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Original article

Secondary succession of *Alnus viridis* (Chaix) DC. in Vanoise National Park, France: coexistence of sexual and vegetative strategies

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Abstract – In the western Alps, *Alnus viridis* expansion on subalpine grasslands brings major modifications in the functioning of ecological systems. The aim of this study was to assess which reproduction strategies were responsible for colonization and persistence of the shrub. Indices of vegetative and sexual reproduction were assessed in four 100 m^2 sites distinguished by the date of *A. viridis* settlement to determine the prevalent strategy as a function of age of the *A. viridis* stand. Results indicated that sexual allocation to reproduction was effective in all situations, whereas layering was absent in the site displaying the most recent *A. viridis* settlement. The number of cones per individual declined significantly from strictly sexual-related individuals to individuals displaying both reproduction strategies. (Mann-Whitney test: $U = 132$: $P = 0.022$). On these grounds we argue that *A. viridis* colonization process on secondary succession is supplied exclusively by sexual reproduction. In contrast, temporal persistence of dense stands is thought to require layering, which is also hypothesized to maintain a mechanism of inhibition towards arboreal coniferous species of late successional stages.

land disuse / reproduction / strategy / subalpine / succession

Résumé – Succession secondaire de *Alnus viridis* (Chaix) DC. dans le parc national de la Vanoise, France : coexistence de stratégies sexuelle et végétative. Dans les Alpes occidentales, l'expansion d'*Alnus viridis* sur pelouses subalpines entraîne des modifications majeures dans le fonctionnement des écosystèmes. Le but de cette étude est de déterminer quelles sont les stratégies de reproduction à l'origine de la colonisation et de la persistance de l'espèce. Des indices de reproduction végétative et sexuée d'individus ont été mesurés dans quatre sites de 100 m^2 différenciés par la date d'installation d'*A. viridis*. Les résultats obtenus indiquent que la production de graines a lieu dans toutes les situations, alors que le marcottage est absent dans le mésosite le plus récemment colonisé par *A. viridis*. Le nombre de cônes produits par individu est par ailleurs plus faible chez les individus qui utilisent une combinaison des reproductions végétative et sexuée que chez les individus à reproduction strictement sexuée (test Mann-Whitney : $U = 132$, $P = 0{,}022$). Sur la base de ces résultats, nous formulons l'hypothèse que la colonisation des pelouses subalpines par *A. viridis* s'appuie exclusivement sur la reproduction sexuée des individus. En revanche, sa régénération sous son propre couvert est essentiellement dépendante de ses capacités de reproduction végétative, également suspectées d'être à l'origine d'un mécanisme d'inhibition vis-à-vis de ses concurrents arborés des stades de succession ultérieurs.

déprise agro-pastorale / reproduction / stratégie / subalpin / succession

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1. INTRODUCTION

Green alder (*Alnus viridis* (Chaix) DC.) is a widely distributed shrub in the northern hemisphere [16, 21] where it is a substantial component of boreal forests, and the subalpine belt in European temperate mountain ranges at the upper treeline. It plays an important role in primary successions, successfully colonizing areas after strong disturbances sensu White & Pickett [36] such as glacial retreat [35]. However, in European mountain areas, current land disuse in the subalpine belt is argued to be one of the main causes of ligneous expansion at the upper treeline [13]. In such a context, *A. viridis* has colonized large areas, as it is recorded on vegetation cartography [3, 9, 28] to the detriment of subalpine grassland. Such singular colonization efficiency in secondary succession is due to its strong ability to spread under a high disturbance regime [15] and implies strong potential expansion in the northern French Alps, where human impact is strong and has fluctuated for decades [4].

One considers the spatial occurrence of *A. viridis* to act as a homogenization process for environmental abiotic parameters at local level, due to its very dense aboveground cover [15]. Such a phenomenon is potentially threatening for the maintenance of biodiversity at the upper treeline, the richness of which is substantially generated by the high level of environmental heterogeneity e.g. [6, 14, 17]. Moreover it is thought to be temporally persistent and thus likely to inhibit the development of arboreal coniferous species [7] and to strengthen negative effects on biodiversity by reducing temporal heterogeneity [33]. For the above reasons the influence of *A. viridis* cover on several biodiversity indicators was investigated and it was suggested that it induces a decline in vascular plant α-diversity, i.e. species richness and species evenness [27] and a decline in the biomass and diversity of macroarthropods active at the soil surface [2]. Yet like most shrubs with strong colonization aptitude after disturbance, *A. viridis* is a light-demanding species [25], which could be interpreted as contradictory with its temporal persistence. Partial explanation of this apparent contradiction was given by underlining the remarkable capacities of individuals to regenerate by resprouting after clear-cutting [15]. However many *A. viridis* stands do not face human-induced clear-cutting, so we hypothesized layering as an alternative strategy used by individuals to persist in time.

The aim of this study was to determine both layering and sexual reproduction processes on a representative sampling of *A. viridis* individuals of variable ages. Results were meant to provide substantial explanation of:

- the respective roles of sexual and vegetative reproduction strategies in explaining the colonization and persistence of *A. viridis* stands;
- the influence of age on the two types of strategies;
- the relations between the two types of strategies.

2. MATERIALS AND METHODS

2.1. Study area

The study was carried out in summer 1999 in the area named “Le Plan du Pré” (*figure 1*), Champagny, inside the Vanoise National Park, France (45° 27’ N, 6° 41’ E). This type of area contained subalpine grassland (1 900 m a.s.l.) surrounded by an *A. viridis* stand considered to be the largest in the French Alps [22]. Located on a north-facing slope under the “Grand Bec de la Vanoise” peak (3 386 m) it is supplied by a large amount of water throughout the year. This phenomenon generated high soil moisture, which, associated with important local pastoral disuse, was favourable to the expansion of *A. viridis* [26].

2.2. Sampling design

A total of 94 *A. viridis* apparent individuals were selected. They were extracted from four contiguous sites, distinguishable by the date of the first *A. viridis* settlement (*table I*), using aerial photographic interpretation. Areas of sites were 100 m^2 (10 by 10 m), which fit the analysis for two reasons: (1) they provided an adequate number of individuals for statistical analyses, (2) they were small enough to maintain relative homogeneity in the age of *A. viridis* stands. Environmental conditions were roughly similar for the 4 sites with respect to altitude and slope gradient, on East to North-East facing slopes (site 4, *table I*); slight variations were noted concerning the topography. All sites faced the same pastoral pressure, currently limited annually to 15 days grazing by a small herd of heifers (Ruffier-Lanche, pers. comm.).

An additional 68 *A. viridis* individuals were selected in “Le Plan du Pré” so as to correlate the age of individuals and trunk circumference. They were randomly selected along a transect representing an ecotone from

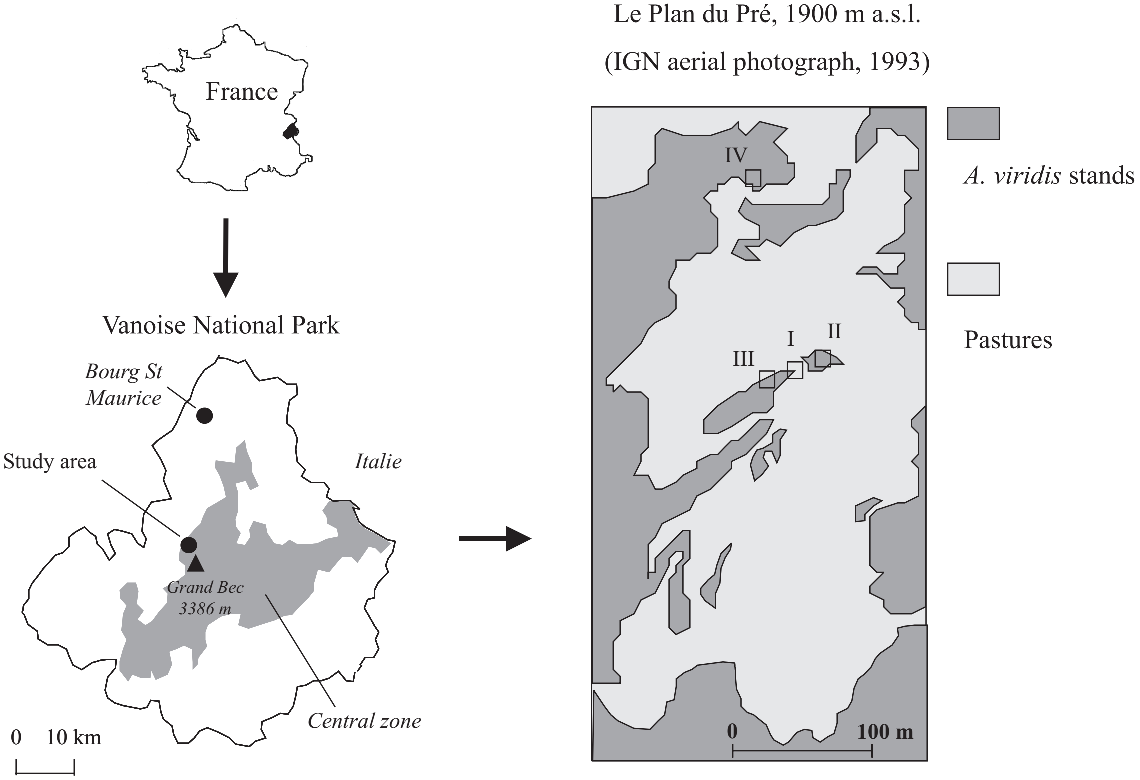

Figure 1. Location of the study area of Le Plan du Pré, inside the Vanoise National Park, Savoie, France.

Table I: Description of the four contiguous sites in Le Plan du Pré.

Sites	1	2	3	4
Exposure (N; °)	100	100	105	55
Altitude (m a.s.l.)	1880	1885	1870	1875
Slope gradient (°)	30°	30°	30°	30°
Alder settlement (years)[i]	< 10	20	30	> 40
Apparent Individuals (A.I.)	12	29	35	23

[i] : on basis of aerial photographic interpretation.

grassland to *A. viridis* stand in order to take into account all the situations occurring in the four sites. Dendrometric study was performed by determining the number of age rings 0.5 m above the ground after cutting trunks of individuals. Results were meant to assess the age of individuals in the 4 sites by measuring their circumferences only, to avoid damaging them.

The floristic composition of the four sites was suggested to give further insight into the stage of *A. viridis* colonization as flora of typical alder stands is well known [24]. It was investigated using a 6-point cover scale for each vascular plant, i.e. +: rare; 1: < 5%; 2: 5–25%; 3: 25–50%; 4: 50–75%; 5: 75% (see Annex). Plant latin names were taken from *Flora Europaea* nomenclature [34].

Respective abundances of species in each site were shown on Annex. Sites I, II and III were dominated by *Agrostis capillaris*, which was interpreted as a residual of former pastoral activity on nutrient-rich subalpine grassland [12]. Abundances of *Dactylis glomerata* and *Anthoxanthum odoratum* in site I underlined herbaceous dominance, and relative nitrogen-rich grassland. The abundance of *Peucedanum ostruthium* and *Rumex alpestris* in site II also characterized a relatively high nitrogen level, but under *A. viridis* canopy. Site III displayed species characteristics of *A. viridis* canopy as well (e.g. *Lamium album* L.), but abundance of *Rubus idaeus* and *Vaccinium vitis-idaea* indicated relative soil xericity. Site IV displayed a typical *A. viridis* stand floristic composition sensu Richard [27], illustrated by the high abundance of *Adenostyles alliariae*, *Cicerbita alpina* and *Viola biflora*, and relative poor species richness. Little evidence of floristic indications related to recent pastoral use was noticed in this site.

2.3. Reproductive strategies

Two methods were available to assess a vegetative reproduction index. The first one consisted of performing comparative genetic analysis on all the individuals, using DNA extracted from leaves. The other method was to give prominence to layering processes, through a mechanical operation [10, 18]. The second method was selected in that it was remarkably suited to *A. viridis* morphology, i.e. apparent individuals were clearly distinguishable and the links between them were easily pointed out (*figure 2*). Consequently all the "apparent individuals" of the 4 sites ($N = 94$) were tagged, aged, and their canopy areas were assessed. Then the area surrounding the trunk of each individual was dug, from 0.5 to 1 m deep, to determine the potential occurrence of vegetative links between individuals. Overall, four types of related individuals were examined (see *figure 2*):

AI: "apparent individuals", separated from one to another at first sight;

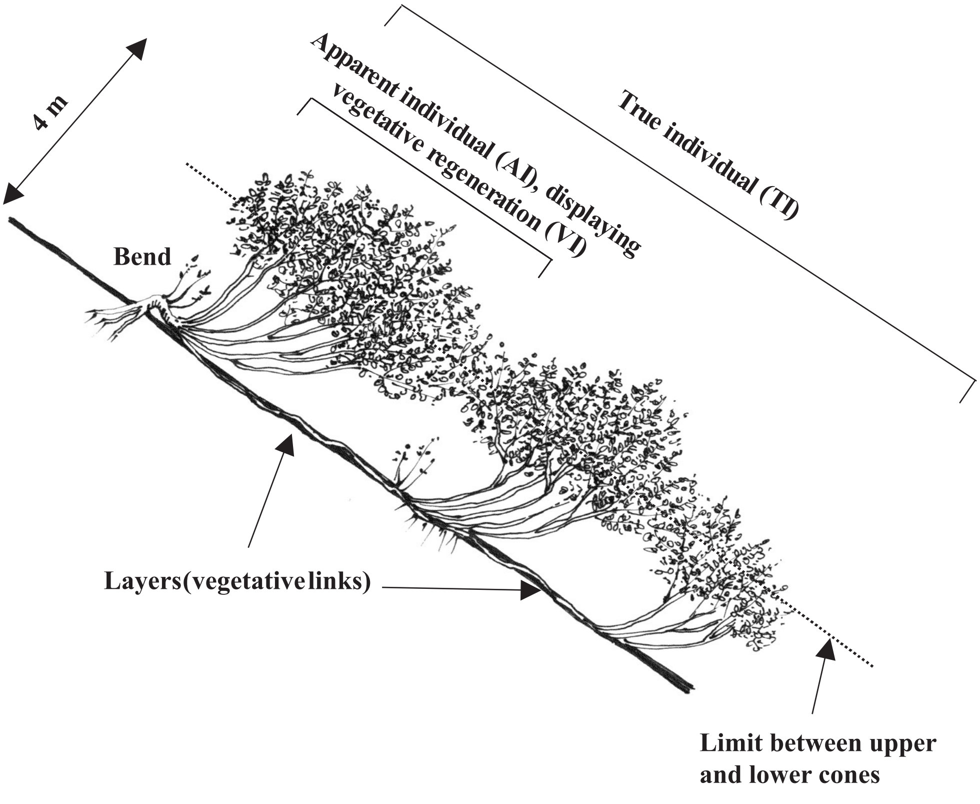

Figure 2. Representation of an *A. viridis* individual in site IV of Le Plan du Pré. The three principal units are "apparent individuals" (AI), they are linked with a vegetative link buried in the litter. The origin of the individual is represented by a bend separating the trunk and the roots.

TI: "true individuals", classified as individuals after assessment of vegetative links;

VI: "vegetative individuals", AI which displayed vegetative links with other AI;

SI: "sexual individuals", AI with no vegetative links; SI + VI = AI.

Considering sexual reproduction, *A. viridis* seeds are available at the beginning of autumn. They are inserted in female cones which are fertilized by pollen from male cones in spring [22]. Both types of cones can be found on every mature individual (monoecious species). Sexual reproduction was thus estimated by the total number of cones (male + female) per individual on twenty-eight individuals. Individual selection was intended to display good representation of VI/SI and sites. Beyond these two constraints, sampling was randomly conducted within the 94 AI previously studied.

Male and female cones were individualized, and were also divided into two categories: "upper cones", located in the upper part of the foliage of individuals, and "lower cones" in the lower part of the foliage (see limit in *figure 2*). These parameters provided different indices of sexual reproduction. The study was carried out in early summer when both male and female cones are fully available [22].

2.5. Data analysis

The relationship between trunk circumference and age of individuals ($n = 68$) was tested by linear regression, as well as the relationship between cone production and age of individuals ($n = 28$).

Non-parametric analyses were preferred to ANOVA and T-tests to determine the significance of the effects of sites and individual reproductive strategy on quantitative variables. This choice was made after considering that the required conditions for performing parametric tests could be not fulfilled. Global effects of sites (four classes of individuals) on lower/upper cones ratio, female/male cone ratio, total number of cones and age of individuals were tested by Kruskal-Wallis analysis, taken as a k-sample non-parametric test. The effects of vegetative strategy (two classes: VI and SI) on the total number of cones and the age of individuals were tested by U Mann-Withney analysis, as a two-sample non-parametric test.

3. RESULTS

3.1. Preliminary dendrometric study

The 68 "test-individuals" were ranged between 3 and 57 years. Their trunk circumference depended significantly on their age. Linear relation (*figure 3*: $R^2 = 0.72$, $P < 0.001$) provided roughly the same explanation rate as logarithmic relation. Upon the basis of this result, age of individuals was estimated by measuring their circumference at 0.5 m above the soil.

3.2. Date of settlement

The age of the 94 AI was ranged between 1 and 67 years and their distribution varied from 12 in site I to 35 in site III. Relation between age and individuals distributed in the four sites was highly significant (*figure 4*: *K*-value = 50.60, $P = 0$). In accordance with Mann-whitney tests, all sites were different from each other considering the age of AI, except for the pair II and III ($U = 391$, $P = 0.115$).

3.3. Cone production

Average production of AI cones (male + female) was significantly related to sites, i.e. age of stands (*figure 5*, *K*-value = 8.51; $P = 0.037$). Mann Whitney tests pointed

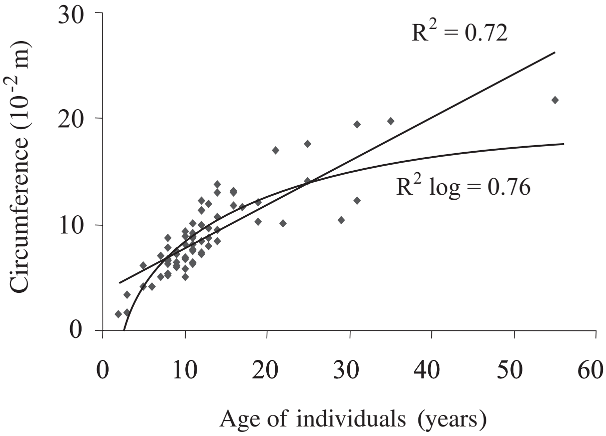

Figure 3. Preliminary results – relations between age and trunk circumference (0.5 m above the ground) of 68 *A. viridis* individuals in Le Plan du Pré, tested with linear and logarithmic regressions.

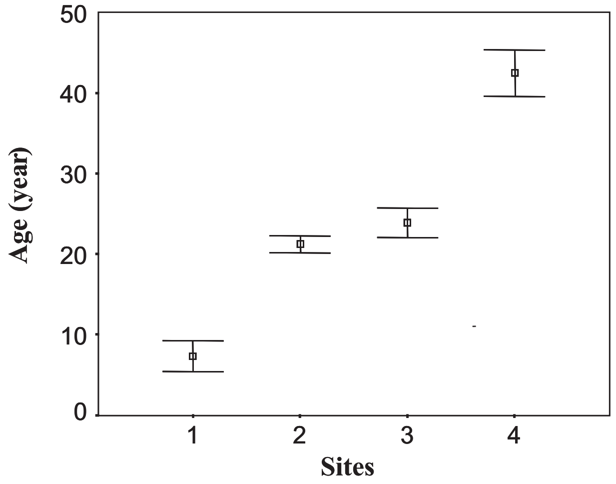

Figure 4. Distribution of *A. viridis* individuals ($n = 94$): relation between age and belonging to sites ($n_1 = 12$; $n_2 = 29$; $n_3 = 35$; $n_4 = 23$), tested with Kruskal-Wallis analysis (K-value = 50.60, $P = 0$). Error bars indicate standard errors.

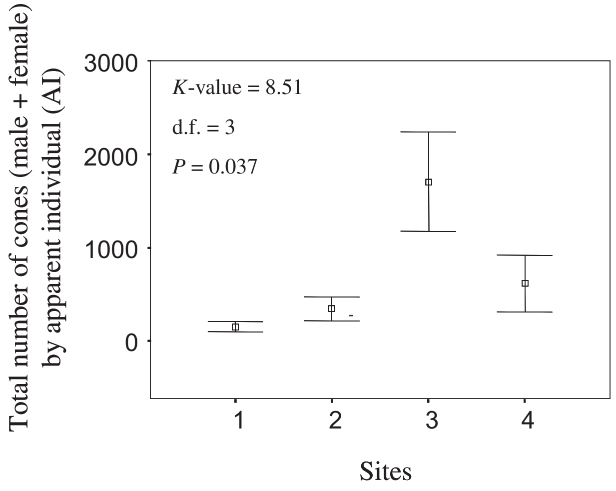

Figure 5. Relations between cone production and individuals related (a) to sites, tested with Kruskal-Wallis analysis (error bars indicate standard errors); (b) to age of individuals ($n = 28$), tested with linear R^2.

out that average cone production in site III was significantly more important than in other sites (see *table II* for significance of Mann-Whitney analyses) which indicated an unimodal relation between cone production and sites. At the same time, the age of AI did not significantly influence cone production ($R^2 = 0.112$, $P = 0.082$).

In contrast, strong evidence of relationship was pointed out between AI classified in sites and female/male cone ratios (*figure 6a*, K-value = 18.09, $P = 0$). In particular site IV yielded a ratio significantly lower than that of sites I and II (*table II*, Mann-Whitney tests), interpreted as a severe deficit in female cone production (ratio = 0.17). The female/male cone ratio in site II was significantly lower than that of site I ($U = 7$, $P = 0.026$). On the whole the relationship was linked to a linear model.

The lower/upper cone ratios of AI also declined significantly with age of sites. It was illustrated in *figure 6b* with a significant Kruskal Wallis test (K-value = 10.41, $P = 0.015$) and in *table II* with an average ratio significantly lower in site IV than in site I ($U = 11$, $P = 0.031$) and site II ($U = 9$, $P = 0.016$).

3.4. Relation between sexual and vegetative indices

A total of 16 VI were found among the 94 AI considered in the study. VI were absent in site I, while 5 VI were recorded in site II, 1 in site III, and 10 in site IV. In order to assess the possible correlation between sexual reproduction and vegetative reproduction, the average number of VI cones (male + female) was matched to the average number of SI. Results on *figure 7a* showed that SI provided a significantly larger number of cones than VI, tested by Mann-Whitney analysis ($U = 132$, $P = 0.022$). On the other hand, testing the effect of age of apparent individuals against their SI or VI classification did not reveal any significant difference (*figure 7b*; $U = 72$; $P = 0.505$).

4. DISCUSSION

4.1. Methodological considerations

The linear correlation observed between the circumference and age of *A. viridis* (*figure 3*) corroborated the fact that circumference assessment can be a useful tool for estimating the age of individuals of several ligneous species without damaging them, as suggested by [29]. More tests at regional level could generate a valuable circumference-age model for *A. viridis* in the Alps. The relative matching of the date of *A. viridis* settlement assessed both by aerial photographs and indirect dendrometric analysis reinforced the efficiency of the dendrometric method in dating this type of site.

Table II: Mann Whitney tests: significance of sexual indices variation between pairs of sites considered as two independent samples. *M*: mean rank values. *U*: number of times a value in group a precedes a value in group b, when values are sorted in ascending order.

Sites		Average cone production				Female/male cone ratio				Lower/upper cone ratio			
a	b	*U*	*P*	M_a	M_b	*U*	*P*	M_a	M_b	*U*	*P*	M_a	M_b
1	2	16	0.318	6.29	8.71	7	0.026	10.00	5.00	17	0.383	8.57	6.43
1	3	0	0.003	4	10	7	0.106	8.00	4.40	8	0.149	7.86	4.60
1	4	25	0.536	7.57	9.22	1	0.000	12.86	5.11	11	0.031	11.43	6.22
2	3	4	0.030	4.57	9.20	8	0.149	5.14	8.40	6	0.073	8.14	4.20
2	4	31	1	8.57	8.44	7	0.008	12.00	5.78	9	0.016	11.71	6.00
3	4	8	0.060	10.40	5.89	1	0.002	11.80	5.11	13	0.240	9.40	6.44

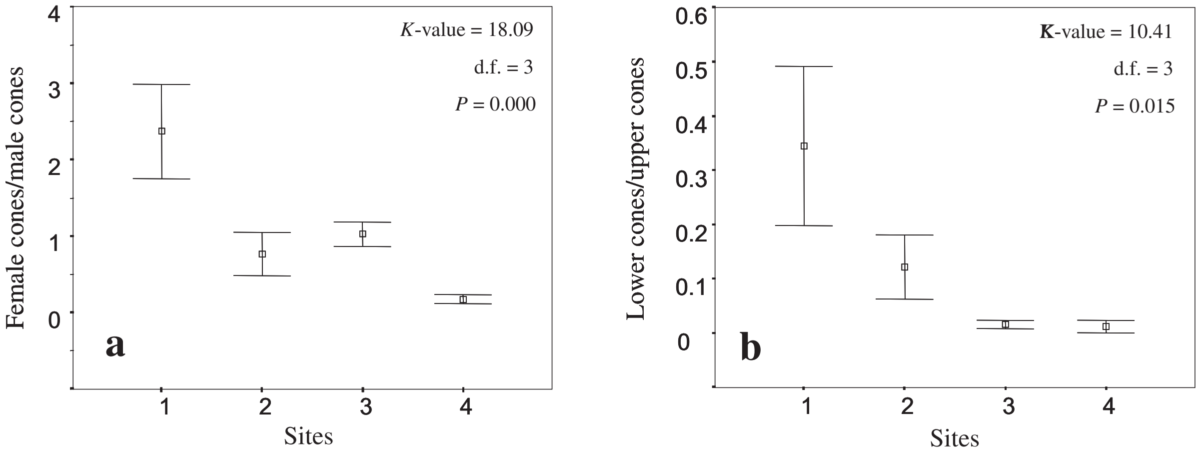

Figure 6. Indices of sexual reproduction strategy in accordance with sites ($n = 28$) – changes (a) in the female/male cone ratio and (b) in the lower/upper cone ratio. Relations tested with Kruskal-Wallis analysis. Error bars indicate standard errors.

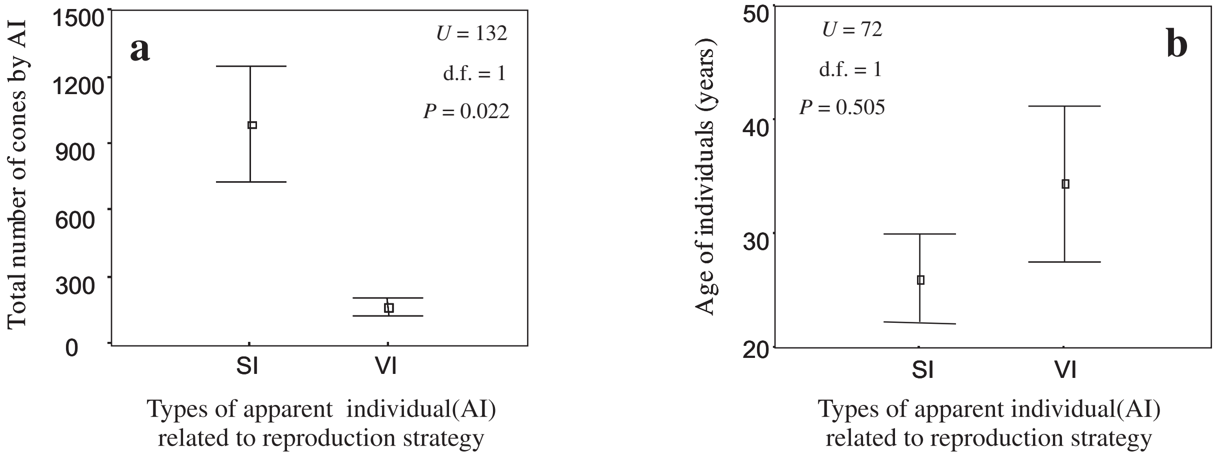

Figure 7. Relations between reproductive strategy of individuals and (a) sexual allocation, (b) age. Error bars indicate standard errors. 1: class of individuals not related to vegetative reproduction strategy ($n = 19$); 2: class of individuals related to vegetative reproduction strategy ($n = 9$). Relations tested with U Mann-Whitney analyses.

Consequently it supported the initial hypothesis considering that the four spatial sites represented a chronological gradient of *A. viridis* settlement.

4.2. Vegetative reproduction

Our results first demonstrated the effectiveness of vegetative regeneration in *A. viridis* stands due to layering. This phenomenon was easily distinguishable from resprouting in that an apparent individual originated by layering (VI) is composed of several trunks clearly separated from its origin, itself composed of several trunks, while resprouting was identified with shoots surrounding the clump of trunks (see *figure 2*). Consequently shape analysis of *A. viridis* individuals is an efficient method of recording the occurrence of layering in this case.

Second, individuals displaying a vegetative reproduction strategy occurred only in sites II, III and IV, that is to say where *A. viridis* settlement had been effective for 20 years at least. Consequently it would be considered that this type of reproduction strategy is not used as a colonization strategy on subalpine grasslands, in contrast for example with several *Ericacae* such as *Vaccinium sp.* or *Rhododendron ferrugineum* [19].

4.3. Sexual reproduction

A. viridis (male + female) cone production depended significantly on the age of the sites (*figure 5*). However this type of relationship is not easily interpretable in that it was unimodal and probably influenced by sampling effects and growth effects.

In contrast, consideration of the female cone/male cone ratio declined linearly with the age of the sites (*figure 6a*), which was interpreted as representing a substantial change in the reproductive strategy of *A. viridis*. This type of phenomenon occurred with a significant decrease in the lower/upper cone ratio from site I to site IV (*figure 6b*). Consequently, on the grounds that no sexual shoots were recorded under the *A. viridis* canopy on the site and more generally under all *A. viridis* stands visited by the authors, we hypothesize that allocation to sexual reproduction in dense alder stands is meant to colonize areas with no canopy cover. For these purposes cone production is promoted at the top of the canopy for the sexual material to be better dispersed. The absence of sexual shoots under *A. viridis* canopy is explained by the light-demanding character of the species [1].

4.4. Changes in resources allocated to reproduction

The significant drop in (male + female) cone production pointed out from SI to VI was interpreted as the occurrence of partial replacement in the allocation to reproduction strategies of *A. viridis* individuals. It was not assignable to differences in age, which was proved to be insignificant. Such a relationship seems to support the constraints and tradeoffs concept [32]: *A. viridis* would have a limited resource rate generated by the subtraction of photosynthesis – respiration. The allocation to reproduction is thus limited and the emergence of the vegetative reproduction strategy illustrated by layering in this study probably induces reduction of the resources allocated to sexual reproduction.

4.5. Colonization and persistence

The chronological occurrence of both reproduction strategies is efficient in secondary successions, as cited for the dominant species in human post-disturbed habitats in Central Europe [20]. Our data did not highlight chronological replacement of reproduction strategies, but hinted that layering was not effective during the first *A. viridis* development stages. Colonization processes are thus dependent on sexual reproduction, which is particularly efficient without ligneous canopy cover [11]. On the other hand, persistence of *A. viridis* cannot rely on sexual reproduction which is inhibited by its own canopy [1]. Yet the life span of *A. viridis* individuals is generally approximately 60 years and relatively homogeneous [23, 30] which in our opinion is not sufficient to justify its lasting distribution throughout a large part of the northern hemisphere. Layering is consequently thought to be the strategy used by *A. viridis* to persist over its individuals life span. We hypothesize that such a regeneration strategy could also help to maintain the inhibition process sensu Connell & Slatyer [8] towards arboreal late successional such as *Picea* sp. cited by Callaway & Walker [5].

Consequently *A. viridis* would take advantage of the availability of two reproduction strategies, both potentially dominant under different constraints. Such functioning is characteristic of pioneer species on primary successions in mountain ranges, which colonize nutrient-poor soils after glacial retreat by using sexual reproduction, and persist with the activation of their vegetative reproduction abilities, as shown for *Epilobium fleischeri* Hochst., an herbaceous mountain species [31]. As for

Rhododendron ferrugineum L. which displays similar characteristics [10]. The *A. viridis* model could thus be considered as an extension of the Stöcklin and Baümler model on secondary successions, i.e. subalpine grasslands in the western Alps.

Considering that the effects of *A. viridis* development on many components of biodiversity is strong [1, 2], such potential persistence of stands is about to induce major changes in the functioning of subalpine ecosystems.

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