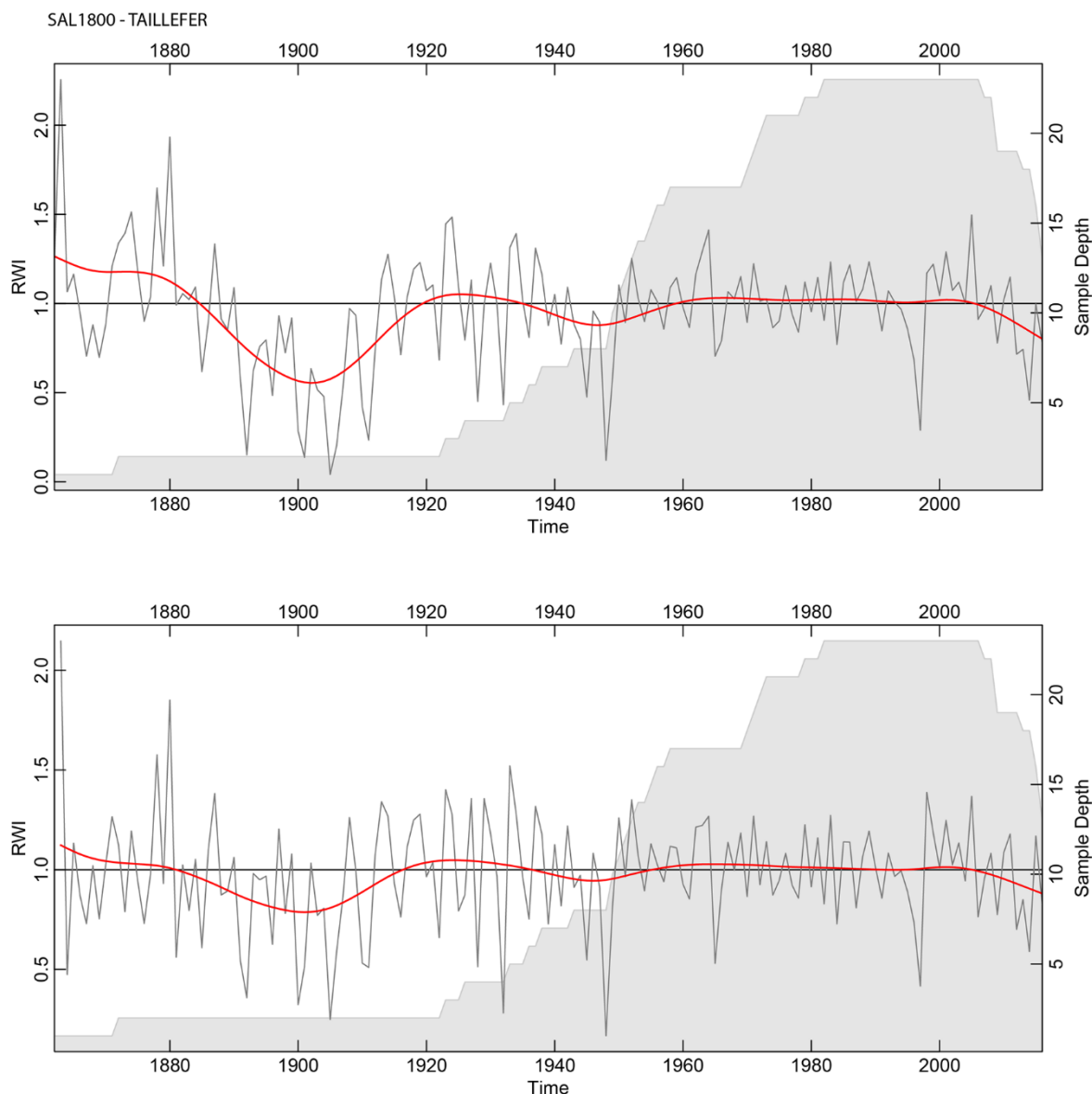


Figure S1 : Chronologie de largeurs de cernes SAL1800 (Taillefer) de *R. ferrugineum*, standardisée (Ring-width indices, RWI, trait gris) à l'aide d'une fonction de type exponentielle négative. La standardisation permet d'enlever une grande part de la variance due à d'autres facteurs que le climat. Le panneau supérieur correspond à la chronologie standardisée classique (utilisée dans le cadre de cette thèse), le panneau inférieur correspond à la chronologie standardisée résiduelle, visualisable ici à titre indicatif. La version résiduelle est produite de la même manière que la version classique, mais dans ce cas, les séries moyennées sont des résidus de la modélisation autorégressive des séries de mesures standardisées. Cela permet d'évacuer la persistance dans les séries temporelle, c-à-d l'autocorrélation. Une courbe de type spline (trait rouge) de période = 30 ans a été ajustée sur les chronologies de manière à suivre l'évolution décennale des largeurs de cernes. Les plages grises correspondent au nombre de sections incluses dans la chronologie (Sample Depth).

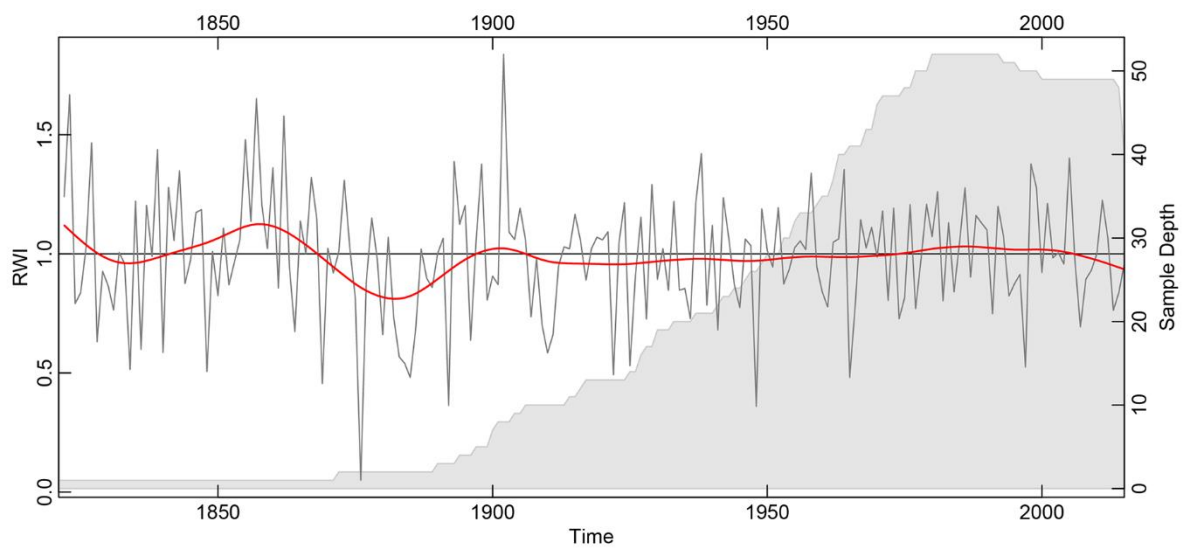
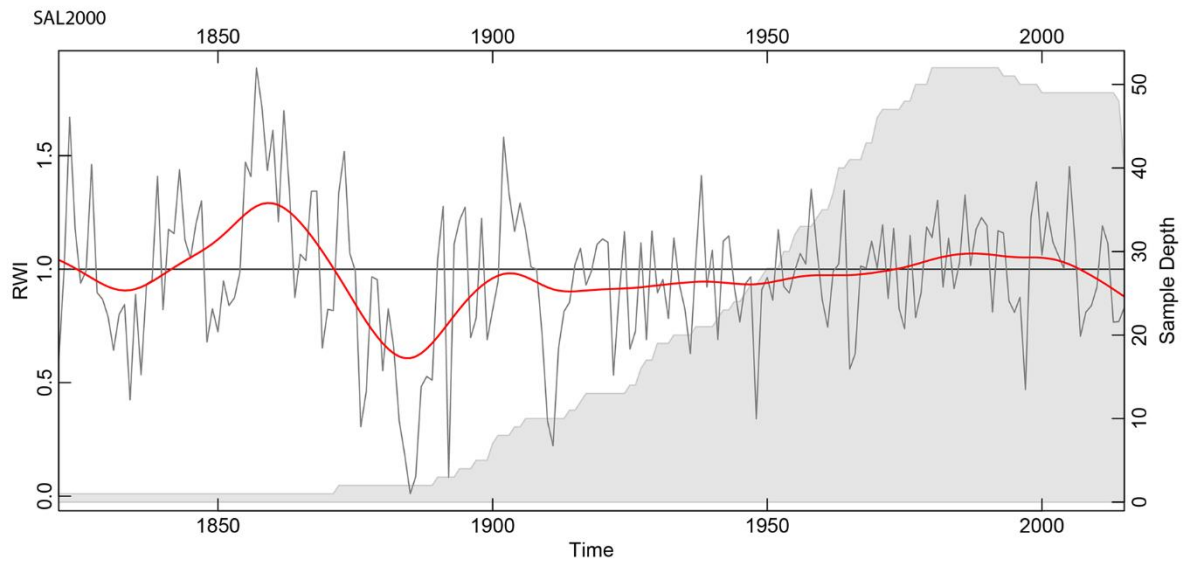


Figure S2 : Idem figure S1 pour SAL2000 (Taillefer)

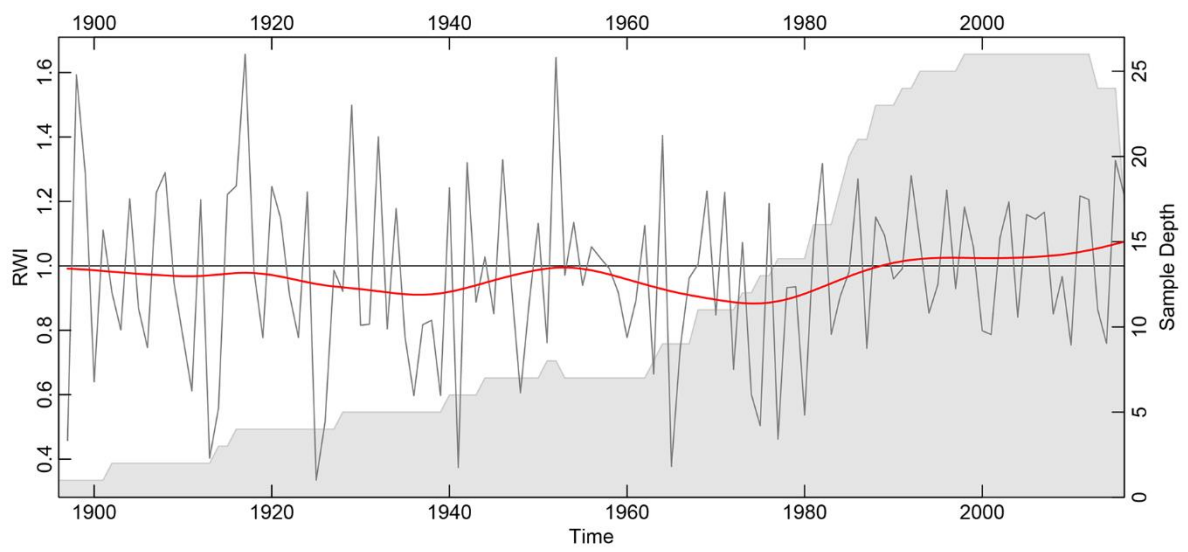
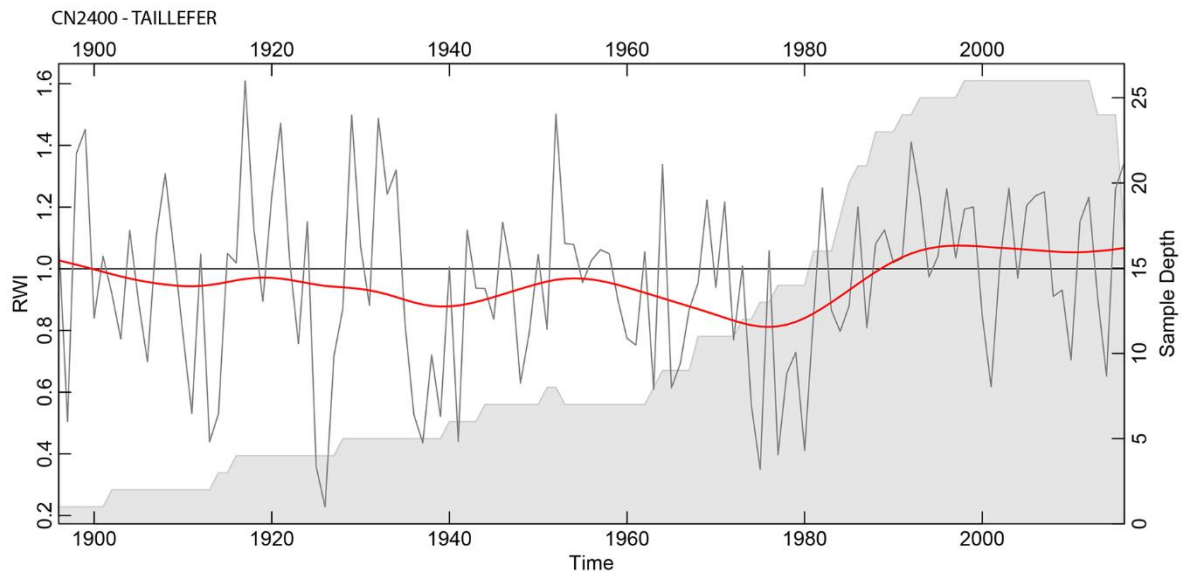


Figure S3 : Idem figure S1 pour CN2400 (Taillefer)

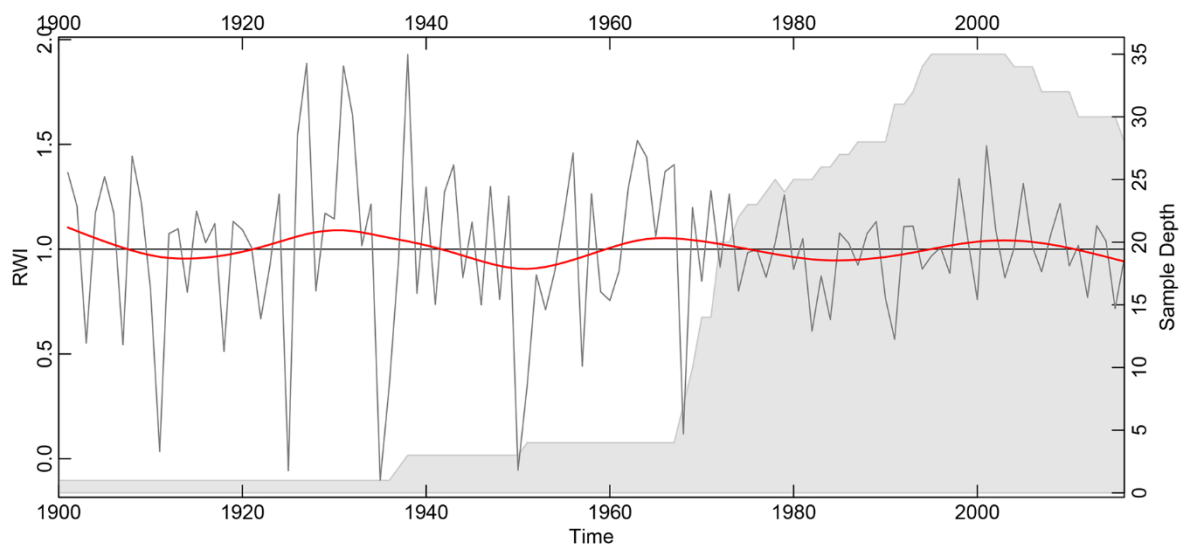
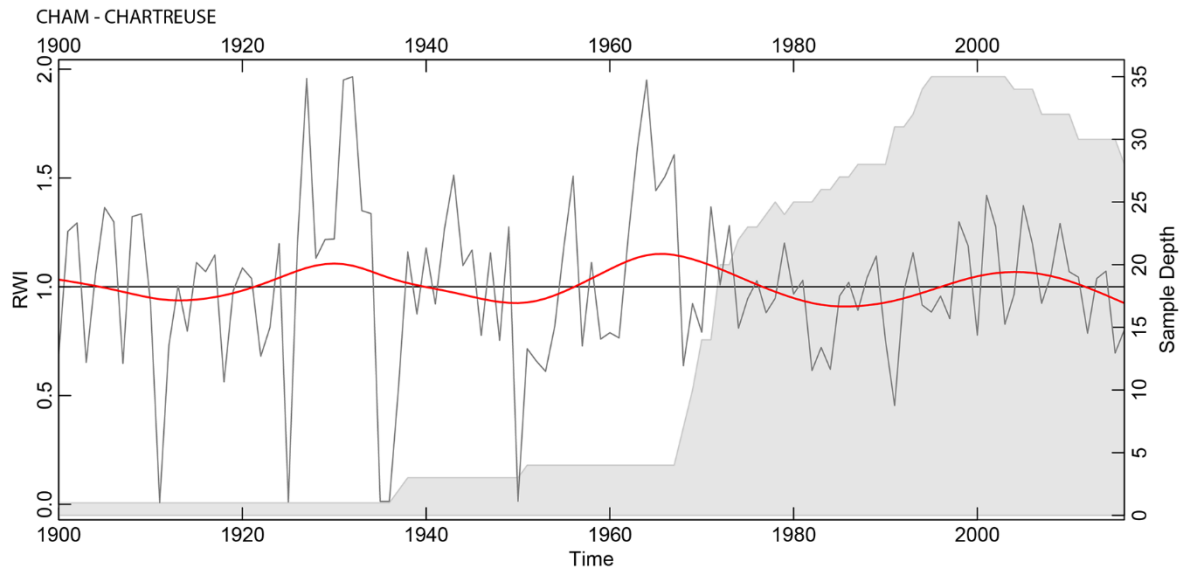


Figure S4 : Idem figure S1 pour CHAM (Chartreuse)

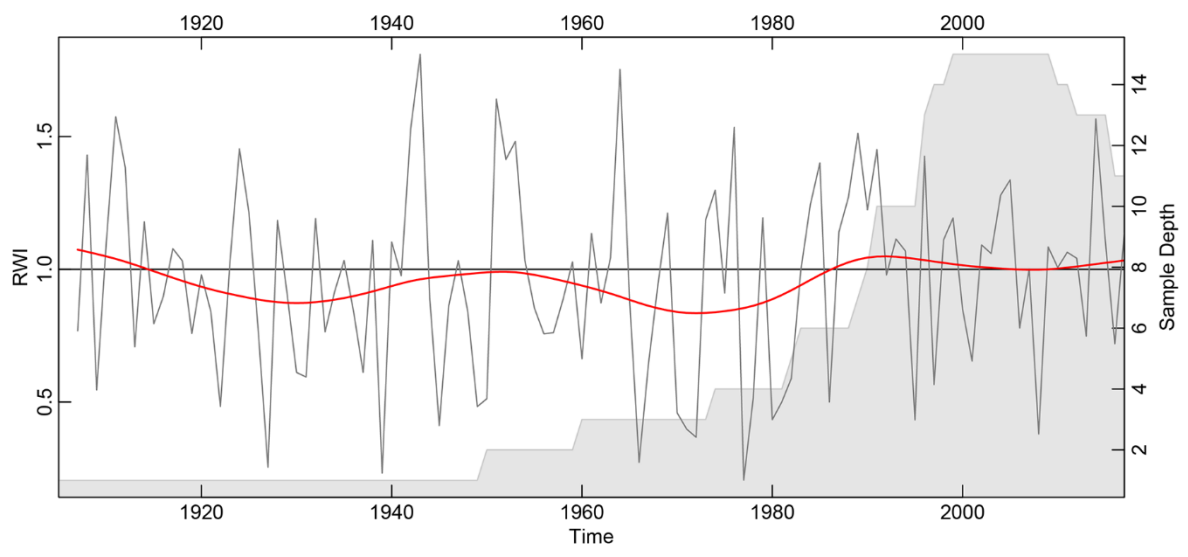
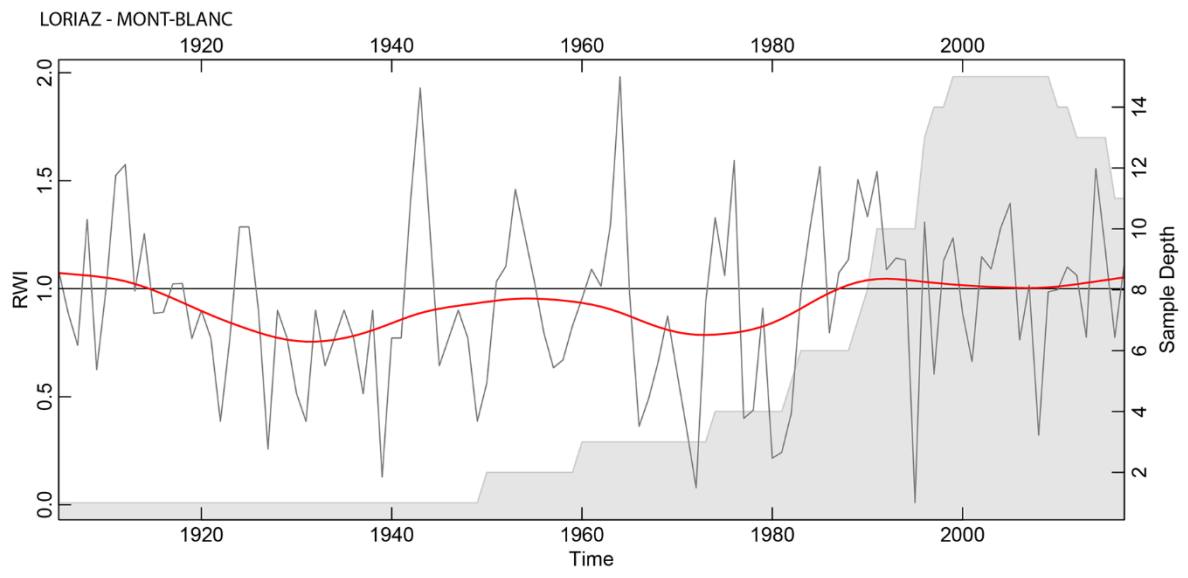


Figure S5 : Idem figure S1 pour LORIAZ (Mont-Blanc)

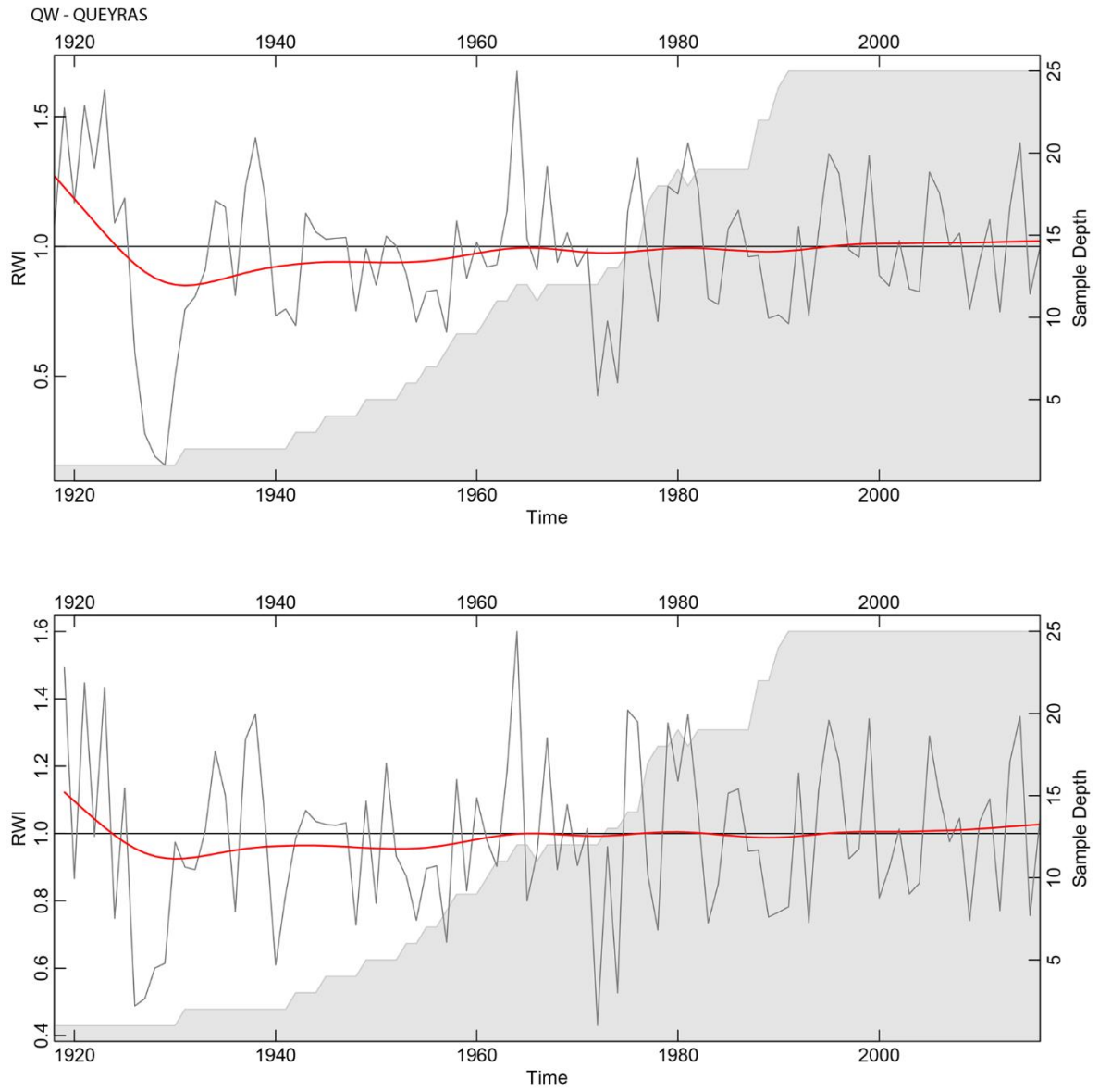


Figure S6 : Idem figure S1 pour QW (Queyras)

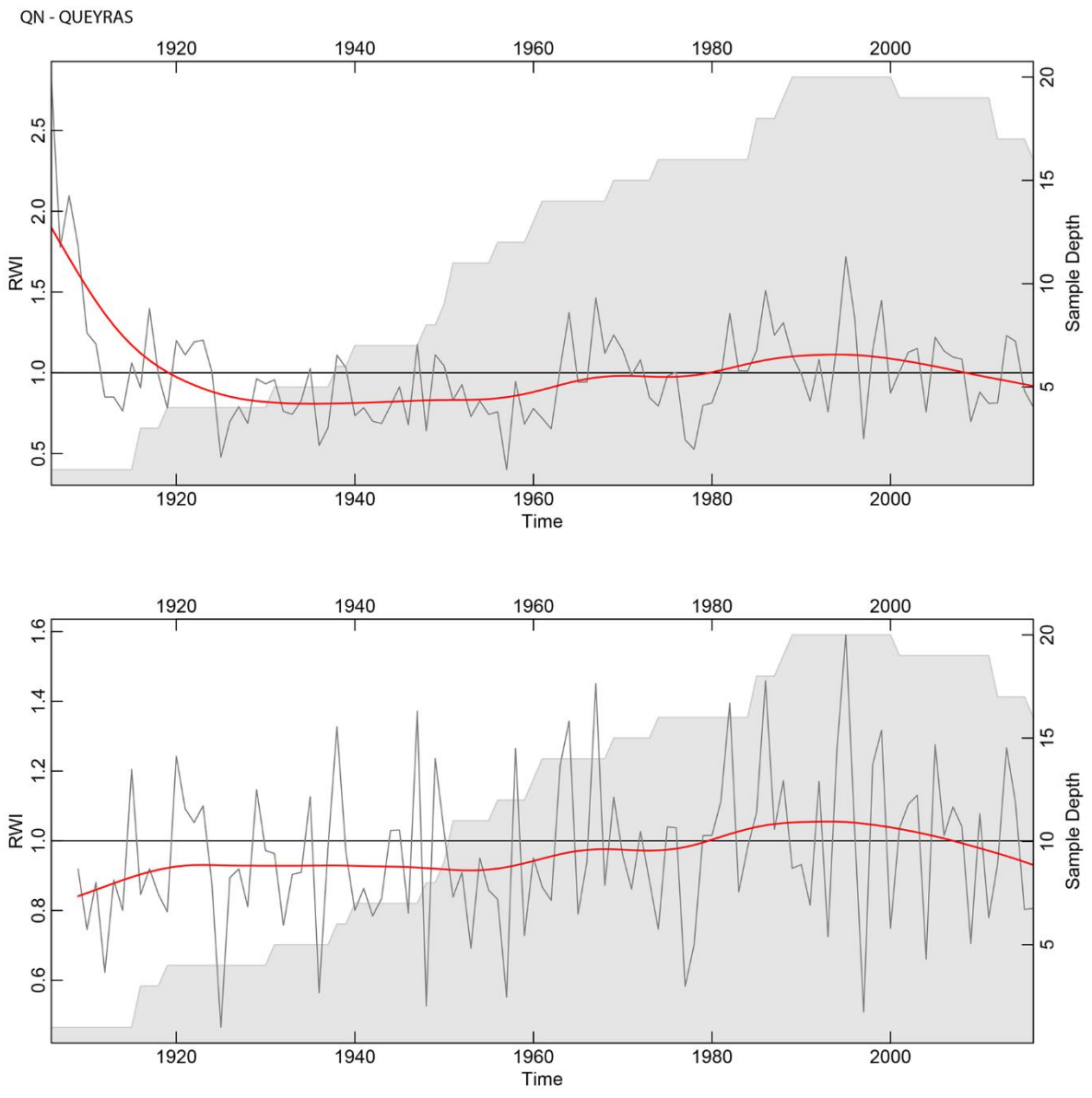


Figure S7 : Idem figure S1 pour QN (Queyras)

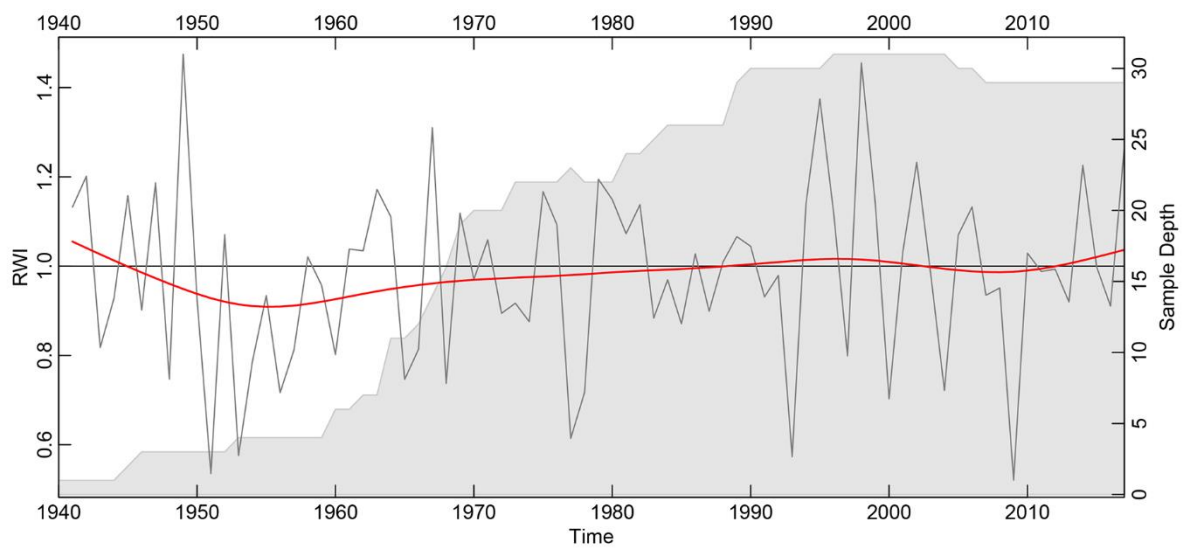
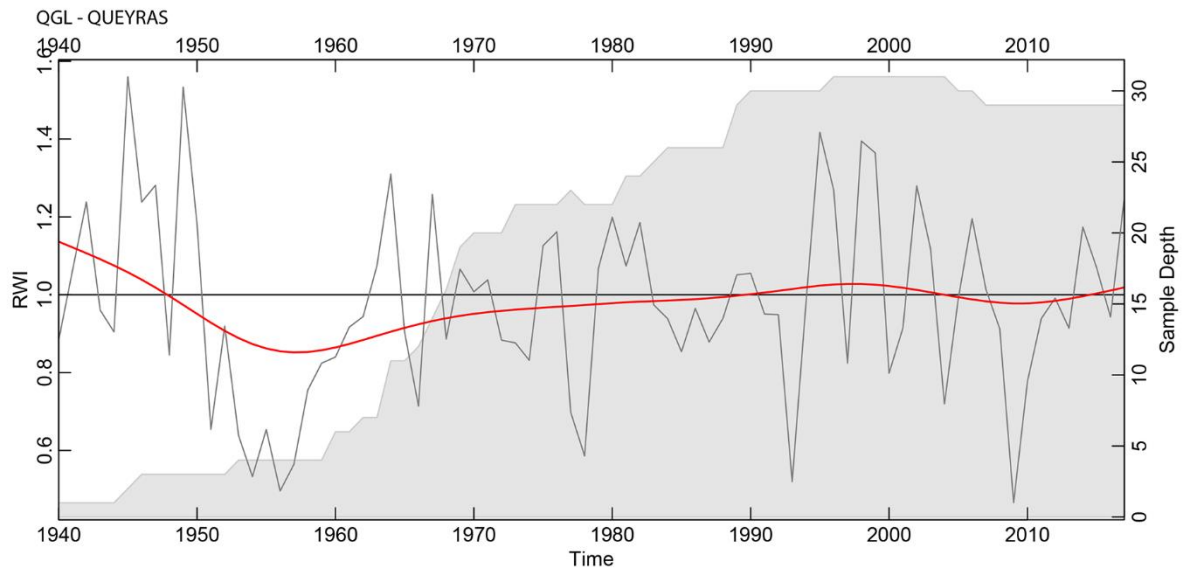


Figure S8 : Idem figure S1 pour QGL (Queyras)

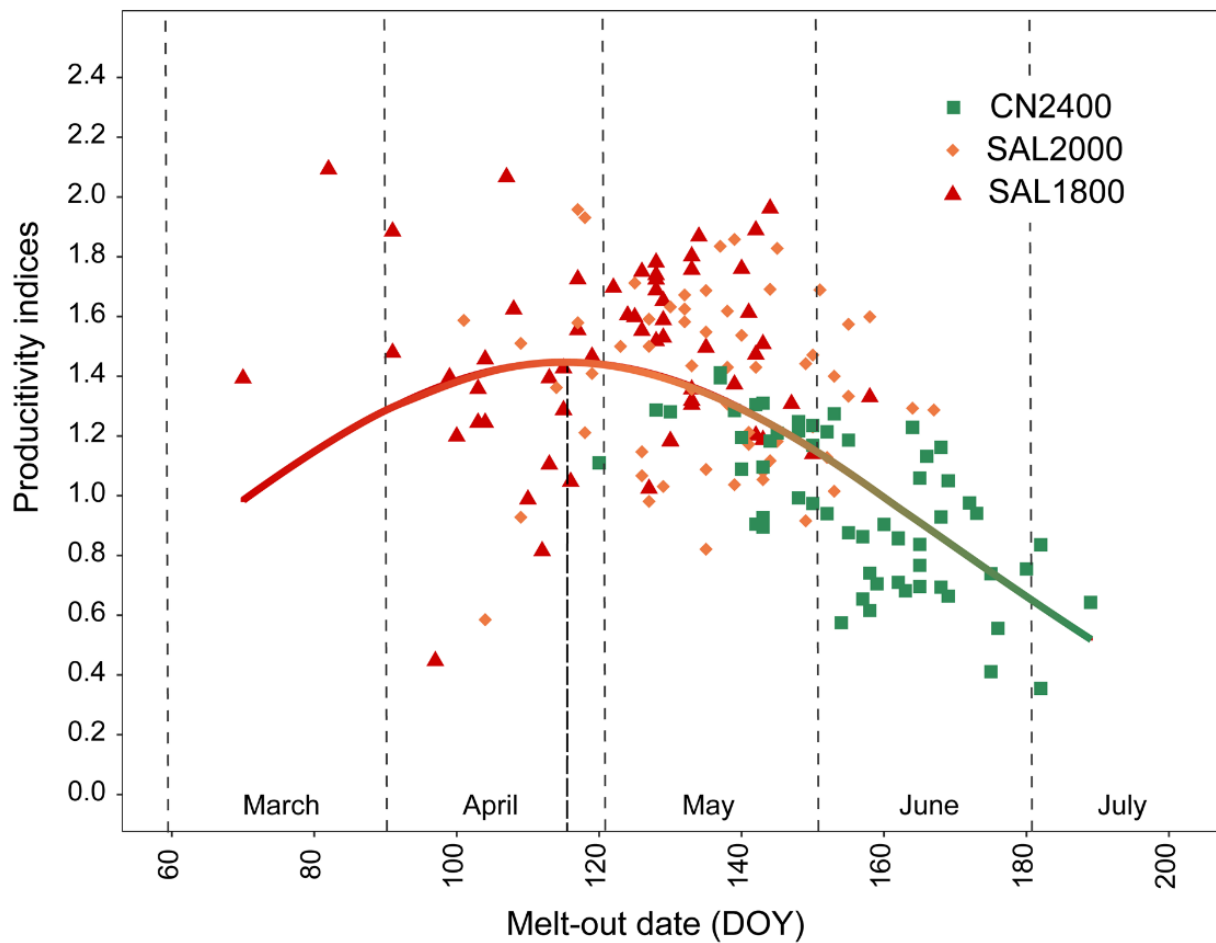


Figure S9 : Relation entre les chronologies de largeur de cernes standardisées du Taillefer, pondérées par un facteur multiplicatif (afin de prendre en compte les différences de productivité des différents sites situés à différentes altitudes, SAL1800, SAL2000 et CN2400) et les dates de déneigement, ajustée par une courbe gaussienne. Le facteur de pondération est extrait à partir des valeurs de productivité calculées au paragraphe 3.1 du 3^e chapitre. Une date de déneigement optimale pour la croissance radiale peut-être estimée autour de la fin avril dans le massif du Taillefer. On observe une forte variabilité de largeur de cernes pour des dates de déneigement les plus précoces.

Annexe

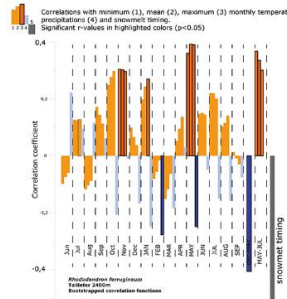
Poster présenté au colloque Wood Formation and tree adaptation to climate (Orléans, 23-25 mai 2018).

Wood formation in rhododendrons at the stress line: Take a shrub to the limit

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In this study, **electronic micro-dendrometers** were used to monitor the **variations in stem diameter** of 11 *Rhododendron ferrugineum* (Rf) individuals located at 1800, 2100 and 2500m asl in the Taillefer Massif (French Alps) and at 1700m asl at Vicdessos (French Pyrenees). In addition, ground-level temperature was recorded for each individual. The results presented here are focused on **the 2500m site**. They cover the period October 2016 - October 2017.

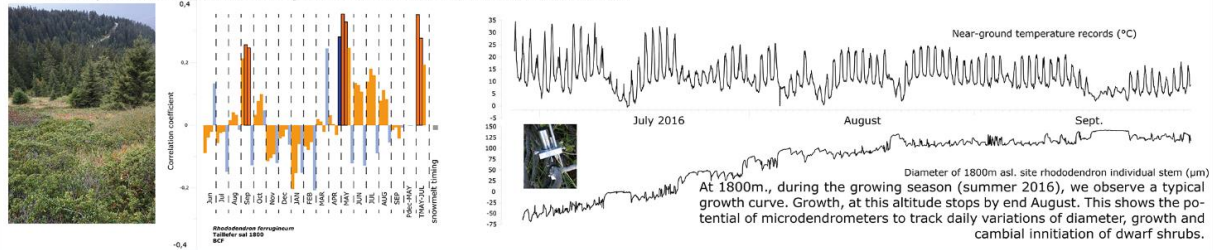
1- Results of the dendroecological approach: Climate-growth relationships (1960-2016)



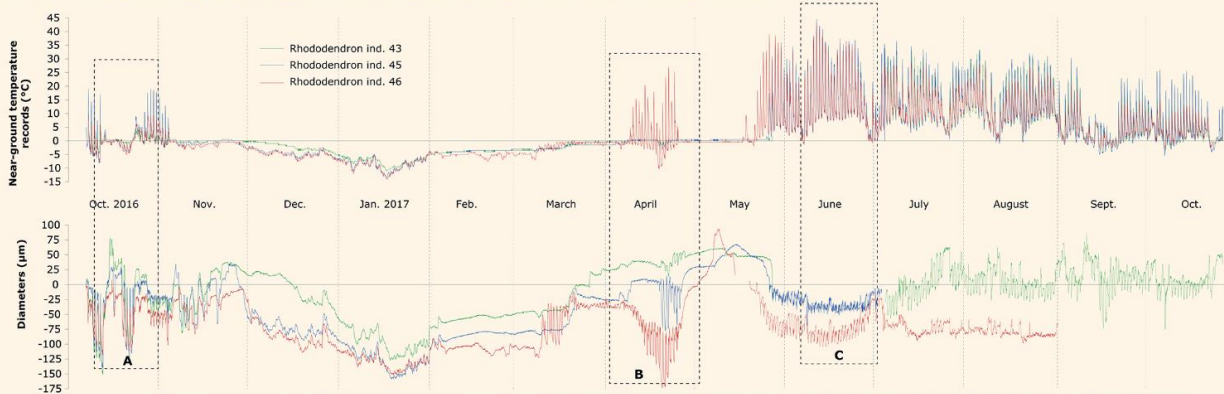
Context:

- High-latitude and **high-altitude ecosystems** are adapted to high level of environmental constraints and are therefore amongst the **most sensitive to on-going climate change**. Numerous studies demonstrated that recent global warming leads to an increase in shrubs cover and productivity at the Arctic and Alpine treelines since the 1980s (ie 'shrubification').
- Dendroecological studies along an altitudinal gradient in the Taillefer massif (French Alps) reveal that *R. ferrugineum* growth was significantly and **positively associated with May temperature and negatively correlated with winter precipitations** at 2500m asl.
- Daily-resolved and homogenized series of temperature, precipitation and snow cover depth from the SAFRAN-CROCUS datasets - for the period 1959-2016 - further confirm that both climatic parameters are the main drivers for **snowmelt** and subsequent **growing season length** at this altitude.
- However, the dendroecological analyses that approximate relationships between tree rings and climate by a time-invariant function consider the underlying processes as a black-box (Guiot et al., 2014). In this context, the monitoring approach developed here is **complementary to the correlation function** analyses to document the **ecophysiological response** of rhododendrons to meteorological/climatic fluctuations.

2- A first try at 1800m in summer : the potential of microdendrometers on dwarf shrubs



3- One-year hourly monitoring of three rhododendrons shrubs stem diameter variations at 2500m asl.



Raw curves of diameters variations and temperatures are strongly snowpack-dependants. The gaps in the middle or at the end of the records corresponds to (1) loss of the signal or (2) aberrant values due mechanical moving of the sensor.



October 2016: Very contrasted conditions

- No snowcover -> freeze/thaw cycles (beginning of the month)
- **High amplitude contractions (125µm)**
- First snowfalls (13th and 14th)
- **Rehydration of the stems**
- Warm temperatures during the day do not allow snowcover persistence (Only until the 19th). No snowcover -> freeze/thaw cycles (19th - 24th)
- **Moderate contractions**
- End October: positive temperatures (days and nights)
- **Transpiration for all individuals**

April 2017: The week without snow

- Warmer temperature and shallow snowpack lead to an exceptionally early snowmelt. Individuals have to endure a prolonged period without protection against frost modulated by their microtopographic position. Rf46 undergoes the longest period.
- **High amplitude contractions are observed for Rf46 and Rf45**
- Sunny days and probably frozen soil
- **Transpiration during the day -> Rf45 and Rf46 lose water.**
- Snowfalls the 27th. **Rehydration of all stems**

June 2017: Heat wave for the rhododendrons

- Globally warm temperatures
- Summer rain the 16th, the 26th and wet weather at the end of the month
- After a period directly after snowmelt when all individuals (Rf45 and Rf46) seem to lose water, they seem to recover in June.
- **Rf46 is growing (cambial initiation about the 19th) whereas Rf45 does not make wood.**

In conclusion, our study demonstrates the **complementarity of dendroecological and ecophysiological approaches** to assess the response of shrub growth to (micro)climatic variability in alpine environments. The monitoring of dwarf shrubs at high altitude/latitude yet remains a technical and scientific challenge and further investigations are needed.

From a technical point of view, the main challenges are related to the improvement of the sensor reliability - electronic components and batteries - in extreme humidity and temperature conditions. Amongst the 11 microdendrometers installed at the different sites, only 5 operated for the winter, 4 ran out of battery and two lost the data before the end of the winter.

From a scientific point of view, we expect that our approach will permit to better assess the role of microclimatic fluctuations on the ecophysiology of alpine and arctic dwarf shrubs in the continuum ground-snowpack-plant-atmosphere.

Résumé

Les écosystèmes alpins, comme la toundra arctique, subissent un réchauffement accentué par rapport au reste du globe. En Arctique, une approche dendroécologique basée sur l'analyse des relations entre la croissance annuelle radiale et le climat a permis de mettre en évidence les paramètres climatiques qui contrôlent l'expansion des arbustes nains (ligneux bas). Ces changements au sein de la toundra ont de vastes répercussions sur l'albédo, le manteau neigeux, le sol, le microclimat au niveau du sol ainsi que sur le cycle du carbone et le climat à l'échelle planétaire. Les Alpes européennes se sont considérablement réchauffées ces dernières décennies, et ce de manière non-linéaire, avec un point d'inflexion situé à la fin des années 80. Par analogie avec l'Arctique, nous émettons l'hypothèse qu'à haute altitude la diminution des contraintes climatiques (hausse des températures estivales, diminution de l'enneigement) favorise une augmentation de la croissance radiale des ligneux bas. Afin de valider cette hypothèse, huit populations de *Rhododendron ferrugineum* L. (Ericaceae) ont été prélevées dans des sites, le long de gradients topoclimatiques et dans des massifs caractérisés par des niveaux de continentalité représentatifs des Alpes françaises. Afin de caractériser finement la réponse de *R. ferrugineum* au changement, les chronologies de largeur de cernes établies pour chaque population ont été comparées aux séries météorologiques en utilisant les approches statistiques courantes en dendrochronologie (fonctions de corrélation) mais également sur la base de modèles empruntés à l'écologie (modèles linéaires mixtes, modèles d'équations structurelles).

Le premier chapitre de la thèse met en évidence le potentiel dendroécologique de *R. ferrugineum*. Sur la base de fonctions de corrélation, il a permis de démontrer que les températures estivales étaient le principal facteur limitant de la croissance radiale d'une population de *R. ferrugineum* échantillonnée dans le massif du Taillefer (Alpes françaises, 2000 m d'altitude) mais également une très forte sensibilité de cette population aux précipitations hivernales, phénomène non observé sur une population d'arbre (*Picea abies*) située à proximité. Dans le deuxième chapitre, l'échantillonnage initial a été complété par des prélèvements réalisés sur deux placettes étagées le long d'un gradient altitudinal (1800-2400 m). La comparaison de la croissance radiale de *R. ferrugineum* et des séries nivo-météorologiques locales issues de la base de données SAFRAN-crocus au moyen de modèles d'équations structurelles démontre une forte hétérogénéité spatiale et temporelle de la réponse des ligneux bas aux fluctuations du climat. La population en limite altitudinale supérieure (2400 m) est très sensible à la durée de saison végétative et à la température estivale. Cette sensibilité décroît fortement à plus basse altitude (1800, 2000 m) en relation avec l'augmentation du stress lié aux gels printaniers depuis la fin des années 1980. De la même manière, l'affaiblissement des relations cernes-climat au cours des deux dernières décennies est attribué à un phénomène de divergence similaire à celui observé dans les populations d'arbres en Arctique. Le troisième chapitre est consacré à l'analyse de populations prélevées dans le massif du Queyras (Alpes françaises du sud) où l'aridité estivale liée à la continentalité est plus marquée que dans le Taillefer. Les résultats obtenus sur deux populations localisées sur des versants ouest et nord montrent le rôle déterminant de la situation topoclimatique sur la réponse de *R. ferrugineum* au climat et l'impact négatif de l'augmentation de la sévérité des vagues de chaleur et de la sécheresse estivale sur la population exposée à un rayonnement solaire important. Le quatrième chapitre intègre les huit populations échantillonnées dans les Alpes. Il démontre une forte non-linéarité de la réponse de *R. ferrugineum* au changement climatique à l'échelle des Alpes françaises. Cette non-linéarité est modulée par le topoclimat. La croissance radiale des ligneux bas, régie par la température avant les années 1980 semble ainsi dorénavant contrainte par l'accessibilité à l'eau et par les événements de gel printanier. Le chapitre de conclusion synthétise les résultats de ce travail mais met également en évidence ses limites et propose des perspectives de recherche. Malgré des avancées importantes pour la compréhension du rôle du réchauffement climatique sur la croissance des ligneux bas en montagne, il souligne que les résultats obtenus reposent sur des corrélations statistiques et insiste sur la nécessité d'approfondir les connaissances sur l'écophysiologie des ligneux bas en montagne. En ce sens, il plaide pour une approche multi-échelle regroupant télédétection (productivité des landes arbustives), approche dendroécologique (réponse au climat et profondeur temporelle) et suivi microclimatique et dendrométrique des ligneux bas (mécanismes physiologiques) qui permettrait une analyse approfondie du verdissement alpin.