



## Associations between canopy and understory species increase along a rainshadow gradient in the Alps: habitat heterogeneity or facilitation?

R. Michalet<sup>1,\*</sup>, Ch. Rolland<sup>1</sup>, D. Joud<sup>1</sup>, D. Gafta<sup>2</sup> and R.M. Callaway<sup>3</sup>

<sup>1</sup>Laboratoire Ecosystèmes et Changements Environnementaux, Centre de Biologie Alpine, Université Joseph Fourier, BP 53 X, F- 38 041 Grenoble, France; <sup>2</sup>Department of Plant Biology, Babes-Bolyai University, 42 Republic Street, 3400 Cluj-Napoca, Romania; <sup>3</sup>Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA; \*Author for correspondence

Received 3 April 2001; accepted in revised form 23 October 2001

**Key words:** *Abies alba*, Beta diversity, Canonical correspondence analysis, Climate, Correspondence analysis, *Picea abies*, Plant community

### Abstract

Spatial associations among overstory and understory species tend to increase on gradients from wet to dry climates. This shift in the strength of spatial associations has usually been attributed to shared abiotic requirements between canopy species and understory assemblages within communities and/or to an increase in habitat heterogeneity in dry climates and therefore higher beta diversity. On another hand, more important positive effects of tree canopies on understory species in drier climates may also explain stronger associations and higher beta diversity. We examined these three hypotheses along a strong rainshadow gradient that occurs from the wet external Alps to the dry inner Alps by analyzing with correspondence analysis and canonical correspondence analysis the species composition of 290 relevés of forests dominated to different degrees by *Abies alba* and *Picea abies*. We found important differences in climatic requirements for *Abies* and *Picea*, with *Abies* occurring in warmer and drier habitats than *Picea*. The understory species associated with these two species showed similar correlations with temperature but not with moisture, with understory species of *Picea*-communities having stronger xeric affinities than understory species of *Abies*-communities. We found no significant associations between canopy species and understory composition in the external Alps despite the fact that *Abies* and *Picea* occurred in substantially different environments. In contrast, *Abies* and *Picea* occurred in more similar environments in the inner Alps, but the understory assemblages associated with either *Abies* or *Picea* were significantly different. This increase in canopy-understory associations was in part determined by strong differences in moisture between southern and northern aspects in the inner Alps, which affected both canopy and understory species distributions. However, differences between the canopy effects of *Picea* and *Abies* also appeared to contribute to stronger associations between canopy and understory species, and consequently to increase beta diversity. This pattern only occurred on southern aspects of the inner Alps but was highly significant. Our results suggest that species distributions may be continuous on the wet ends of moisture gradients but discrete on dry ends. Relatively discrete communities at stressful ends of gradients appear to develop as a result of both habitat differentiation and the positive effects of overstory species.

### Introduction

The absence of strong correlation between canopy tree species and understory species (Lippmaa 1939; Whittaker 1951, 1956; Bratton 1975; Hicks 1980; McCune and Antos 1981; Bradfield and Scagel 1984;

Rheinhardt 1992) has been used to argue for a “loose” organization of communities and the “individualistic” behavior of species assemblages (Gleason 1926). Conversely some European phytosociologists have proposed that at least at small scales, groups of species (i.e. *synusiae* or unions) can be delineated into

“real communities” (Lippmaa 1939; Barkman 1978; Gillet and Gallandat 1996; Gillet et al. 1999). Since the 1950’s most ecologists have embraced an individualistic Gleasonian concept of community organization, primarily due to the overwhelming preponderance of continuous distributions of species on environmental gradients (Curtis 1959; McIntosh 1967; Whittaker 1967; Peet 1981; Austin 1985). However, in the last ten years many experimental studies have demonstrated positive interactions in plant communities (see reviews by Callaway (1995); Callaway and Walker (1997)) suggesting that species are not always independent of each other. Callaway (1997) argued that continuous correlations are not proof of fully independent communities because species can either compete, have no effect on each other, or have strong positive relationships depending on the environmental conditions at particular locations along environmental gradients (see Bertness and Callaway (1994); Brooker and Callaghan (1998)).

Some gradient analyses suggest that the mesic ends of moisture gradients tend to show clear continua in species distributions, whereas more discrete assemblages often occur on the xeric ends of the gradients. For example, Whittaker (1960) and del Moral and Watson (1978) found that correlations between canopy and understory species increased with continentality in forest communities. del Moral and Watson (1978) concluded that canopy and understory species may have more similar, and more restricted, requirements in dry environments. Whittaker (1960) and McCune and Antos (1981) argued that abiotic effects of aspect, elevation, and slope are stronger in dry climates than in wet climates. Indeed, beta diversity is correlated with the “steepness” of the environmental gradients, which is higher in dry areas (Whittaker 1960) than in wet ones (Whittaker 1956). Stronger associations between canopy and understory species may also be due to stronger positive interactions in dry climates, as suggested by Bertness and Callaway (1994), and observed repeatedly for savanna trees (Vetaas 1992; Callaway 1995). If the relative strength of associations among species changes along climate gradients, perhaps common ground can be established for integrating the concepts that have produced the theory behind the individualistic and phytosociological classification approaches.

We examined correlations among climate, canopy species, and understory species in *Picea abies*-*Abies alba* forests of the European Alpine chain using a set of 290 relevés. *Picea abies* and *Abies alba* provide a

conservative system in which to study species-specific effects (see Callaway (1998a)), because these two genera are generally considered to be in the same “functional group” (Bugmann 1996). Both *Abies alba* and *Picea abies* occur along the entire rainshadow gradient which constitutes the main climatic gradient of the European Alpine chain (Ozenda 1985; Pache et al. 1996a; Gafta and Pedrotti 1998). In the wet and thermally buffered climates of the external Alps both species generally occur in the same communities, and in particular at the mountain belt where *Fagus sylvatica* is abundant (Kuoch 1954). In contrast, in the dry and thermally contrasted climates of the inner Alps, from which deciduous trees are excluded, different communities have been described, either dominated by *Abies alba* or *Picea abies* (Braun-Blanquet et al. 1954; Bartoli 1966; Michalet et al. 1998). This increase in beta diversity suggests that the strength of associations between canopy and understory species may change along the rainshadow gradient of the Alpine chain. We will focus on two questions: 1) Are there more significant differences between the understory assemblages of *Abies alba* and *Picea abies* in the inner Alps than in the external Alps? 2) Which mechanisms may affect the strength of associations between canopy and understory species along this rainshadow gradient: more similar requirements, higher habitat heterogeneity or positive interactions?

## Materials and methods

### *Vegetation data*

We used 290 phytosociological relevés that had been collected by different researchers using standardized phytosociological methodology (Braun-Blanquet 1932; Westhoff and van der Maarel 1978). These relevés were distributed throughout the south-western and north-eastern European Alps, and encompass the climatic variability of the entire Alpine chain (Pache et al. 1996a) and the phytosociological diversity of *Picea-Abies* forests (see Michalet et al. (1998) for references and geographical positions). We chose the 290 plots from a larger group of 2000 relevés in *Picea-Abies* forests by randomly subsampling clusters described by Michalet et al. (1998). We reduced sample size to have approximately a similar number of relevés in each community type. *Abies* and *Picea* were always dominant, but other tree species occurred

as rare or subcanopy species including *Fagus sylvatica*, *Acer pseudoplatanus*, *Acer platanoides*, *Acer campestre*, *Acer opalus*, *Quercus petraea*, and *Quercus humilis* in the external Alps, and *Larix decidua*, *Pinus sylvestris*, *Pinus uncinata*, and *Pinus cembra* in the inner Alps. The nomenclature of taxa is that used in *Flora Europaea* by Tutin et al. (1964–1980). Beta diversity (the extent of differentiation of communities along environmental gradients, Whittaker (1972)), was measured in the two rainshadow sectors. We used the formula developed by Whittaker (1972) for sets of samples characterized by many habitat axes:  $BD = Sc/Sm$ , in which  $Sc$  is the number of species in the composite sample (combining a number of relevés) and  $Sm$  is the mean number of species in the relevés. Because we used a similar number of samples per composite sample, we avoided the negative effect of sample size which is an inherent problem with this formula (Whittaker 1972).

#### *Environmental data*

Three topographic variables were sampled with the relevés: elevation, aspect (8 classes) and substrate (3 classes, either limestone, or calcareous shale and marls, or siliceous). Substrate types were coded in order of their moisture availability (Michalet et al. 2002).

We used 7 climatic variables which were estimated for specific plots extrapolating data from grids of climate stations in the region over a 30 year period (1951–1980). Climate variables were minimum temperatures for January ( $T_{Jan-min}$ ) and July ( $T_{Jul-min}$ ), maximum temperatures for January ( $T_{Jan-max}$ ) and July ( $T_{Jul-max}$ ), Gams coefficients in winter ( $G_{winter}$ ) and the year ( $G_{year}$ ), and a summer aridity index ( $Arid_{summer} = P_{summer}/(T_{max} + 10)$ ). The Gams (1932) index is a measure of rainshadow effect in mountainous areas and its main purpose is to allow a geographical comparison of precipitation while controlling for the effect of elevation. This index,  $G$ , expressed in degrees, and with the formula:  $Cotangent(G) = P/A$  ( $P$  is precipitation in mm and  $A$  is elevation in m), was initially used by taking into account the annual rainfall only (Gams 1932; Ozenda 1985), but its seasonal calculation may offer biologically more meaningful interpretation. The modified winter Gams angle has been shown to be the best index for the precipitation components of continentality (Michalet 1991), and the modified summer Gams angle has been shown to have a more direct relationship to the water require-

ments of plant species during the growing season (Pache et al. 1996a). The original Gams index has been shown to be accurate only for elevations between 900 m and 1600 m, i.e. the range within which precipitation increases linearly with elevation (Ozenda 1985). Therefore, along with the classic “coefficient of hygric continentality” (Gams 1932) we used two modified forms of the Gams index (Michalet 1991; Pache et al. 1996b) below and above the elevation thresholds previously mentioned. We calculated Gams angles for each relevé, using the closest climate station. With these values, the elevation of the relevés and the inverse Gams formula, the summer precipitation was estimated at each site, to calculate the  $Arid_{summer}$  values.

Douguedroit and de Saintignon (1970) proposed different lapse rates (vertical thermal gradients) for southern slopes and valley bottoms, in the southern French Alps. Although there are too few climate stations on northern aspects to calculate specific lapse rates, they argued that lapse rates of northern slopes were much closer to the lapse rates of valley bottoms than to that of southern slopes. Using 300 climate stations of different elevations and topographic positions (110 southern slopes and 190 valley bottoms), from different alpine sectors, we calculated, with linear regressions, the lapse rates and TSL (temperature at sea level in °C) values for the minimum and maximum for January and July, in both topographic positions (Table 1). We then selected 33 climate stations that were close to our forest stands to locally calibrate the temperatures of the 290 relevés, using the closest climate station recordings (as “TSL” values), the different lapse rates, and the difference in elevation between the climate stations and the plots. When the relevé and the climate station used to calculate the temperature of the relevé were on different aspects, a correction was applied to the values of the climate station (at sea level) to approximate the effect of aspect. Three main aspects were distinguished, north (NE, N, E), south (SW, S, W) and intermediate (NW, SE). We used the lapse rates of valley bottoms in calculations on north aspects and separate intermediate lapse rates for intermediate aspects.

#### *Multivariate analyses*

To assess the ecological requirements of the understory species multivariate analyses were conducted on all subcanopy species including herbs, shrubs and understory trees, with the exception of *Abies alba* and

Table 1. Lapse rates and values at sea level (TSL) for minimum and maximum temperatures of January and July for southern aspects and valley bottoms.

	Minimum temperature		Maximum temperature	
	January	July	January	July
South lapse rates	-0.498	-0.581	-0.504	-0.682
South TSL	0.74	18.32	7.53	29.21
Valley bottom lapse rates	-0.516	-0.633	-0.41	-0.698
Valley bottom TSL	-2.08	17.44	5.21	29.64

*Picea abies*, which were removed from the data matrix. Only species with a frequency greater than 5/290 were included in the data matrix which reduced outlier effects. Braun-Blanquet's coefficients, with rare species coded 0.5, were used for species abundance classes. The final floristic matrix (243 species  $\times$  290 relevés) was analysed with correspondence analysis (CA) using ADE-4 software (Thioulouse et al. 1991). Pearson's correlation coefficients (Afifi and Clark 1990) were calculated between relevés scores on CA axes and the 10 variables (3 topographic variables and 7 climatic variables) of the "environmental" matrix. We also added total tree cover and *Picea* and *Abies* abundances as variables in the second matrix in order to estimate the relative importance of these canopy species to the composition of the understory. We also conducted a canonical correspondence analysis (CCA) (ter Braak 1986; Lebreton et al. 1988) with the same software in order to graphically depict relationships among environmental variables. The statistical significance of the CCA was tested with a Monte-Carlo permutation test. Due to the fact that CCA is constrained by the abiotic variables in a second matrix (Okland 1996; McCune 1997) we have emphasized the CA.

#### Statistical analyses of environmental variables and relevé scores

We evaluated the environmental requirements of both canopy species by comparing mean values of each of the 10 environmental variables and "total tree cover" for each of three formation types that differed in the relative abundance of *Picea* and *Abies*: 1) *Picea*-dominated forests (*Abies* < 5%, i.e. Braun-Blanquet's coef. 0.5), 2) Mixed (both species  $\geq$  5%), 3) *Abies*-dominated forests (*Picea* < 5%).

The steepness of the environmental gradients (1. below), as well as correlations between canopy species and understory composition (2. below) were

analysed in both the external Alps and the inner Alps, by dividing the relevés into two equal parts, based on their scores on the first axis of the CA. This rather arbitrary but unbiased and conservative approach produced two distinct groups of relevés. 137 of the 145 relevés of the external Alps had negative scores on CA axis 1, whereas all the 145 relevés of the inner Alps had positive scores on CA axis 1 (see Figure 1).

1. We first correlated relevé scores to environmental variables for the external and inner groups on CA axis 1, independently of formation types, in order to understand the relationship of the steepness of the environmental gradients to understory composition in both rainshadow sectors. We used separate linear regressions for each of the rainshadow sectors to test the relationship between the values of elevation and aspect with the relevé scores on CA axis 1 (Figure 2). For the variable "substrate", which had only three discrete classes, we used ANOVA to compare the relevé scores on CA axis 1 for these three classes for each of the two groups on CA axis 1. "Total tree cover" was also analysed using ANOVA for "open", "intermediate", and "closed" classes for the two rainshadow sectors (Figure 2).
2. Because the analyses described above indicated that correlations between aspect and understory assemblages were strong in the inner Alps, we analysed the correlations between canopy species and understory composition in each rainshadow sector for two classes of aspect (south-facing aspects and north-facing aspects with intermediate aspects included in the latter): we compared the mean values of the relevé scores on the first axis of the CA, for the three formation types described in the preceding paragraph, in each of these four ecological conditions (two rainshadow sectors and two aspects). Because of low sample sizes for some classes on southern aspects, we combined the for-

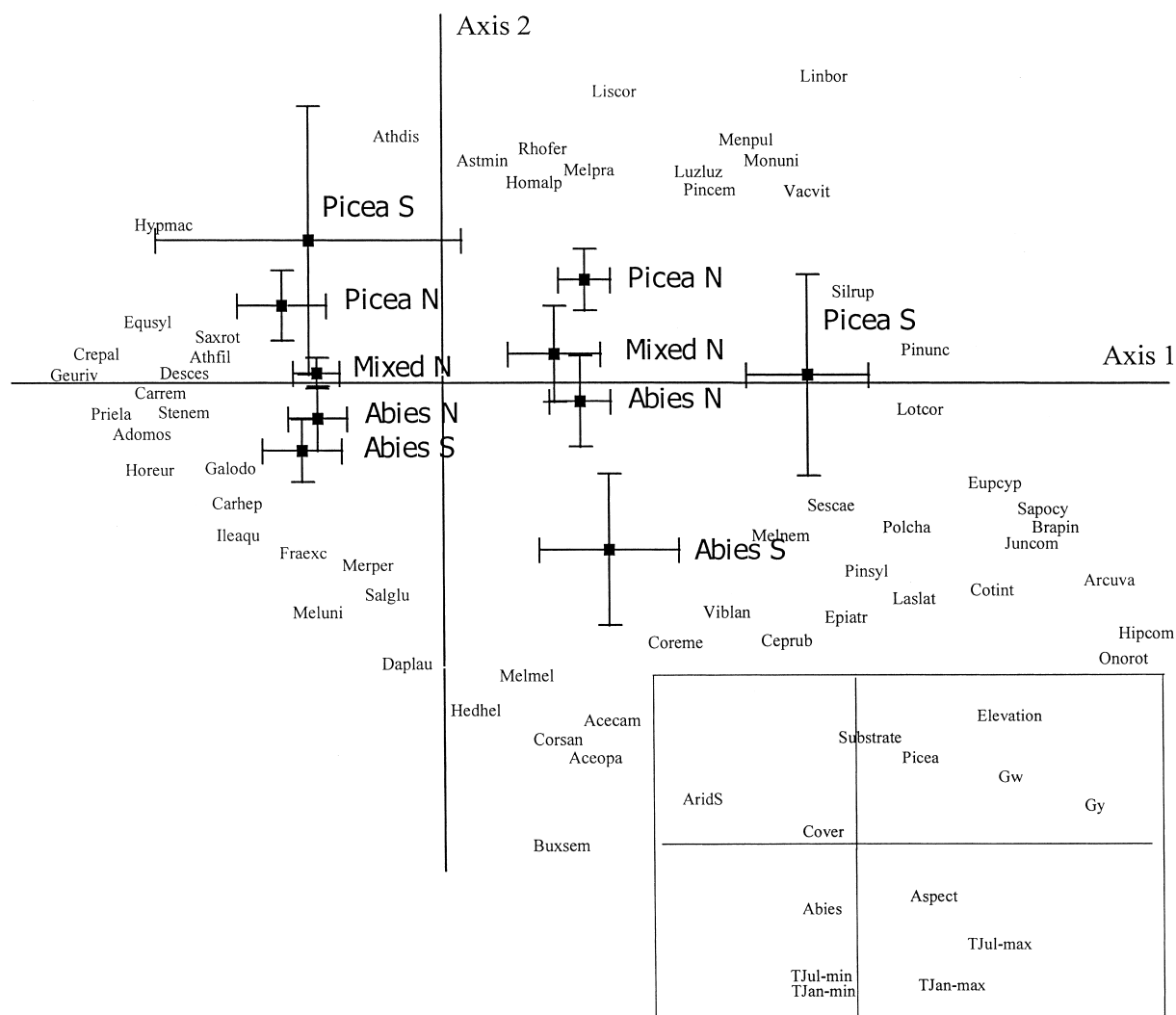


Figure 1. : Correspondence analysis showing 1) the means and 95% confidence limits for understory assemblages associated with *Picea*, mixed or *Abies* canopies, on different aspects and in the two rainshadow sectors (external Alps in the negative side of axis 1 and inner Alps in the positive side of axis 1), 2) dominant species distributions, 3) environmental variables scores in the inset, for axes 1 and 2. Acecam: *Acer campestre*, Aceopa: *Acer opalus*, Adomos: *Adoxa moschatellina*, Arcuva: *Arctostaphylos uva-ursi*, Astmin: *Astrantia minor*, Athdis: *Athyrium distentifolium*, Athfil: *Athyrium filix-femina*, Brapin: *Brachypodium pinnatum*, Buxsem: *Buxus sempervirens*, Carhep: *Cardamine heptaphylla*, Carrem: *Carex remota*, Ceprub: *Cephalanthera rubra*, Coreme: *Coronilla emerus*, Corsan: *Cornus sanguinea*, Cotint: *Cotoneaster integerrimus*, Crepal: *Crepis paludosa*, Daplau: *Daphne laureola*, Desces: *Deschampsia cespitosa*, Epiatr: *Epipactis atrorubens*, Equisyl: *Equisetum sylvaticum*, Eupcyp: *Euphorbia cyparissias*, Fraexc: *Fraxinus excelsior*, Galodo: *Galium odoratum*, Geuriv: *Geum rivale*, Hedhel: *Hedera helix*, Hipcom: *Hippocrepis comosa*, Homalp: *Homogyne alpina*, Horeur: *Hordelymus europaeus*, Hypmac: *Hypericum maculatum*, Ileaqu: *Ilex aquifolium*, Juncom: *Juniperus communis*, Laslat: *Laserpitium latifolium*, Linbor: *Linnaea borealis*, Liscor: *Listera cordata*, Lotcor: *Lotus corniculatus*, Luzluz: *Luzula luzuloides*, Melmel: *Melittis melissophyllum*, Melnem: *Melampyrum nemorosum*, Melpra: *Melampyrum pratense*, Meluni: *Melica uniflora*, Menpul: *Mentha pulegium*, Merper: *Mercurialis perennis*, Monuni: *Moneses uniflora*, Onorot: *Ononis rotundifolia*, Pincem: *Pinus cembra*, Pinsyl: *Pinus sylvestris*, Pinunc: *Pinus uncinata*, Polcha: *Polygala chamaebuxus*, Priela: *Primula elatior*, Rhofer: *Rhododendron ferrugineum*, Salglu: *Salvia glutinosa*, Sapocy: *Saponaria ocymoides*, Saxrot: *Saxifraga rotundifolia*, Sescae: *Sesleria caerulea*, Silrup: *Silene rupestris*, Stenem: *Stellaria nemorum*, Vacvit: *Vaccinium vitis-idaea*, Viblan: *Viburnum lantana*.

mation types “Mixed” and “*Abies*” into one formation, and compared it to the “*Picea*” formation, in the southern exposure. We checked the effect of habitat heterogeneity on these correlations by

comparing mean values of the main environmental variables for these different formation types in each of the four ecological conditions (Table 4). This allowed us to determine whether or not un-

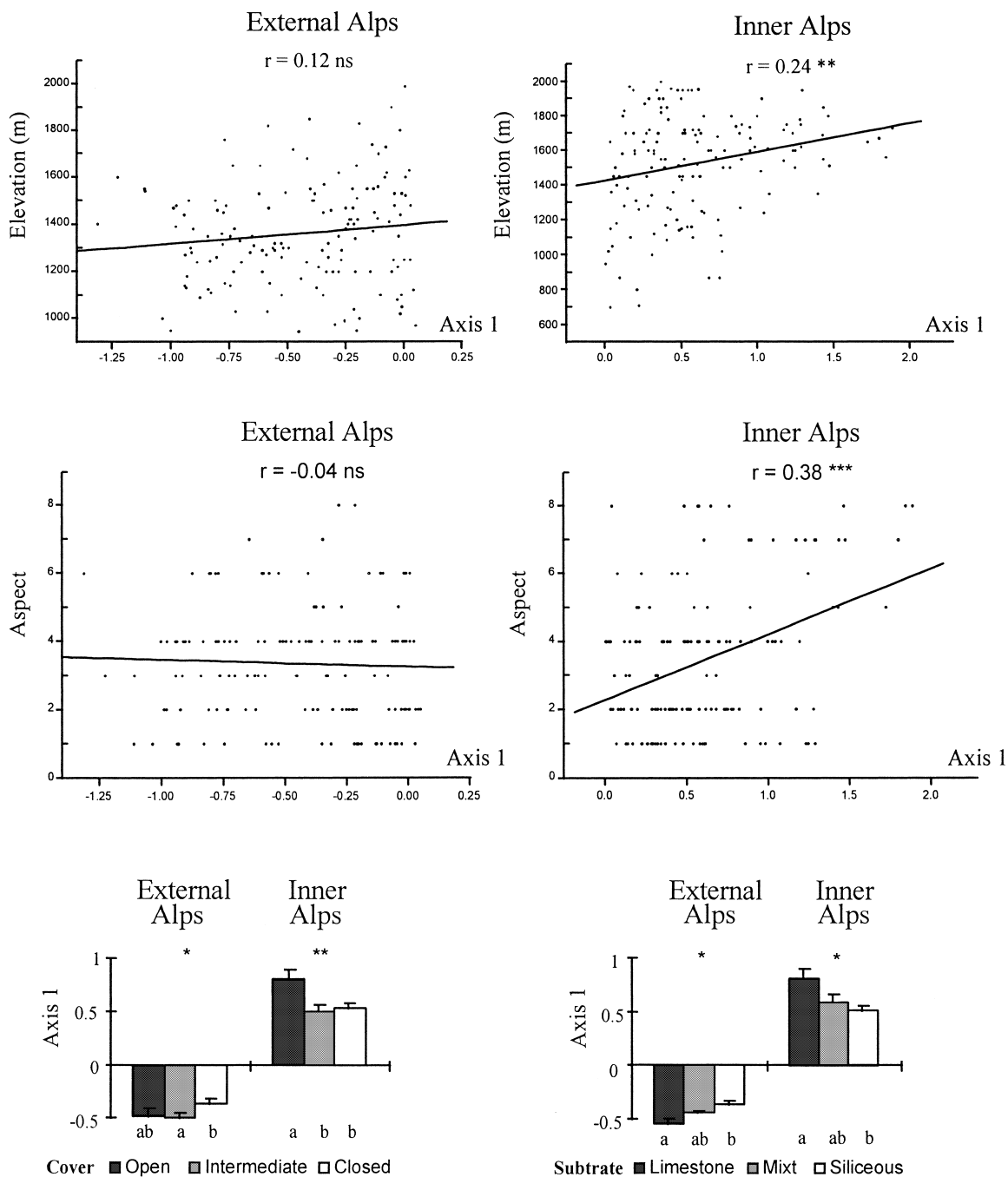


Figure 2. : Regressions between relevé scores on CA axis 1, in both rainshadow sectors represented on axis 1 (external and inner Alps), and elevation and aspect, and means (and standard errors) of CA-axis 1 scores of relevés on the three substrate types (right) and with three classes of cover (open:  $< 60\%$ , intermediate:  $60\% \leq x < 80\%$ , closed:  $\geq 80\%$ ), on both sides of axis 1 (external and inner Alps). Statistical significances of ANOVAs are given above bars (\*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ ) and Tukey's tests below (ns: non-significant).

derstorey assemblages associated with formation types were also correlated with the physical environment. Statistical significances of all compari-

sons of means were tested by ANOVA followed by Tukey's HSD *post hoc* tests, using SPSS (1997).

Table 2. Means and standard errors for elevation, aspect, substrate,  $G_{\text{winter}}$ ,  $G_{\text{year}}$ ,  $T_{\text{Jan-min}}$ ,  $T_{\text{Jan-max}}$ ,  $T_{\text{Jul-min}}$ ,  $T_{\text{Jul-max}}$ ,  $\text{Arid}_{\text{summer}}$  and Cover for the three formation types (*Picea*: *Abies* abundance  $\leq 0.5$ , *Abies*: *Picea* abundance  $\leq 0.5$ , Mixed: other relevés).

	<i>Picea</i>	Mixed	<i>Abies</i>
Elevation***	1573 $\pm$ 28.5 <sup>a</sup>	1391 $\pm$ 25.4 <sup>b</sup>	1374 $\pm$ 24.8 <sup>b</sup>
Aspect ns	3.5 $\pm$ 0.2	3.2 $\pm$ 0.2	3.5 $\pm$ 0.2
Substrate***	2.4 $\pm$ 0.1 <sup>a</sup>	2.4 $\pm$ 0.1 <sup>a</sup>	2.0 $\pm$ 0.1 <sup>b</sup>
$G_{\text{winter}}$ ns	46.1 $\pm$ 1.5	46.0 $\pm$ 1.1	47.5 $\pm$ 1.0
$G_{\text{year}}$ ns	46.0 $\pm$ 1.3	43.2 $\pm$ 1.0	46.3 $\pm$ 1.1
$T_{\text{Jan-min}}$ ***	-7.7 $\pm$ 0.2 <sup>a</sup>	-6.4 $\pm$ 0.2 <sup>b</sup>	-6.3 $\pm$ 0.3 <sup>b</sup>
$T_{\text{Jan-max}}$ ***	0.4 $\pm$ 0.2 <sup>a</sup>	1.4 $\pm$ 0.1 <sup>b</sup>	2.1 $\pm$ 0.1 <sup>c</sup>
$T_{\text{Jul-min}}$ ***	6.5 $\pm$ 0.2 <sup>a</sup>	8.3 $\pm$ 0.2 <sup>b</sup>	8.8 $\pm$ 0.2 <sup>b</sup>
$T_{\text{Jul-max}}$ **	19.2 $\pm$ 0.2 <sup>a</sup>	20.0 $\pm$ 0.2 <sup>b</sup>	20.8 $\pm$ 0.2 <sup>c</sup>
$\text{Arid}_{\text{summer}}$ **	60.2 $\pm$ 3.5 <sup>a</sup>	57.6 $\pm$ 2.4 <sup>a</sup>	46.6 $\pm$ 2.2 <sup>b</sup>
Cover ns	68.5 $\pm$ 1.8	70.5 $\pm$ 1.6	70.5 $\pm$ 1.7

ns: non-significant

\*:  $p < 0.05$

\*\* :  $p < 0.01$

\*\*\*:  $p < 0.001$ . Means with different letters were significantly different (Post-ANOVA Tukey's tests).

## Results

### Ecological requirements of canopy species

*Abies* was absent or rare at the sites with the lowest  $T_{\text{Jan-min}}$  (coldest sites) and *Picea* at the sites with the lowest  $\text{Arid}_{\text{summer}}$  (driest sites) (Table 2). *Picea*-dominated and Mixed forest were also less common on limestone (driest substrate) than *Abies* formations. Mean values of  $T_{\text{Jan-max}}$ ,  $T_{\text{Jul-min}}$  and  $T_{\text{Jul-max}}$  also demonstrated a gradual increase from *Picea*- to *Abies*-dominated forests. *Picea*-dominated forests occurred 200 m higher in elevation than *Abies*-dominated and Mixed forests. Aspect,  $G_{\text{year}}$ ,  $G_{\text{winter}}$  and cover did not differ between *Abies*- and *Picea*-dominated forests.

### CA on understory species

Eigenvalues for the three first axes of the CA were 0.05, 0.05 and 0.03, respectively.  $G_{\text{year}}$  was highly correlated with the first axis ( $r = 0.47$ ,  $P < 0.001$ ), which demonstrated strong differences between the communities of the external Alps (low  $G_{\text{year}}$ ) and the communities of the inner Alps (high  $G_{\text{year}}$ ) (Figure 1, Table 3). Summer drought ( $\text{Arid}_{\text{summer}}$ ) was also highly correlated with this first axis ( $r = -0.37$ ,  $P < 0.001$ ). *Geum rivale*, *Crepis paludosa*, *Carex remota*, *Equisetum sylvaticum*, *Deschampsia cespitosa* were

associated with the negative side of the first axis (Figure 1). These species are common in communities from the north-western external Alps (Kuoch 1954), where summers are wet and cool ( $T_{\text{Jul-max}}$  significantly correlated with the first axis). The species that contributed the most to the positive part of the first axis (*Ononis rotundifolia*, *Arctostaphylos uva-ursi*, *Polygala chamaebuxus*, *Silene rupestris*) occur in the communities from the drier inner valleys of the south-western Alps (Briançonnais, Maurienne). These shade intolerant species are common in xeric *Pinus*-dominated communities and in grasslands, as do *Hippocrepis comosa*, *Euphorbia cyparissias*, *Juniperus communis*, *Lotus corniculatus*, which were also associated with this side of the first axis.

The second axis of the CA differentiated between group of species that are also common in low-elevation oak forests (*Quercus humilis*) of the south-western Alps (*Buxus sempervirens*, *Acer opalus*, *Acer campestre*, *Cornus sanguinea*, *Melittis melissophyllum*, *Coronilla emerus*), versus subalpine species (*Rhododendron ferrugineum*, *Astrantia minor*, *Homogyne alpina*) and emphasized species from the north-eastern Alps (*Listera cordata*, *Linnaea borealis*). Temperature variables were highly correlated with this axis, in particular  $T_{\text{Jan-min}}$  ( $r = -0.42$ ,  $P < 0.001$ ),  $T_{\text{Jan-max}}$  ( $r = -0.41$ ,  $P < 0.001$ ), and  $T_{\text{Jul-min}}$  ( $r = -0.38$ ,  $P < 0.001$ ). Elevation was also correlated with CA axis 2 ( $r = 0.34$ ,  $P < 0.001$ ). Calcareous substrates and southern aspects were correlated with the cold-intolerant species, and siliceous substrates and northern aspects with the subalpine species. The relative abundances of *Picea* and *Abies* were not correlated with the first axis, whereas *Picea* ( $r = 0.22$ ,  $P < 0.01$ ) and *Abies* ( $r = -0.19$ ,  $P < 0.05$ ) were correlated in an almost reverse direction with CA axis 2.

### Steepness of the environmental gradients in each rainshadow sector

Linear regressions between elevation and aspect and CA axis 1 scores were not significant in the external Alps, but these regressions were significant in the inner Alps, with aspect showing the most striking differences between the rainshadow sectors (Figure 2). The ANOVA for the relevé scores for the three cover classes demonstrated a significant difference for total tree cover in both rainshadow sector, as did the ANOVA on substrate types (Figure 2). In the inner Alps the highest scores (i.e. the most xeric understories) were for relevés on limestone, on southern as-

Table 3. Pearson correlation coefficients for CA-axes and environmental variables and correlation coefficients for CCA-axes and environmental variables.

Variables	CA			CCA		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Elevation	0.24**	0.34***	0.22**	0.69***	0.45***	0.03 ns
Aspect	0.10 ns	-0.16*	0.02 ns	0.03 ns	-0.29**	0.44***
Substrate	-0.05 ns	0.28**	-0.08 ns	0.08 ns	0.50***	0.07 ns
G <sub>winter</sub>	0.29**	0.17*	-0.11 ns	0.56***	0.03 ns	-0.51***
G <sub>year</sub>	0.47***	0.09 ns	0.01 ns	0.84***	-0.21**	-0.28**
T <sub>Jan-min</sub>	-0.15*	-0.42***	-0.11 ns	-0.57***	-0.60***	0.42***
T <sub>Jan-max</sub>	0.12 ns	-0.41***	-0.01 ns	-0.04 ns	-0.80***	-0.18*
T <sub>Jul-min</sub>	-0.15*	-0.38***	-0.20*	-0.55***	-0.57***	-0.11 ns
T <sub>Jul-max</sub>	0.22**	-0.29**	-0.10 ns	0.17*	-0.72***	-0.38***
Arid <sub>summer</sub>	-0.37***	0.11 ns	0.04 ns	-0.56***	0.52***	0.38***
Cover	-0.12 ns	0.02 ns	-0.13 ns	-0.20*	0.07 ns	-0.43***
<i>Abies</i>	-0.12 ns	-0.19*	-0.06 ns	-0.30***	-0.28**	-0.60***
<i>Picea</i>	0.09 ns	0.22**	0.05 ns	0.25**	0.35***	0.53***

ns: non-significant

\*:  $p < 0.05$

\*\* :  $p < 0.01$

\*\*\*:  $p < 0.001$ .

pects, at high elevations, and with low tree cover. In contrast, in the external Alps relevés on limestone and with low cover had lower scores and there were no differences for elevation and aspect. These results indicate that the steepness of the complex environmental gradients was higher for understory species in the inner Alps than in the external Alps.

#### Canopy-understory correlations in the CA

In the external Alps there were no significant correlations between formation type and understory relevé scores, despite strong variations in climatic conditions for the formations (Table 4): 1) on both aspects in the external Alps, elevation and Arid<sub>summer</sub> had significant higher values for *Picea* forests than for *Abies* forests, 2) G<sub>year</sub> and G<sub>winter</sub> were lower in *Picea* forests only on northern aspects, 3) substrate type was correlated with formation type on south-facing aspects. In contrast, in the inner Alps there were strong correlations between formation types and relevé composition on south-facing aspects, but not on northern aspects, and there were weaker correlations between formation types and climatic variables: 1) only Arid<sub>summer</sub> was significantly higher for *Picea* formations than for *Abies* formations and only on north-facing aspects, 2) on south-facing aspects *Picea*-dominated formations had much higher relevé scores than *Abies*-

dominated and Mixed formations (Figure 1), and elevation and G<sub>year</sub> both had higher values for *Picea* formations than for the other formations. Although *Picea*-understory species appeared to be much more drought-tolerant than *Abies*-understory species on south-facing aspects in the inner Alps, there was no differences in summer drought (Arid<sub>summer</sub>) between sites, which suggests that elevation compensated for rainshadow on the southern aspects in the inner Alps.

Figure 3 presents these differences among rainshadow sectors more synthetically: 1) there was much higher moisture in *Picea* sites than in *Abies* sites on both aspects but no correlations between canopy and understory species in the external Alps, 2) there was marginally higher moisture for *Picea* sites than for *Abies* sites on north-facing aspects in the inner Alps, but no correlations between canopy and understory species, 3) there were strong correlations between canopy and understory species despite no differences in moisture between *Picea* and *Abies* sites on south-facing aspects in the inner Alps.

The increase in correlation between canopy and understory species along the rainshadow gradient is corroborated by measurements of beta diversity, with a higher value in the inner Alps (8.52) than in the external Alps (6.6).



Table 4. Means ( $\pm 1$  SE) of relevé scores for the two groups in different rainshadow sectors (the two sides of CA axis 1), for the three formation types (*Picea*: *Abies* abundance  $\leq 0.5$ , *Abies*: *Picea* abundance  $\leq 0.5$ , Mixed: other relevés) on northern aspects (including intermediate aspects), for two formation types (*Picea*: *Abies* abundance  $\leq 0.5$ , *Abies*: other relevés) in southern aspects and means of elevation (m), aspect (1 = NE, 2 = N, 3 = E, 4 = NW, 5 = SE, 6 = W, 7 = S, 8 = SW), substrate (1 = limestones, 2 = calcareous shales, marls, 3 = siliceous substrates), cover (%),  $C_{year}$ ,  $G_{winter}$  and  $Arid_{summer}$  for these ten relevé groups. Letters indicate results of Tukey's tests, within each aspect ( $p < 0.05$ ).

	Inner Alps									
	External Alps					Inner Alps				
	Northern aspect		Southern aspect		Sample size	Northern aspect		Southern aspect		Sample size
Physionomy	<i>Picea</i>	<i>Abies</i>	Mixed	<i>Picea</i>		<i>Abies</i>	<i>Picea</i>	<i>Abies</i>	Mixed	
CA axis 1 scores	-0.54 $\pm$ 0.08	-0.41 $\pm$ 0.04	-0.41 $\pm$ 0.04	-0.41 $\pm$ 0.05	-0.41 $\pm$ 0.05	-0.44 $\pm$ 0.21	-0.47 $\pm$ 0.07	0.55 $\pm$ 0.05	0.44 $\pm$ 0.08	0.53 $\pm$ 0.05
Elevation (m)	1480 $\pm$ 48.5 <sup>a</sup>	1329 $\pm$ 28.1 <sup>b</sup>	1329 $\pm$ 28.1 <sup>b</sup>	1337 $\pm$ 30.8 <sup>b</sup>	1337 $\pm$ 30.8 <sup>b</sup>	1598 $\pm$ 75.3 <sup>a</sup>	1278 $\pm$ 42.6 <sup>b</sup>	1575 $\pm$ 42.8	1495 $\pm$ 59.3	1415 $\pm$ 75.8
Aspect	2.9 $\pm$ 0.3	2.7 $\pm$ 0.2	2.7 $\pm$ 0.2	2.9 $\pm$ 0.2	2.9 $\pm$ 0.2	6.0 $\pm$ 0.0	6.4 $\pm$ 0.2	2.5 $\pm$ 0.2	2.6 $\pm$ 0.3	2.8 $\pm$ 0.2
Substrate	2.0 $\pm$ 0.2 <sup>a</sup>	2.5 $\pm$ 0.1 <sup>b</sup>	2.5 $\pm$ 0.1 <sup>b</sup>	2.2 $\pm$ 0.1 <sup>ab</sup>	2.2 $\pm$ 0.1 <sup>ab</sup>	2.3 $\pm$ 0.4 <sup>a</sup>	1.5 $\pm$ 0.2 <sup>b</sup>	2.6 $\pm$ 0.1 <sup>a</sup>	2.4 $\pm$ 0.1 <sup>ab</sup>	2.0 $\pm$ 0.1 <sup>b</sup>
Cover (%)	73.0 $\pm$ 3.1	70.9 $\pm$ 2.1	70.9 $\pm$ 2.1	73.1 $\pm$ 2.4	73.1 $\pm$ 2.4	57.5 $\pm$ 2.5	69.1 $\pm$ 4.4	69.0 $\pm$ 2.4	70.6 $\pm$ 3.0	63.3 $\pm$ 2.9
Gy (°)	32.6 $\pm$ 2.1 <sup>a</sup>	38.7 $\pm$ 1.0 <sup>b</sup>	38.7 $\pm$ 1.0 <sup>b</sup>	41.4 $\pm$ 1.0 <sup>b</sup>	41.4 $\pm$ 1.0 <sup>b</sup>	31.8 $\pm$ 2.2	33.8 $\pm$ 1.8	52.4 $\pm$ 1.2	54.0 $\pm$ 1.4	55.2 $\pm$ 1.2
Gw (°)	34.0 $\pm$ 2.0 <sup>a</sup>	3.6 $\pm$ 1.3 <sup>b</sup>	3.6 $\pm$ 1.3 <sup>b</sup>	43.9 $\pm$ 1.2 <sup>b</sup>	43.9 $\pm$ 1.2 <sup>b</sup>	34.8 $\pm$ 2.3	34.8 $\pm$ 2.1	53.0 $\pm$ 1.9	54.6 $\pm$ 1.9	55.6 $\pm$ 0.9
Arid Summer	95.6 $\pm$ 6.5 <sup>a</sup>	67.2 $\pm$ 3.0 <sup>b</sup>	67.2 $\pm$ 3.0 <sup>b</sup>	56.8 $\pm$ 3.5 <sup>c</sup>	56.8 $\pm$ 3.5 <sup>c</sup>	113.2 $\pm$ 14.6 <sup>a</sup>	67.5 $\pm$ 4.7 <sup>b</sup>	41.2 $\pm$ 1.6 <sup>a</sup>	36.5 $\pm$ 2.6 <sup>ab</sup>	31.6 $\pm$ 2.2 <sup>b</sup>

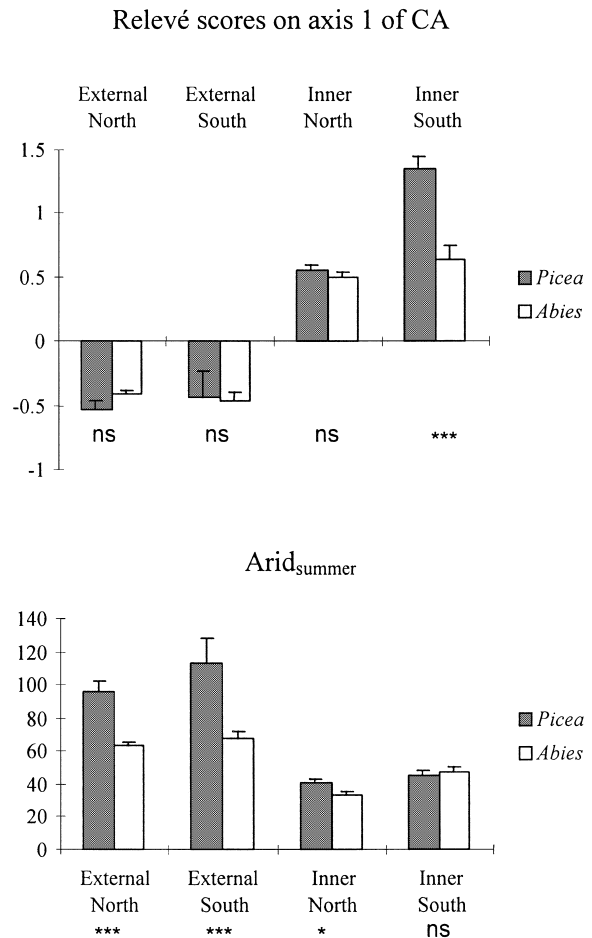


Figure 3. : Means (and standard errors) for relevé scores on CA-axis 1 and for  $Arid_{summer}$  for the two formation types (*Picea*: *Abies* abundance  $\leq 0.5$ , *Abies*: other relevés) on both sides of axis 1, and for the two main aspects, north (including intermediate aspects) and south. Statistical significances of ANOVAs are given below bars: ns: non-significant, \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ .

### CCA

The results of the CCA showed similar relationships among relevés and environmental variables on axes 1 and 2, but correlations between formation types and understory assemblages were more evident on axis 3. Eigenvalues for the three CCA axes were 0.22, 0.20 and 0.12, respectively and Montecarlo test with 1000 permutations indicated that the CCA ordination was significant ( $p < 0.001$ ). The correlations shown in Table 3 show that CCA axis 1 was primarily explained by rainshadow effect and summer aridity, and CCA axis 2 by winter temperature. Although these general patterns were similar to those of the CA, the strength

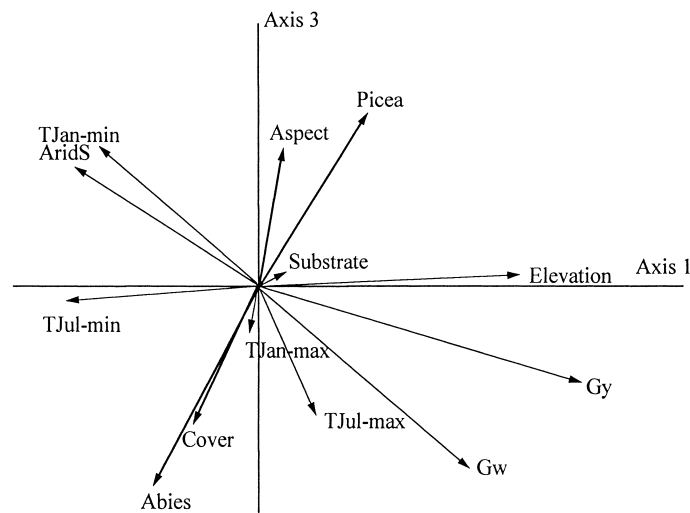


Figure 4. : Environmental variables scores on 1–3 axes of the CCA.

of the correlations for elevation and minimum temperatures ( $T_{\text{Jan-min}}$  and  $T_{\text{Jul-min}}$ ) with axis 1 increased in the CCA, and decreased on axis 2. This pattern suggests a significant rotation of the cloud from CA to CCA and a less clear separation in the CCA between rainshadow effect and aridity on axis 1 and elevation and temperature on axis 2. As a consequence, the correlations for both canopy species, *Picea* and *Abies*, were significant with both axes 1 and 2 in CCA versus only with axis 2 in CA.

CCA axis 3 was different from CA axis 3 and the highest correlations with this axis were for the two canopy species (Figure 4 and Table 3;  $-0.60$  for *Abies* and  $0.53$  for *Picea*). The other most correlated environmental variables ( $P < 0.001$ ) were  $G_{\text{winter}}$  ( $-0.51$ ), aspect ( $0.44$ ), cover ( $-0.43$ ),  $T_{\text{Jan-min}}$  ( $0.42$ ),  $T_{\text{Jul-max}}$  ( $0.38$ ) and  $\text{Arid}_{\text{summer}}$  ( $0.38$ ). However, the main contribution of the CCA axis 3 was the differentiation between closed *Abies*-dominated forests on north-facing aspects and open *Picea*-dominated forests on south-facing aspects.

## Discussion

Our results demonstrated that associations between the abundance of two conifers, *Picea abies* and *Abies alba*, and particular understory plant assemblages were stronger in the xeric inner Alps than in the mesic external Alps. This increase in species-specific association appeared to be due to both higher habitat heterogeneity and the stronger biotic influence of tree canopies in the dry rainshadow sector. In the wetter

external Alps, the species composition of understory assemblages did not differ substantially between *Picea*- and *Abies*-dominated forests even though these forests occurred in substantially different climates. These results suggest that the buffering effects of tree canopies may actually reduce habitat heterogeneity in wet regions. In the drier inner Alps the species composition of understory communities differed substantially between *Picea*- and *Abies*-dominated forests even though these forests occurred in relatively similar climates, and in particular on south-facing aspects. These results suggest that tree canopies may create more habitat heterogeneity in dry regions. The parallel increase in beta diversity supports the hypothesis that understory assemblages were more discrete in the inner Alps than in the external Alps. These results corroborate those of Whittaker (1960) for the Siskiyou Mountains and del Moral and Watson (1978) for the Cascade Mountains, and both of these North American mountain ranges also have strong rainshadow gradients. A large number of correlative studies conducted in mesic areas, as north-west Europe (Lippmaa 1939), the Appalachian chain (Whittaker 1956; Bratton 1975; Rheinhardt 1992), the Northern Rockies (McCune and Antos 1981; Bradfield and Scagel 1984) and Vancouver Island (Klinka et al. 1996; Qian et al. 1997) have observed weak or non-existent canopy-understory associations.

del Moral and Watson (1978) argued that the increase in canopy-understory correlations along the strong rainshadow gradient of the Cascades ranges was due to the smaller size and cover of the trees on the dry end of the gradient. The smaller trees were

hypothesized to poorly buffer the effect of climate on understory species, relative to large trees, exposing the understory species on the dry ends of gradients more directly to habitat heterogeneity; canopy trees and understory species may have more similar environmental requirements on the dry ends of gradients than on wet ends, which may explain stronger associations among canopy and understory species (del Moral and Watson 1978). Whittaker (1960) and McCune and Antos (1981) hypothesized that increased canopy-understory associations were the result of steeper environmental gradients in dry climates (i.e. the effect of aspect is stronger in dry climates) which in turn cause higher beta diversity among communities. On another hand, strong associations between canopy and understory species may be due to stronger positive and species-specific biological interactions in dry climates, as suggested by Bertness and Callaway (1994) and Callaway (1998a). We will examine successively these three hypotheses.

*Do canopy species and understory species have more similar requirements on the dry ends of gradients?*

ANOVAs performed on environmental variables with the three formations as treatments (Table 2) indicated clear differences in climatic requirements between *Picea* and *Abies*. *Abies* was dominant in drier habitats and *Picea* in colder habitats. Our results are supported by dendroecological studies of both species (Becker 1989; Bert and Becker 1990; Desplanque et al. 1998; Rolland et al. 1998, 1999, 2000). Ecophysiological studies on seedlings of *Abies lasiocarpa* and *Picea engelmannii* (Noble and Alexander 1977; Knapp and Smith 1981; Shea 1985) and of *Abies balsamea* and *Picea rubens* (McIntosh and Hurlley 1964) suggest that similar differences exist between other *Picea* and *Abies* species.

The two primary factors correlated with understory composition of *Picea* and *Abies* forests were also drought and cold temperatures, respectively. Results of both the CA and the CCA showed that both of these direct factors were primarily determined by rainshadow effect and elevation, which have been shown in other studies to be the most important complex factors, associated with the organization of forest communities in the Alpine chain (Ozenda 1985; Gafta and Pedrotti 1998; Michalet et al. 1998). Regarding the relationship between cold temperatures (which increased along CA axis 2) and both trees and

their associated understory assemblages, the correlation was positive for *Picea*, but negative for *Abies* (Figure 1, Table 3). This suggests that, for temperature, the requirements for understory species and for canopy species were consistent. In other words *Picea* and its understory were both cold-tolerant and *vice versa* for *Abies*. In contrast, the understory correlations with moisture along CA axis 1 were inconsistent with the moisture requirements for the canopy species discussed above. The most drought-tolerant assemblages did not occur below *Abies*, the most drought-tolerant tree species, but below *Picea* which is less drought-tolerant than *Abies*.

Differences in water requirements between canopy and understory species have been observed by several authors even in wet climates (Whittaker 1956; Bratton 1975; Hicks 1980; McCune and Antos 1981) and for these "Gleasonian" ecologists this has been a strong argument against the holistic concept of community organization. The argument was strengthened by the experiments of Chapin and Shaver (1985). However, we found that canopy and understory species had different moisture requirements in the sites where the correlation between the canopy species and understory assemblages was the highest. Therefore dissimilar requirements of canopy and understory species are not necessarily an argument for fully individualistic communities.

*Does habitat heterogeneity explain stronger canopy-understory associations on the dry ends of gradients?*

Whittaker (1960) and McCune and Antos (1981) thought that increased correlations among canopy and understory species in relatively dry conditions, and the resulting beta diversity, were due to higher habitat heterogeneity caused by more contrasting effects of other environmental factors such as aspect or slope in dry climates. Our results also indicate that the effects of aspect, elevation, substrate and cover were more pronounced at the dry end of the rainshadow gradient in the inner Alps than at the wet end in the external Alps. Many studies have shown strong effect of aspect (Bartoli 1966; Noble and Alexander 1977; Ustin et al. 1984; Rolland et al. 1999) or substrate (Braun-Blanquet et al. 1954; Bartoli 1966; Whittaker and Niering 1968) on understory species in dry areas but not wet ones.

In our study, if habitat heterogeneity was a primary driver of canopy-understory correlations, we would

have observed an increase in habitat heterogeneity for both the understory species and the canopy species, which we did not. Our results (Figure 3, Table 4) showed the converse; *Picea* and *Abies* forests occurred in more heterogeneous conditions in the external Alps than in the inner Alps. But, in contrast understory assemblages occurred in less heterogeneous conditions in the external Alps than in the inner Alps. However, to be unbiased and conservative, we divided the dataset somewhat arbitrarily into only two parts, with the intermediate Alps shared in these two parts. This may have obscured differences in the habitat distribution between *Abies* and *Picea*. Indeed pure *Abies* communities were almost absent from the very inner Alps on south-facing aspects, and were restricted to the intermediate Alps (see Table 4; means of 44.5 for  $G_{\text{year}}$  for southern aspect, versus 55.2 for the northern aspect). Conversely, *Picea* was present on both aspects (similar mean of 52.4 for  $G_{\text{year}}$  for both aspects) in both rainshadow sectors. Consequently, the increase in correlation between canopy and understory assemblages in our chosen group for the inner Alps, to which we have attributed species-specific canopy effects may also have been affected by the steepness of the gradient of aspect driving different canopy species and understory assemblages on different aspects. However the steepness of the gradient of moisture induced by substrate types was unlikely to increase correlations between canopy species and understory assemblages because the most xeric understory was preferentially on limestone in the inner Alps (Figure 2) and *Picea* communities on siliceous rocks (Table 4). High positive correlations of *Picea* and aspect on CCA axis 3 and very low correlation of substrate (and elevation) confirm this argument (Figure 4, Table 3). Cover was significantly negatively correlated to CCA axis 3, probably because trees had lower covers on southern aspects than on northern aspects. However, there was no significant differences in cover between *Picea* and *Abies* formations (Table 4).

Human impact may also have enhanced the effect of habitat heterogeneity on canopy-understory correlations and increased beta diversity in the inner Alps. Historical studies by Desplanque (1997) have shown that *Abies* is more affected than *Picea* by deforestation and she concluded that this may explain its rarity on south-facing aspects in the inner Alps as compared to *Picea*.

#### *Are species-specific canopy effects on the understory stronger in the inner Alps?*

The large difference in the composition of the understory assemblages for *Picea* versus *Abies* on the rainshadow gradient (CA axis 1 scores, Figure 1) that occurred on the southern aspects of the inner Alps suggests that the increase in canopy-understory correlations was not only determined by the steepness of the moisture gradient. The sites had similar moisture conditions ( $\text{Arid}_{\text{summer}}$ , Figure 3) but the canopy of *Abies* appears to have created more mesic and buffered microclimatic conditions for the understory than that of *Picea*. This pattern was not observed at either of the sites in the external Alps, where moisture was much higher (Figure 3), nor at sites on northern aspects of the inner Alps, despite no differences in  $\text{Arid}_{\text{summer}}$  between *Abies* and *Picea* forests at these sites (Figure 3). Facilitation has been hypothesized to increase in stressful conditions (Bertness and Callaway 1994) and several experimental studies have supported this model on gradients of moisture (Berkowitz et al. 1995; Greenlee and Callaway 1996), elevation (Callaway 1998b) or both (Choler et al. 2001). Shade has been shown to be important in facilitative interactions in stressful environments, especially when the stress is due to drought (Noble and Alexander 1977; Selter et al. 1986; Vetaas 1992; Callaway et al. 1996; Greenlee and Callaway 1996; Suzan et al. 1996; Holmgren et al. 1997; Weltzin and McPherson 1999).

In savannas, where the climate is hotter and dryer than the communities studied here, the effect of tree canopies on understory environment can be striking (Vetaas 1992), but such differences have rarely been shown in mesic forests. Species-specific effects in a wide variety of forest types have been shown for nutrients (Alban 1982; Beatty 1984; Boettcher and Kalisz 1990; Dzwonko and Loster 1997; Finzi et al. 1998), snow accumulation (Veblen et al. 1979) and soil temperature and moisture (Beatty 1984). Differences in species-specific effects appear to be more common when tree species are different morphologically, such as evergreen versus deciduous *Nothofagus* (Veblen et al. 1979), conifers versus deciduous trees (Beatty 1984; Boettcher and Kalisz 1990), or nitrogen-fixing versus non nitrogen-fixing species (Dzwonko and Loster 1997). Beatty (1984) found no microclimate differences among deciduous trees in mesic *Acer-Fagus* forests. In the dry inner French Alps Michalet et al. (2001) found differences in humus types, nitrogen availability, soil fauna between

*Pinus sylvestris* and *Abies alba* communities in similar abiotic conditions. Although morphologically different canopy species can have strong differences in their effects on understory assemblages (Veblen et al. 1979; Hicks 1980; Sydes and Grime 1981; Beatty 1984; Boettcher and Kalisz 1990; Dzwonko and Loster 1997), the relationships among canopy species and understory tend to be weaker in mesic climates (McIntosh and Hurlley 1964; Klinka et al. 1996). In contrast, in arid regions a number of studies have indicated that the effects of trees and shrubs on understory assemblages may be species-specific (Hutto et al. 1986; McAuliffe 1988; Franco and Nobel 1989; Callaway 1995; Suzan et al. 1996; Callaway 1998a).

Shade intolerant species in general transmit more light in their understory than shade tolerant species (Messier et al. 1998), which have a higher efficiency of leaf display (Canham 1989; Cornelissen 1999; Bond et al. 1999). No data are available on differences in light penetration between *Abies alba* and *Picea abies* and the two species are similar enough to have been placed in the same functional group (Bugmann 1996), as have other *Abies* and *Picea* pairs, despite well documented differences in shade tolerance between the genera (McIntosh and Hurlley 1964; Shea 1985; Veblen 1986; Okitsu et al. 1995; Busing 1996; Kneeshaw and Burton 1997; Takahashi 1997). *Abies alba* and *Picea abies* have different crown architectures, with the former having a more rounded apex and the latter a more conical canopies. These differences could contribute to differences in light penetration, water throughfall, and microclimatic conditions in the understory.

Our large-scale correlative study does not allow us to conclude on the relative importance of the positive effects of canopy species and the effect of habitat heterogeneity in increasing spatial associations between canopy and understory species. Further studies are needed to quantify the importance of these positive effects in explaining the occurrence of discrete communities in dry environments: small-scale sampling of understory vegetation near and away from trees, more precise measurements of tree density and removal of specific canopy tree species in different positions along the rainshadow gradient. Bertness and Callaway (1994) proposed that facilitation increases with abiotic stress and Callaway (1997) argued that positive interactions can be reconciled with continuum theory. Our results suggest that a continuum may shift to more discrete communities along a gradient of abiotic stress due to a combined effect of increas-

ing habitat heterogeneity and the biological effects of different canopy species. In his 1960 study in the Siskiyou Mountains of northern California, where the effect of rainshadow is much stronger than in the Great Smoky Mountains, Robert Whittaker, the dean of continuum theory, described discrete communities. He concluded that "the limitations inherent in any approach or system may suggest the desirability of applying more than one approach to a given study when this is feasible-of supplementing a study in gradient analysis with consideration of classification as in the present work".

### Acknowledgements

We thank Gérard Cadel, Carole Desplanque, Gilles Pache, Guy Pautou, Anne Petetin and Lucien Richard for providing us unpublished relevés or environmental data. The comments of J. Stephen Brewer and two anonymous reviewers greatly improved the manuscript.

### References

- Affi A.A. and Clark V. 1990. Computer-aided multivariate analysis. Lifetime Learning Publications, Belmont.
- Alban D.H. 1982. Effects of nutrient accumulation by aspen, spruce and pine on soil properties. *Soil Science Society of American Journal* 46: 853–861.
- Austin M.P. 1985. Continuum concept, ordination methods, and niche theory. *Annual Review of Ecology and Systematics* 16: 39–61.
- Bartoli Ch. 1966. Etudes écologiques sur les associations forestières de la Haute-Maurienne. *Annales des Sciences Forestières* 23: 433–479.
- Barkman J.J. 1978. Synusial approaches to classification. In: Whittaker R.H. (ed.), *Classification of Plant Communities*. Junk, The Hague, pp. 111–165.
- Beatty S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65: 1406–1419.
- Becker M. 1989. The role of climate on present and past vitality of silver fir forests in the Vosges mountains of northeastern France. *Canadian Journal of Forest Research* 19: 1110–1117.
- Berkowitz A.R., Canham C.D. and Kelly V.R. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. *Ecology* 76: 1156–1168.
- Bert G.D. and Becker M. 1990. Dendroécologie du sapin dans le Jura. *Annales des Sciences Forestières* 47: 395–412.
- Bertness M.D. and Callaway R.M. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9: 191–193.

- Boettcher S.E. and Kalisz P.J. 1990. Single-tree influence on soil properties in the mountains of eastern Kentucky. *Ecology* 71: 1365–1372.
- Bond B.J., Farnsworth B.T., Coulombe R.A. and Winner W.E. 1999. Foliage physiology and biochemistry in response to light gradients in conifers with varying shade tolerance. *Oecologia* 120: 183–192.
- Bradfield G.E. and Scagel A. 1984. Correlations among vegetation strata and environmental variables in subalpine spruce-fir forests, southeastern British Columbia. *Vegetatio* 55: 105–114.
- Bratton S.P. 1975. A comparison of the beta diversity functions of the overstory and herbaceous understory of a deciduous forest. *Bulletin of Torrey Botanical Club* 102: 55–60.
- Braun-Blanquet J. 1932. Plant sociology, the study of plant communities. Mc Graw-Hill, New York, Transl. By G.D. Fuller and H.S. Connard.
- Braun-Blanquet J., Pallmann H. and Bach R. 1954. Pflanzenzoologische und Bodenkundliche Untersuchungen in Schweizerischen Nationalpark und seine Nachgebieten II. *Ergebnung Wissenschaften Untersuchungen Schweizer Nationalparks* 4: 1–199.
- Brooker R.W. and Callaghan T.V. 1998. The balance between positive and negative plant interactions and its relationships to environmental gradients: a model. *Oikos* 81: 196–207.
- Bugmann H. 1996. Functional types of trees in temperate and boreal forests: classification and testing. *Journal of Vegetation Science* 7: 359–370.
- Busing R.T. 1996. Estimation of tree replacement patterns in an Appalachian *Picea-Abies* forest. *Journal of Vegetation Science* 7: 685–694.
- Callaway R.M. 1995. Positive interactions among plants. *The Botanical Review* 61: 306–349.
- Callaway R.M. 1997. Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia* 112: 143–149.
- Callaway R.M. 1998a. Are positive interactions species-specific? *Oikos* 82: 202–207.
- Callaway R.M. 1998b. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. *Oikos* 82: 561–573.
- Callaway R.M., De Lucia E.H., Moore D., Nowak R. and Schlesinger W.H. 1996. Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert versus montane pines. *Ecology* 77: 2130–2141.
- Callaway R.M. and Walker L.R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78: 1958–1965.
- Canham C.D. 1989. Different responses to gap among shade-tolerant tree species. *Ecology* 70: 548–550.
- Chapin F.S. and Shaver G.R. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* 66: 564–576.
- Choler Ph., Michalet R. and Callaway R.M. 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* 82: 3295–3308.
- Cornelissen J.H.C. 1999. A triangular relationship between leaf size and seed size among woody species: allometry, ontogeny, ecology and taxonomy. *Oecologia* 118: 248–255.
- Curtis J.T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison.
- del Moral R. and Watson A.F. 1978. Gradient structure of forest vegetation in the Central Washington Cascades. *Vegetatio* 38: 29–48.
- Desplanque C. 1997. Dendroécologie comparée du sapin et de l'épicéa dans les Alpes internes franco-italiennes. Univ. J. Fourier, Grenoble 1, France.
- Desplanque C., Rolland C. and Michalet R. 1998. Dendroécologie comparée du sapin (*Abies alba* Mill.) et de l'épicéa (*Picea abies* Karst.) dans une vallée alpine française. *Canadian Journal of Forest Research* 28: 737–748.
- Douguedroit A. and de Saintignon M.-F. 1970. Méthode d'étude de la décroissance des températures en montagne de latitude moyenne: exemple des Alpes françaises du sud. *Revue de Géographie Alpine* 58: 453–472.
- Dzwonko Z. and Loster S. 1997. Effects of dominant trees and anthropogenic disturbances on species richness and floristic composition of secondary communities in Southern Poland. *Journal of Applied Ecology* 34: 861–870.
- Finzi A.C., van Breemen N. and Canham C.D. 1998. Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecological Applications* 8: 440–446.
- Franco A.C. and Nobel P.S. 1989. Effect of nurse plants on the microhabitat and growth of cacti. *Journal of Ecology* 77: 870–886.
- Gafta D. and Pedrotti F. 1998. Fitoclima del Trentino-Alto Adige. *Studi Trentini di Scienze Naturali* 73: 55–111.
- Gams H. 1932. Die Klimatische Begrebzung von Pflanzenarealen und die Verteilung der hygrischen Kontinentalität in den Alpen. *Zeitschrift der Gesellschaft für Erkunde* 56.
- Gillet F. and Gallandat J.-D. 1996. Integrated synusial phytosociology: some notes on a new, multiscale approach to vegetation analysis. *Journal of Vegetation Science* 7: 13–18.
- Gillet F., Murisier B., Buttler A., Gallandat J.-D. and Gobat J.-M. 1999. Influence of tree cover on the diversity of herbaceous communities in subalpine wooded pastures. *Applied Vegetation Science* 2: 47–54.
- Gleason H. 1926. The individualistic concept of the plant association. *Bulletin of Torrey Botanical Club* 53: 7–26.
- Greenlee J.T. and Callaway R.M. 1996. Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. *The American Naturalist* 148: 386–396.
- Hicks D.J. 1980. Intrastrand distribution patterns of southern Appalachian cove forest herbaceous species. *American Midland Naturalist* 104: 209–223.
- Holmgren M., Scheffer M. and Huston M. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78: 1966–1975.
- Hutto R.L., McAuliffe J.R. and Hogan L. 1986. Distributional associates of the saguaro (*Carnegiea gigantea*). *Southwestern Naturalist* 31: 469–476.
- Klinka K., Chen H.I.H., Wang Q. and de Montigny L. 1996. Forest canopies and their influence on understory vegetation in early-seral stands on West Vancouver Island. *Northwest Science* 70: 193–200.
- Knapp A.K. and Smith W.K. 1981. Factors influencing understory seedling establishment of Engelmann spruce and subalpine fir in southeast Wyoming. *Canadian Journal of Botany* 60: 2753–2761.
- Kneeshaw D.D. and Burton P.J. 1997. Canopy and age structure of some old sub-boreal *Picea* stands in British Columbia. *Journal of Vegetation Science* 8: 615–626.

- Kuoch R. 1954. Wälder der Schweizer Alpen im verbreitungsgebiet der Weibtanne. *Mitteilungen der Schweizerischen Anstalt für das forstliche Versuchswesen* 30: 133–314.
- Lebreton J.D., Chessel D., Prodon R. and Yoccoz N. 1988. The analysis of species environment relationships by canonical correspondence analysis. I. Quantitative environmental variables. *Acta Oecologica Generalis* 9: 53–67.
- Lippmaa T. 1939. The unistratal concept of plant communities (the unions). *American Midland Naturalist* 21: 111–145.
- McAuliffe J.R. 1988. Markovian dynamics of simple and complex desert plant communities. *The American Naturalist* 131: 459–490.
- McCune B. 1997. Influence of noisy environmental data on canonical correspondence analysis. *Ecology* 78: 2617–2623.
- McCune B. and Antos J.A. 1981. Correlations between forest layers in the Swan Valley, Montana. *Ecology* 62: 1196–1204.
- McIntosh R.P. 1967. The continuum concept of vegetation. *The Botanical Review* 33: 130–187.
- McIntosh R.P. and Hurlley R.T. 1964. The spruce-fir forests of the Catskill Mountains. *Ecology* 45: 314–326.
- Messier C., Parent S. and Bergeron Y. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *Journal of Vegetation Science* 9: 511–520.
- Michalet R. 1991. Nouvelle synthèse bioclimatique des milieux méditerranéens. Application au Maroc septentrional. *Revue d'Ecologie Alpine* 1: 45–60.
- Michalet R., Cadel G., Joud D., Pache G., Pautou G. and Richard L. 1998. Synthèse phytécologique des forêts de l'Arc Alpin. *Ecologie* 29: 99–104.
- Michalet R., Gandoy C., Cadel G., Girard G., Grossi J.-L., Joud D. et al. 2001. Modes de fonctionnement d'humus des forêts sempervirentes des Alpes internes françaises. *Comptes Rendus de l'Académie des Sciences Paris Sciences de la Vie* 324: 59–70.
- Michalet R., Gandoy C., Joud D., Pagès J.-P. and Choler Ph. 2002. Plant community composition and biomass on calcareous and siliceous substrates in the northern French Alps: comparative effects of soil chemistry and water status. *Arctic Antarctic and Alpine Research* 34: 102–113.
- Noble D.L. and Alexander R.R. 1977. Environmental factors affecting natural regeneration of Engelmann spruce in the Central Rocky Mountains. *Forest Science* 23: 420–429.
- Okitsu S., Ito K. and Li C. 1995. Establishment processes and regeneration patterns of montane virgin coniferous forest in northeastern China. *Journal of Vegetation Science* 6: 305–308.
- Okland R.H. 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? *Journal of Vegetation Science* 7: 289–292.
- Ozenda P. 1985. La végétation de la chaîne alpine dans l'espace montagnard européen. Masson, Paris.
- Pache G., Michalet R. and Aimé S. 1996a. A seasonal application of the Gams (1932) method, modified Michalet (1991): The example of the distribution of some important forest species in the Alpine chain. *Dissertationes Botanicae* 258: 31–54.
- Pache G., Aimé S. and Michalet R. 1996b. A simple model for the study of the altitudinal rainfall gradient, applied in the Tyrolian orographic complex. *Revue d'Ecologie Alpine* 3: 13–20.
- Peet R.K. 1981. Forest vegetation of the Colorado Front Range. *Vegetatio* 45: 3–75.
- Qian H., Klinka K. and Sivak B. 1997. Diversity of the understory vascular vegetation in 40 year-old and old growth forest stands on Vancouver Island, British Columbia. *Journal of Vegetation Science* 8: 773–780.
- Rheinhardt R.D. 1992. Disparate distribution patterns between canopy and subcanopy life-forms in two temperate North-American forests. *Vegetatio* 103: 67–77.
- Rolland C., Petitcolas V. and Michalet R. 1998. Changes in radial tree-growth for *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the Alpine timberline since 1750. *Trees Structure and Function* 13: 40–53.
- Rolland C., Michalet R., Desplanque C., Petetin A. and Aimé S. 1999. Ecological requirements of *Abies alba* in the French Alps derived from dendro-ecological analysis. *Journal of Vegetation Science* 10: 297–306.
- Rolland C., Desplanque C., Michalet R. and Schweingrüber F.H. 2000. Extreme tree-rings in fir (*Abies alba* Mill.) and spruce (*Picea abies* (L.) Karst.) stands in relation to climate and space. *Arctic Antarctic and Alpine Research* 32: 1–13.
- Selter C.M., Pitts W.D. and Barbour M.G. 1986. Site microenvironment and seedling survival of Shasta red fir. *American Midland Naturalist* 115: 288–300.
- Shea K.L. 1985. Demographic aspects of coexistence in Engelmann spruce and subalpine fir. *American Journal of Botany* 72: 1823–1833.
- SPSS 1997. SPSS version 7.0 for Windows. SPSS, Chicago, Illinois, USA.
- Suzan H., Nablun G.P. and Patten D.T. 1996. The importance of *Olneya tesota* as a nurse plant in the Sonoran desert. *Journal of Vegetation Science* 7: 635–644.
- Sydes C. and Grime J.P. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. II. An experimental investigation. *Journal of Ecology* 69: 249–262.
- Takahashi K. 1997. Regeneration and coexistence of two subalpine conifer species in relation to dwarf bamboo in the understory. *Journal of Vegetation Science* 8: 529–536.
- ter Braak C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167–1179.
- Thioulouse J., Devillers J., Chessel D. and Auda Y. 1991. Graphical techniques for multidimensional data analysis. In: Devillers J. and Karcher W. (eds), *Applied Multivariate Analysis in SAR and Environmental Studies*. Kluwer Academic Publishers, pp. 153–205.
- Tutin T.G., Heywood V.H., Burges N.A., Moore D.M., Valentine D.H., Walters S.M. et al. 1964–1980. *Flora Europaea*. Cambridge University Press, Cambridge.
- Ustin S.L., Woodward R.A., Barbour M.G. and Hatfield J.L. 1984. Relationships between sunfleck dynamics and red fir seedling distribution. *Ecology* 65: 1420–1428.
- Veblen T.T. 1986. Treefalls and the coexistence of conifers in subalpine forests of the Central Rockies. *Ecology* 67: 644–649.
- Veblen T.T., Veblen A.T. and Schlegel F.M. 1979. Understory patterns in mixed evergreen-deciduous *Nothofagus* forests in Chile. *Journal of Ecology* 67: 809–823.
- Vetaas O.R. 1992. Micro-site effects of trees and shrubs in dry savannas. *Journal of Vegetation Science* 3: 337–344.
- Weltzin J.F. and McPherson G.R. 1999. Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. *Ecological Monographs* 69: 513–534.

- Westhoff V. and van der Maarel E. 1978. The Braun-Blanquet approach. In: Whittaker R.H. (ed.), *Classification of plant communities*. Junk, The Hague, pp. 297–399.
- Whittaker R.H. 1951. A criticism of the plant association and climax concepts. *Northwest Science* 25: 17–31.
- Whittaker R.H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26: 1–80.
- Whittaker R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279–338.
- Whittaker R.H. 1967. Gradient analysis of vegetation. *Biological Review* 42: 207–264.
- Whittaker R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213–251.
- Whittaker R.H. and Niering W.A. 1968. Vegetation of the Santa Catalina mountains, Arizona. IV: Limestone and acid soils. *Journal of Ecology* 56: 523–544.