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Architecture of the growth and development of the two alpine rhododendron species *Rhododendron hirsutum* and *Rhododendron ferrugineum* as a basis for the verification of the assessed relative and absolute age of aboveground shoots

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Abstract. The two species of alpine rhododendrons: *Rhododendron hirsutum* and *Rh. ferrugineum*, growing in natural conditions (Hohe Tauern and southern Tirol) were studied. The studies were aimed, among others, at the elaboration of a method allowing the assessment of the relative and absolute age of these plants using an algorithm based on the average length of annual increments, and next, at the verification of these data on the basis of the morphological structure of aboveground shoots and the architecture of the growth and development of individuals.

Key words: *Rhododendron hirsutum, Rh. ferrugineum,* relative and absolute age, Hohe Tauern, Tirol, Austria

Introduction

Using the architecture of an individual one may determine the degree of complexity of its morphological structure beginning from the simplest forms, seedlings, to more complicated ones, comprising both aboveground and underground organs. It is characterized by the repeatability of certain modules of growth and development in the life cycle. In a similar meaning this notion was used by Bell and Tomlinson (1980), Hibbs (1981), Remphrey *et al.* (1983a,b), Douglas (1991) and Falińska in her manual (1990). This repeatability (regular sequence of developmental stages) may serve to verify an algorithm allowing the calculation of the relative age of a rhododendron shrub of any species, growing in natural conditions, on the basis of the mean length of the annual increment of shoots (Tumidajowicz and Dawidowicz 1993). This method was applied to two alpine rhododendrons *Rhododendron hirsutum* and *Rh. ferrugineum*. Studies on these species were carried out over about a dozen years in two Alpine regions: Hohe Tauern and southern Tirol (Fig.1). Both examined species grow only in the Alps, above the upper forest limit at altitudes of 1,450-2,320 m a.s.l. (Fig. 2a,b). They show the similar type of growth but differ in the size and habit of shrubs, flowering period, geographical distribution (Fig. 3) and habitat conditions. *Rhododendron ferrugineum* is a calcifuge species growing in the whole Inner Alps and *Rhododendron hirsutum* is a calciphilous species growing locally in the eastern and central Outer Alps.

The aim of the studies conducted in the Alps on the two rhododendron species was: 1) to elaborate an

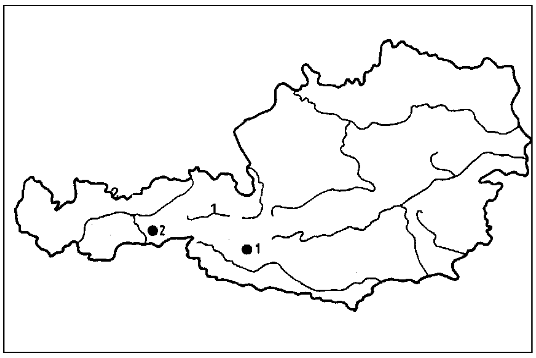

Fig. 1. Location of study areas in the Alps: 1 - Hohe Tauern, 2 – southern Tirol.

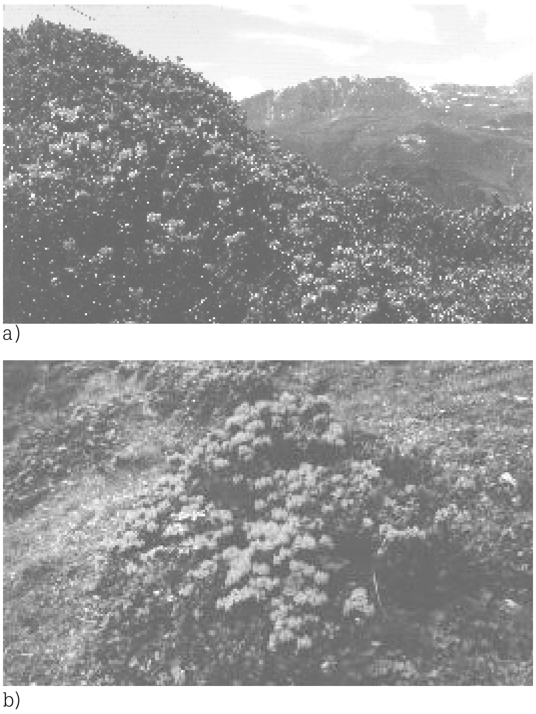

Fig. 2. a) Patch of *Rhododendron ferrugineum* at an altitude of 2,100 m a.s.l. in Tirol. b) *Rhododendron hirsutum* at an altitude of 2,040 m a.s.l. Möslalm (Tirol).

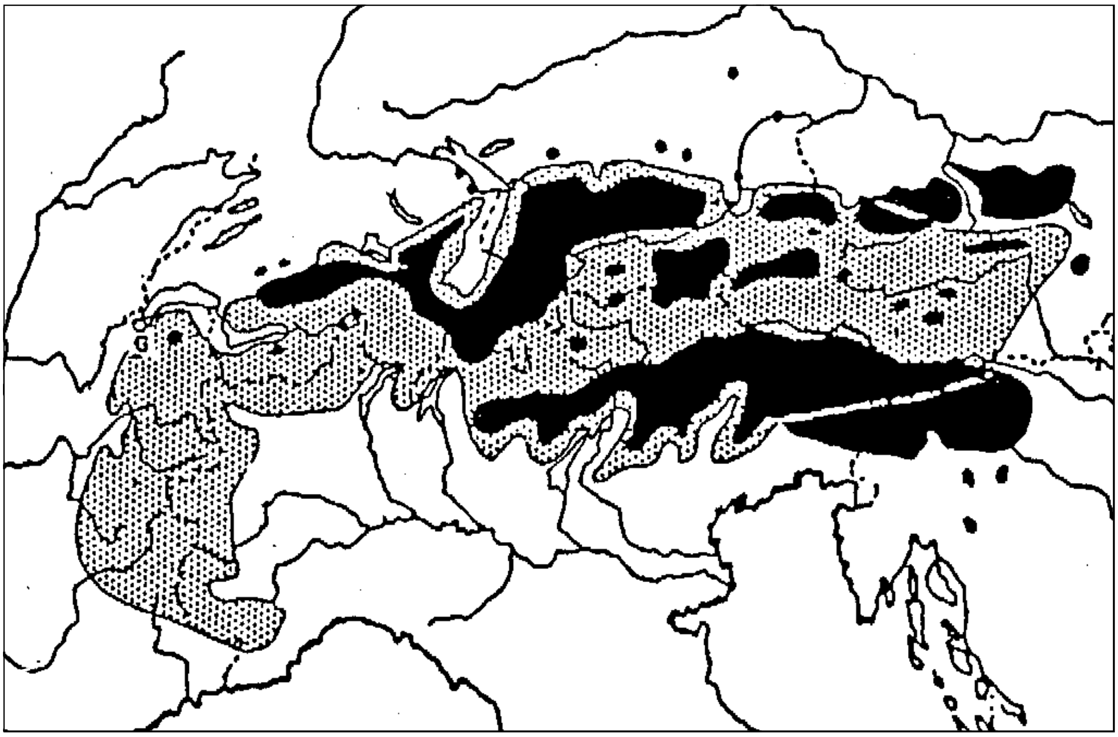

Fig. 3. Geographic ranges of two rhododendron species in the Alps: 1 – *Rhododendron hirsutum* (black areas), 2 – *Rhododendron ferruginerum* (dotted areas) (Ozenda 1988).

algorithm allowing the determination of relative and absolute age (young individuals) of any shrub growing at different altitudes in natural conditions, 2) to verify the results obtained on the basis of the morphological analysis and architecture of particular shoots of an examined shrub, or e.g. one branch, 3) to make an essay at the assessment of age on the basis of: size and structure of particular individuals or their groups at determined altitudes, and 4) to calculate the mean age of populations at selected plots.

Material and methods

Studies on rhododendrons were carried out in the Alps at some tens of localities (7 in Hohe Tauern and 20 in southern Tirol) at different altitudes (1,450–2,320 m a.s.l.) and exposures in the years 1985-87, 1991-92, 1996-98 and 2000. The studies were aimed to elaborate methods allowing the determination of relative and absolute age of long-lived individuals from *Rhododendron hirsutum* and *Rh. ferrugineum* populations, based on an analysis of the length of annual increments of aboveground shoots. To this aim the samples of aboveground shoots were collected randomly along a transect following a contour line. All individuals, occurring on that line, irrespective of their size, were sampled. The aboveground shoots were also collected with the help of a method named "all from a given plot" (from each individual a determined number of the tips of shoots were collected). Particular samples comprised 30–356 twigs collected from each locality. Each sample was analyzed in a following way: measured was the length of annual increments, beginning from the last year, and a distance between successive branches. This allowed the determination of a mean frequency with which a given shoot flowered and checking whether the mean increment did not differ much from the calculated value for the last few years. The number of flowers on the examined twig in a given year, the number of buds for the following year, scars left by flowers from the preceding year and earlier years were noted (Table 1). Counted were also all the leaved ends of shoots, named in this paper "sterile rosettes", which in the following vegetation season would not pass the generative cycle. Simultaneously, the architecture of the growth and development of individuals from the youngest stages (seedlings), through a juvenile stage, to generative and senile stages was examined. Altogether several thousand sketches of particular shoots and all branches were made and their relative or absolute age (juvenile individuals) was determined. At some tens of selected plots the area occupied by 520 shrubs were computed with the help of a planimeter; in this way the resources of the plants per a determined area were calculated.

Results

1. Development of individuals: small and big life-cycle

Seeds collected in the Alps in autumn 1985 and sown on Petri dishes in January 1986 germinated 2 weeks later, reaching in January 1987 from 45% to 65% of the sprouting. Almost all seedlings survived over 1 year in a refrigerator (watered only with distilled water). The schematic course of the growth of an individual from a seedling to the first florescence is shown in Fig. 4. The further development of juvenile individuals, observed in the natural environment, depends on habitat conditions, type of substratum, density etc.(Fig. 5). In

Species	Date of collection, locality	Numb.of examined branches	Total numb. of branches of examined shrubs	Maxim. length of single branch	Mean length of single branch	Number of "sterile rosettes"	Flowers or flower buds in years:				
							1984	1985	1986	1987	1988
Rhododendron hirsutum	2 Aug. 1986 Feldereral 1,701 m a.s.l.	30	370	110	49	974	27	46	90	103	
Rhododenron ferrugineum	11 Sept. 1986 Rauris 1,720 m a.s.l.	30	810	169	66	814	159	69	80	106	
Rhododendron hirsutum	8 Sept. 1986 Krumlthal 1,540 m a.s.l.	30	328	189	92	1,016	58	80	152	112	
Rhododendron ferrugineum	27 Aug. 1986 Laponesalm 1,500 m a.s.l.	30	221	97	62	1,053	38	56	183	122	
Rhododendron irsutum	19 Sept. 1987 Krumlthal 1,640 m a.s.l.	30	470	150	72	1,413	42	97	112	88	189
Rhododendron ferrugineum	7 Aug. 1992 Möslalm 2,040 m a.s.l.	25	305	117	83	1,104	1*	6**	30***		
Rhododendron ferugineum	8 Aug. 1992 Naviser Joch 2,260 m a.s.l.	15	20	58	22	195	3*	1**	4***		

Note * - in 1991, ** - in 1992, *** - in 1993

Table 1. Structure of examined branches, described by their maximum and mean length, number of "sterile rosettes", flowering shoots and flower buds in successive years.

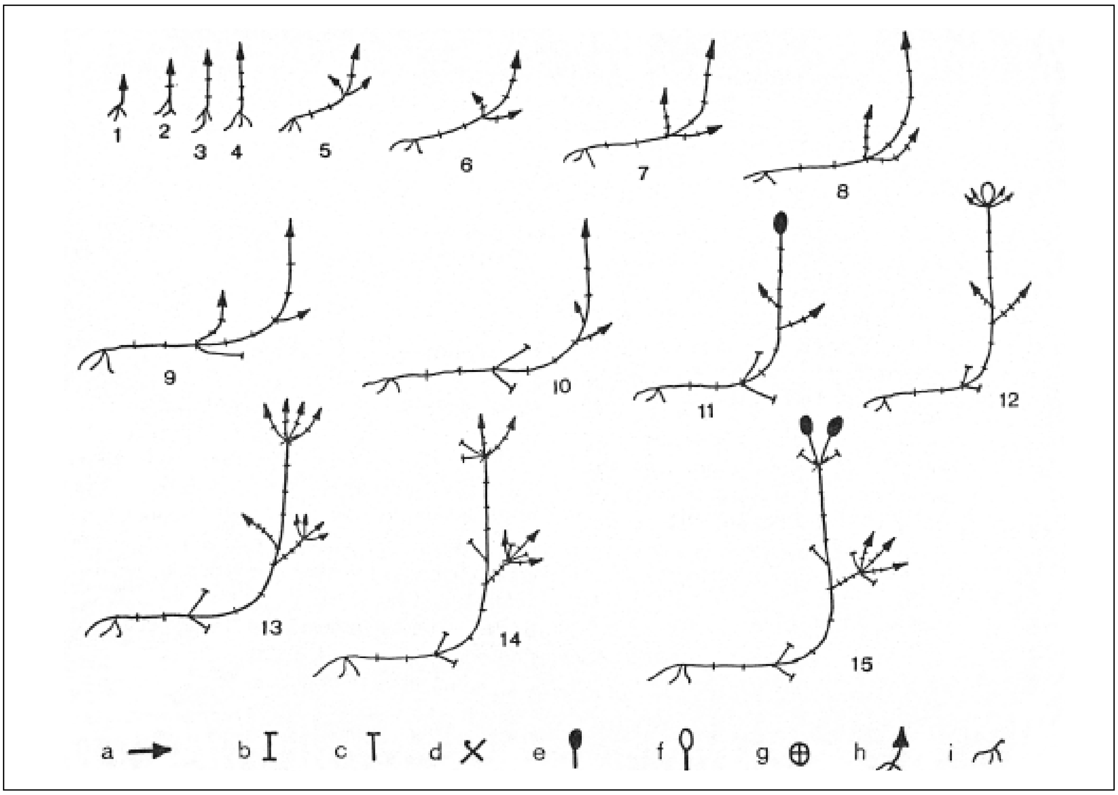

Fig. 4. Scheme of the growth of *Rhododendron hirsutum* from seedling to generative stage. Symbols used in schemes and simplified drawings of single shoots, branches and whole individuals: **a**–direction of growth of shoots ended with leaf rosette, **b**–segment of annual increment, **c**–shoot without, annual increment (withered), **d**–scar left by flowering shoot, **e**–winter flower bud, **f**–flower, **g**–flower bud which withered before flowering, **h**–seedling, **i**–underground organs (roots).

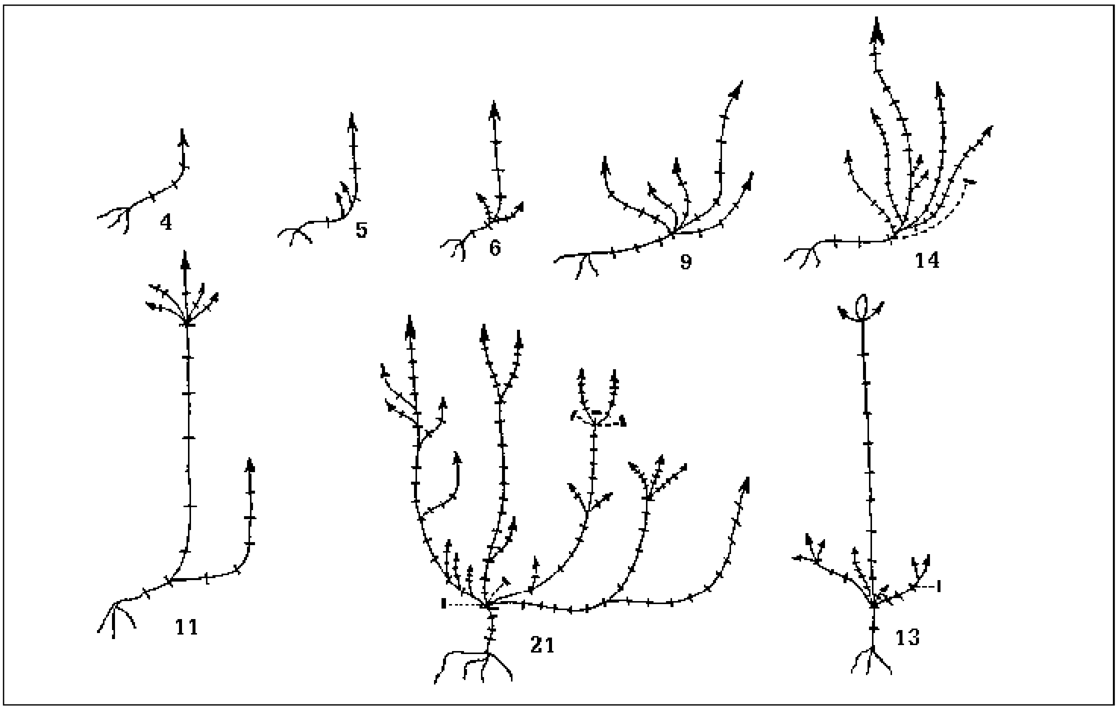

Fig. 5. Schemes of the growth of individuals of *Rhododendron hirsutum* and *Rh. ferrugineum*: different types of branching (numbers denote absolute age of an individual).

the initial period of the development of juvenile individuals a considerable variation of the development of shrubs may occur, from simple, not branched and often procumbent forms to raised shoots with lateral branches, originating already in the 2nd or 3rd year of life (Fig. 5). On the basis of her own observation, the Author has found that the first individuals of generative origin flower between the 12 and 15 year of life. Flowers originate at the tip of a shoot, ending its further growth after shading blossoms. However, new leaved shoots, in the number of 2-7, appear under inflorescences. In successive years, part of them will die, but two of them most often remain, assuming the function of leading shoots. It is the type of pseudodichotomic many-axial growth, which after many years conduces to the formation of a dichotomic fan-shaped shoot. The withering of an inflorescence is marked by a scar in the form of a small tip (torus of inflorescence); lateral branches originate from shoots under the inflorescence (Fig. 6). Part of these shoots wither in successive years; on the remaining ones the first flowers appear after 3-4 years at the earliest (Fig. 7). The shoots blossom with various frequency amounting to 2.79-3.43 years (3.13 years on the average). Each year, in summer, new buds appear on the tips of shoots; next year, part of them will produce the new segments of aboveground shoots together with leaves, and part (usually 1–24%) will flower and end the growth of a given shoot. Under the inflorescence new shoots will originate, forming lateral branches, and this sequence will repeat in successive years on the different fragments of shoots. In this way the kind of a fan will originate; each year this fan loses some withered lateral branches (a few to a dozen or so years old) and the remaining ones will form successive lateral branches. The size of these fans is determined by habitat conditions, e.g. the availability of light, as indicated by field observations. The largest shrubs have many branches but the span of particular fans is rather narrow. Branches within the shrubs have usually less green tips. In the most abundantly flowering shrubs only part of the ends of shoots blossom each year; at the utmost no more than 1/4 of all the ends (Tumidajowicz unpubl.). Already in autumn one may tell how many flowers will be next year. It is a very characteristic sequence in which every few years some terminal shoots with inflorescences end their growth, and new shoots under the inflorescences take over their role. *Rh. ferrugineum* individuals keep leaves for successive 2–2.5 years, i.e.

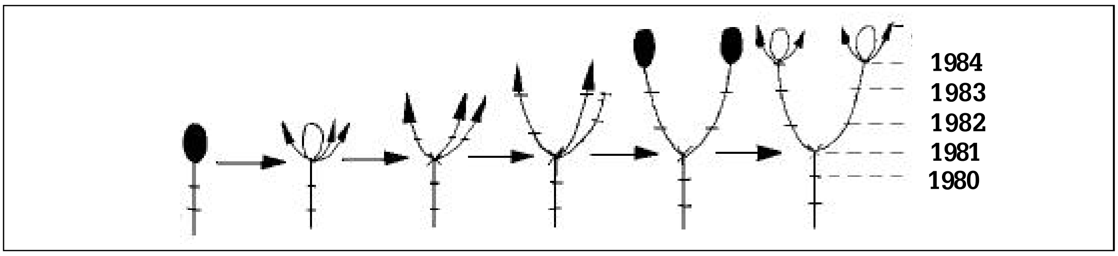

Fig. 6. Scheme of the growth of a generative shoot during 4 years.

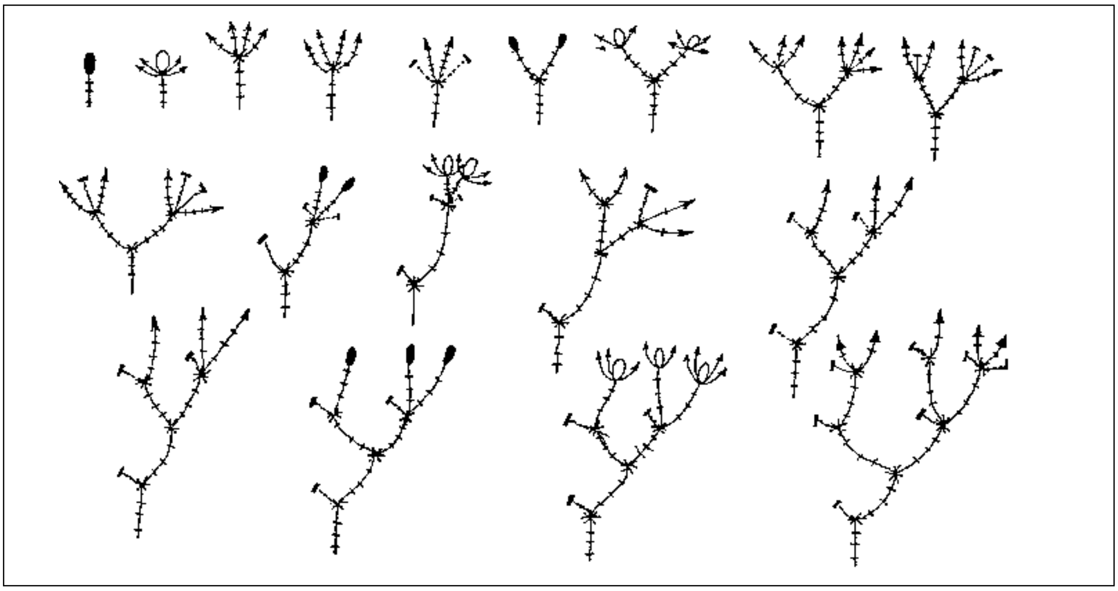

Fig. 7. Schematic development and growth of generative and vegetative shoots in many-years' aspect.

longer than *Rh. hirsutum*, which keeps leaves for about 1.5 year. Rhododendrons are long-lived plants. The long life of these plants is connected with the way of their regeneration. The older are shrubs, the more branches they have. Practically each of them may function. The withering of one or even several branches does not cause the death of the whole shrub. According to the definition, the big life-cycle comprises a period from the germination of a seed to the death of the whole individual – genete. Hence, the big cycle may last hundreds of years and even a thousand years.

2. Assessment of relative age on the basis of permanent aboveground organs

All investigations were aimed at the observation of certain qualitative and quantitative regularities in the examined rhododendron populations in the Alps, allowing the determination of relative age of these plants.

The elaboration of the algorithm based onthe material originated from some tens of populations growing at different altitudes and in different regions of the Alps allowed one to obtain coefficients of the mean annual increments of aboveground shoots for the whole range of the occurrence of rhododendrons in the Alps. The procedure of calculating the relative age of aboveground shoots was shown in the paper by Tumidajowicz and Dawidowicz (1993). The authors devised a formula allowing one in a simple way to determine the relative age of any shrub (W):

$$Ww = K/k \quad (1)$$

$$k = 1/n\ (k1 + \ldots\ldots + kn) \quad (2)$$

where:

K = length of the longest shoot of examined shrub

k = mean length of annual increments,

i.e. $k1 + \ldots\ldots + kn$, (3)

n = number of measurements in particular samples

When the length of branches K is known but it is impossible to measure accurately annual increments in determined shrubs or populations at a given locality, one may accept as k an approximate value equal to 1.07 for *Rhododendron hirsutum* and 1.34 for *Rh. ferrugineum*. These are coefficients, which introduced to the formula, produce the approximate relative age of a given rhododendron shrub (Tumidajowicz and Dawidowicz 1993). The calculated relative age of shrubs, i.e. the age of the aboveground shoots of *Rhododendron,* need verification. Attempts at counting annual rings on discs sampled from both the hypocotyl and other parts of aboveground shoots, whose age was known, did not produced satisfactory results because the observed (under the magnifying glass) pattern of cells on the cross-sections of shoots did not allowed one to distinguish particular annual rings of increments. It was proved that the best method of the verification of the age assessed using the formula, was the architecture of particular shoots (branches) and the knowledge of the processes of growth and development in the rhododendrons from the earliest stages of an individual growth. The next step was an essay at the determination of the age of their genetes, reaching even hundreds of years, and the use of these data in modeling the processes of many-hundred-years' life-history of these plants (Dawidowicz *et al.* 1995).

3. Simple and complex architecture of individuals

The architecture of rhododendrons may be considered in a few categories:

3.1. Development architecture of an individual from a seedling to the first generative stage (Fig. 8)

Individuals entering for the first time into the generative stage may be 12–15 years old. Their main shoot will flower not earlier than about 3 years later and that is why each consecutive lateral shoot will register the age of a given individual. If in juvenile generative individuals the first florescence is found,

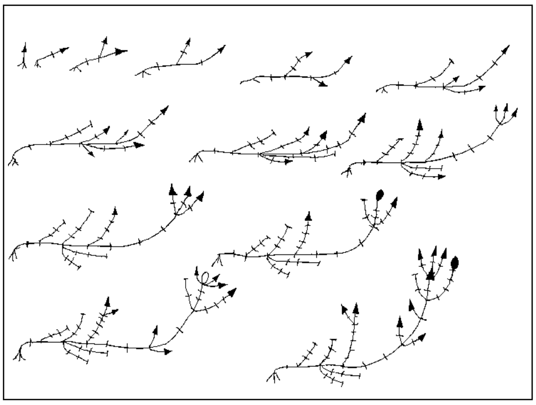

Fig. 8. Scheme of the growth of *Rh. hirsutum* individual and formation of lateral shoots, not preceded by flowering, which will never function as main shoots.

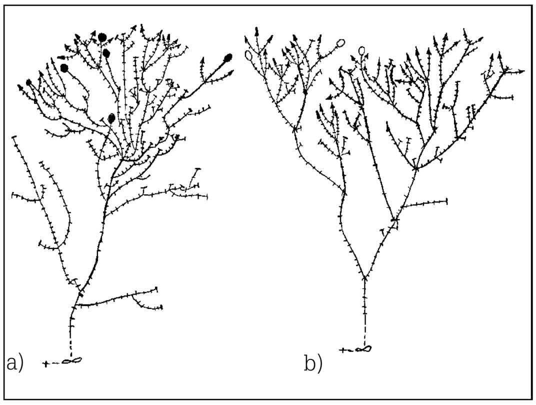

Fig. 9. Schemes of 40–45 year-old branches: a) *Rhododendron hirsutum* b) *Rhododendron ferrugineum.*

then one may assess their absolute age using the formula:

$$WB = (a \times b) + c$$

where:

a = mean number of lateral shoots from several series of one branch
b = coefficient 3.13 (mean frequency with which a given shoot flowers)
c = age in which individuals enter the generative stage (± 12 – 15); it is absolute age.

Usually, there are few individuals such as these in an old population. The morphology of the very aboveground shoots is very useful for the determination of this age (Figs. 4, 5, 8).

3.2 Architecture of a single aboveground shoot (branch) (Figs. 9 a, b and 10 a, b)

Most differentiated, in the terms of architecture, are the apical, youngest parts of branches (Fig. 11 a, b, c). In the oldest fragments of branches, the aboveground shoots between 30 and 40 years of life become with time only a single shoot. Examining the morphological structure of these shoots, one may obtain information on e.g. the percentage of sterile, flowering and withering shoots in a given year and in preceding years (Table 1). To calculate the age of these branches, one should measure annual increments beginning from the youngest ones and going down to the base of a branch. If the measurements are slightly divergent, one should accept a mean from these measurements. Almost all shrubs, after reaching the generative stage, flower each year with different intensity depending on altitude and other factors.

Counting scars which indicate the florescence of the shoot of a given series (this measurement should be repeated for a few series of the same branch), we obtain a value showing the years of flowering and multiplying this value by coefficient 3.13 (frequency of the flowering of shoots), one may obtain the approximate age of a given shrub or branch (Fig. 12). All lateral shoots show how many times has a given branch flowered during its life, which is the percentage of seed capsules it has set, and how many seeds it has produced. For each investigated locality the percentage of seed capsules and the mean production of seeds per one capsule was calculated. This information was used for the construction of mathematical models showing the life-history of rhododendrons, to which strict mathematical rules were applied (Dawidowicz and Tumidajowicz 1992; Dawidowicz *et al.* 1995).

3.3 Architecture of aboveground shoots, which became underground organs (Fig. 13)

Both species of rhododendrons: *Rhododendron hirsutum* and *Rh. ferrugineum* are long-lived plants, hence it is difficult to assess their absolute age. Rhododendrons owe their long life to the characteristic development of aboveground shoots and a very slow growth, on

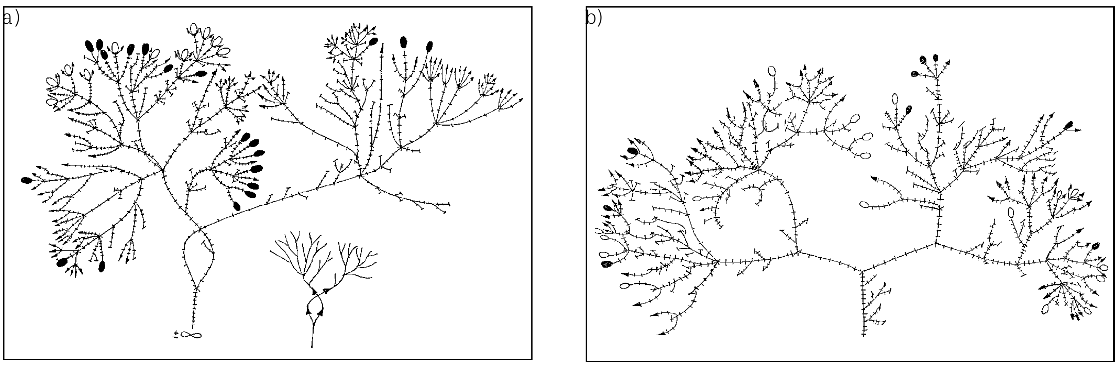

Fig. 10. Schemes of 40–50 year-old branche, a) *Rhododendron hirsutum,* b) *Rhododendron ferrugineum.*

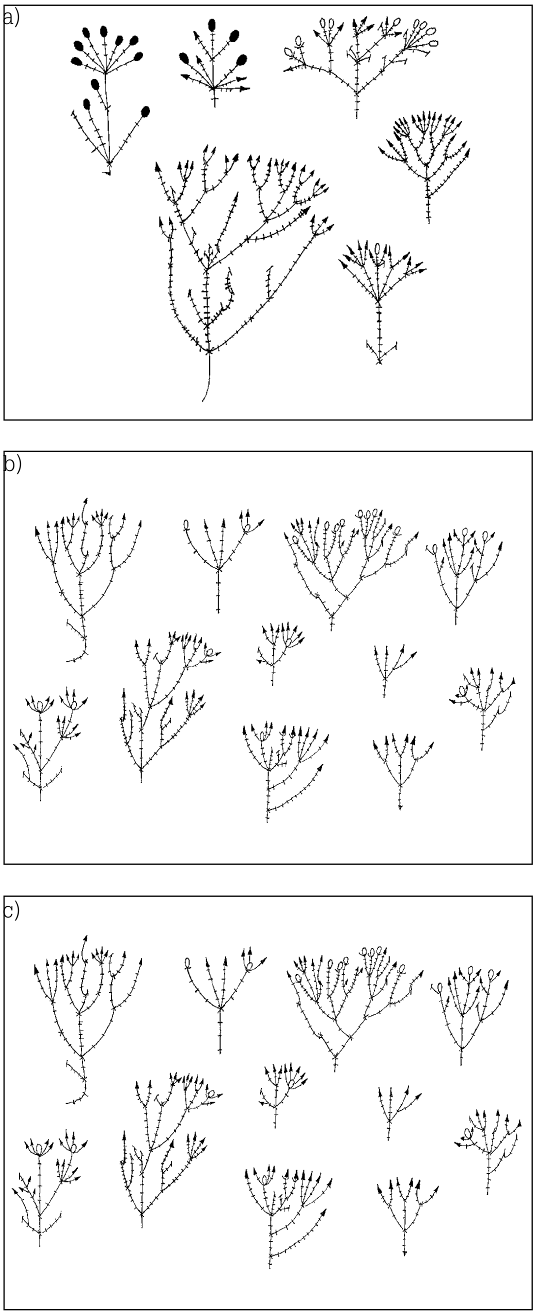

Fig. 11. Differentiation of the tips of terminal shoots of branches included in measurements of annual increments: a, b) *Rhododendron hirsutum,* c) *Rhododendron ferrugineum.*

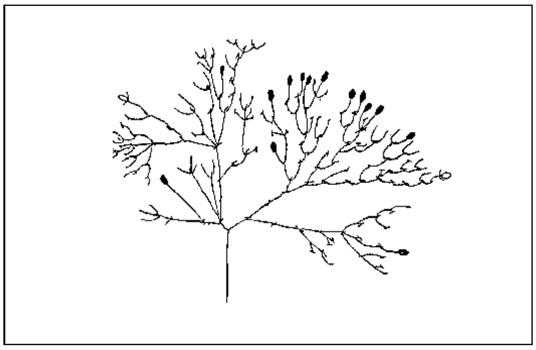

Fig. 12. Scheme of a branch with flowering scars in many-years´ aspect.

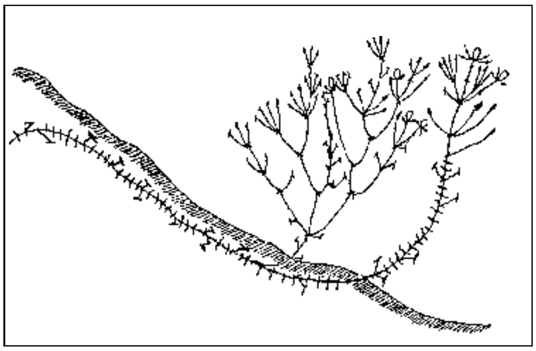

Fig. 13. Scheme of taking roots by aboveground shoots, secondarily underground, under the sward surface.

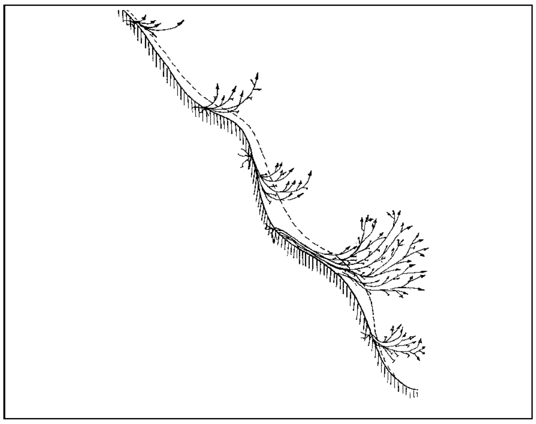

Fig. 14. Scheme of rhododendrons' growth, depending on the inclination of slope and the related phenomenon of the transformation of aboveground to underground

average 1.07-1.34 cm per year, a big resistance to any extreme atmospheric conditions, such as freezing and mechanical damage, e.g. by grazing cattle etc. Their aboveground organs, as shown by earlier studies (Tumidajowicz and Dawidowicz 1993), may function more than 100 years. Rhododendron shrubs growing on slopes, mountain meadows and rocky places are characterized by a more or less horizontal growth. Their aboveground shoots bend depending on slope inclination. These long-lived, procumbent aboveground shoots of rhododendrons are gradually being covered with rock debris transported with melting snow from the higher parts of mountains. The shoots are also being overgrown by sward which in spring and after heavy rains is trodden and showed down by grazing cattle; in this way, these aboveground shoots become with time underground (Fig. 14). Thanks to that phenomenon rhododendrons are long-lived plants and their genetes are practically long-lived. In one of the alpine meadows the author managed to prepare an alive underground shoot, which originally was aboveground. Its length was 3.80 m, of which only 68 cm were above the ground, while the rest, i.e. 3.12 m remained under the soil and rocky debris; this branch was probably over 200 years old.

3.4. Spatial architecture of shrubs depending on exposure, inclination, altitude, structure of sustratum etc. (Fig. 15)

Rhododendron ferrugineum shrubs growing in the lowest parts of the Alps at altitudes of 1,600–1,700m a.s.l. usually have the largest annual increments but

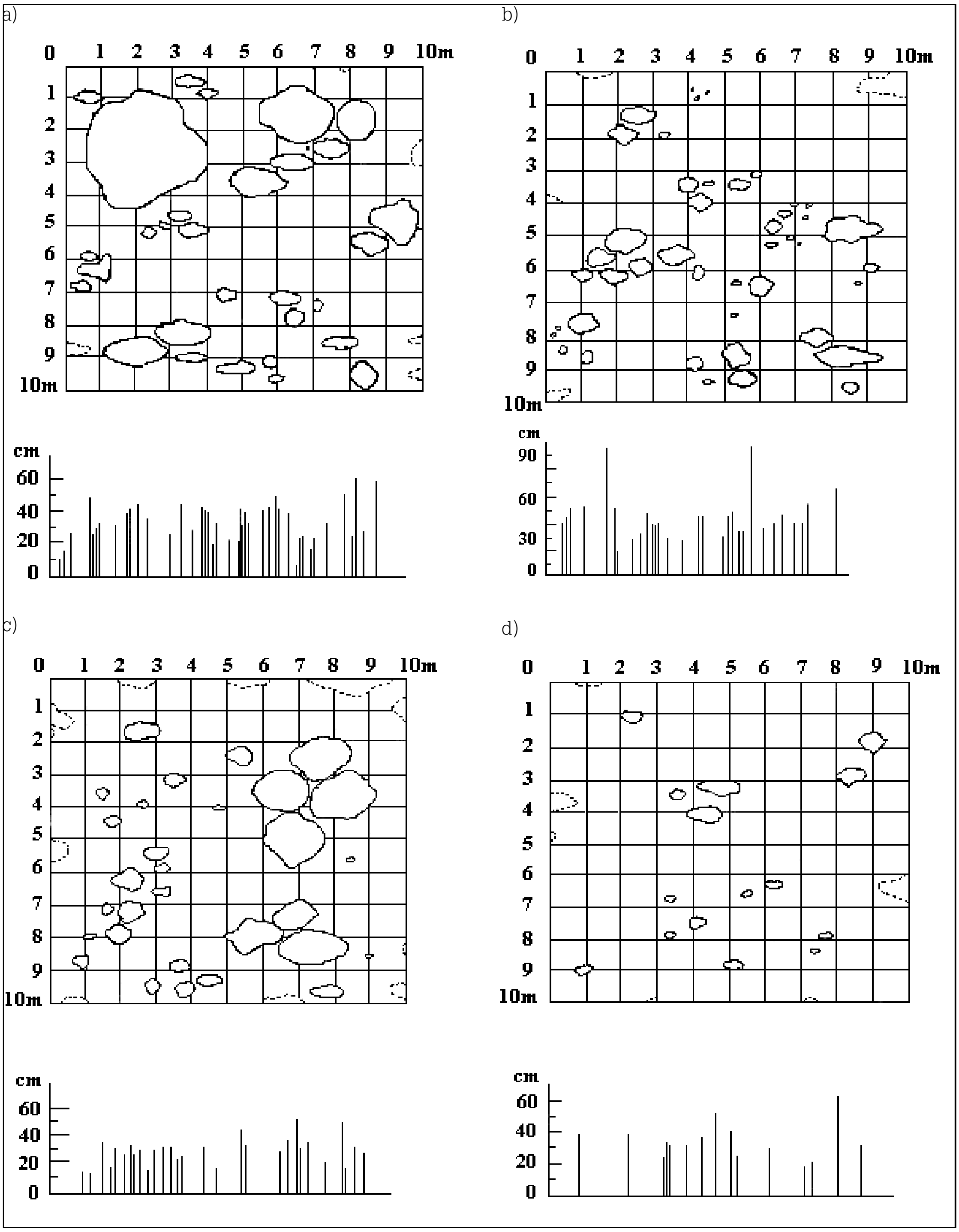

Fig. 15. Area occupied by *Rhododendron hirsutum* and *Rh. ferrugineum*, as computed with the help of a planimeter, for which the height of individuals above the ground and mean relative age of each population were calculated: a) *Rhododendron ferrugineum* Kolm, Saigurn 1820 m a.s.l., mean age 41 years, b) *Rhododendron ferrugineum* Hohalm – Rauris 1720 m a.s.l., mean age 50 t, c) *Rhododendron hirsutum* Krumltal 1640 m. a.s.l., mean age 60 years, d) *Rhododendron hirsutum* Krumltal 1550 m a.s.l., mean age 85 years.

the relative age of their aboveground shoots does not exceed 60–80 years. The oldest individuals one could found were over 120 years old (Tumidajowicz unpubl.). In the Navis valley (soutern Tirol) above 2,100–2,300 m a.s.l. *Rhododendron ferrugineum* shrubs have the smallest size; these are usually relatively small one-shoot shrubs with several lateral branches. Their mean annual increment does not exceed 0.5 cm. The length of annual incrementsin *Rhododendron hirsutum* and *Rh. ferrugineum* in the whole area of the Alps differs depending on altitude, particularly when one compares the highest and lowest situations. For that reason it is advisable to perform at least some tens of measurements in individual study areas to obtain the more precise coefficients of annual increments. To make only approximate measurements, one may use coefficients calculated for the whole of the Alps. Also the size and spatial structure of the whole shrubs of the investigated populations in a given area are useful for the assessment of age (Fig. 15). On the basis of the structure of shrubs

Fig. 16. Horizontal projections (bird´s eye view) of *Rhododentron hirsutum* and *Rh. ferrugineum* populations at different altitudes 1540-2300m a.s.l. Characteristic horizontal structures of these shrubs at different exposures and inclination of slopes in the Alps..

Fig. 17. Cascade-like growth of many-hundreds' year-old individuals of *Rhododendron ferrugineum*.

(horizontal projection of their branches), measuring their length and width, one may calculate the area occupied by particular individuals or their groups and arrange them into size classes. In this way one may calculate the age of each individual or their group, and next, the mean age of the entire population. Examining the distribution of rhododendron shrubs at different altitudes, one may also draw conclusions about the age of these populations, knowing e.g. the mean length of annual increment. The size of these groups and their distribution in the area shows their great differentiation. The groups of rhododendrons, making in places large patches, are composed of many long-lived individuals, now not distinguishable (Fig. 16). Also the cascade-like aboveground shoots streaming on rocks testify to the long-life of these plants (Fig. 17). On the basis of the size of *Rhododendron hirsutum* and *Rh. ferrugineum* shrubs, particularly the size of fans, the number of the ends of sterile and flowering shoots (Table 1), an altitude at which they occur, the length of annual increments, the architecture and the number of branches, one may conclude about an approximate absolute and relative age, making the use of both formulas and all direct and indirect methods that were discussed above.

Discussion

During the last years the architecture of individuals, both the underground and above ground organs, particularly of shrubs and dwarf-shrubs, became one of the methods employed to solve many dynamic problems in plants, such as the assessment of the rate of growth of rametes and whole individuals, and their relative and absolute age, or the registration of morphological changes of individuals in time, observations of the colonization of new areas, e.g. in *Arctostaphylos uva – ursi*, whose particular segments of annual increments allow the precise assessment of the rate of colonization (Remphrey *et al.* 1983a). The repeatability and regularity of these structures allowed the construction of a simulation model, which showed the growth of samples similar to those observed in the nature (Remphrey *et al.* 1983b).

The regularity of these structures was described in rhizomorphic plants, such as *Medeola virginiana, Oxalis corniculata, Alpinia speciosa* and others highly-organized species and used for the simulation models of branching (Bell and Tomlinson1980). One of the plants of the clonal type of growth, for which the simulation model of the growth of genete was also constructed on the basis of the architecture of underground organs, was *Dentaria glandulosa* (Dąmbski and Tumidajowicz 1983, 1985; Tumidajowicz and Dąmbski 1984). The repeated type of growth was also observed in three North-American species of *Tsuga*, forming structures containing elements of the series of architectonic models (Hibbs 1981). The method of architectonic analysis was used for *Salix setchelliana* (Douglas 1991). The architecture of this species was examined to find whether the existing parameters of the clonal growth differ from the factual age. It appeared that the examined clones could be arranged according to age on the basis of their size. To the architectonic structures of the repeated model of growth belong the two rhododendron species, *Rhododendron hirsutum* and *Rh. ferrugineum*, in which one may observe the repeating from year to year sequence, allowing the assessment of the age of their rametes.

In the investigated populations the age of perennial plants play an important role and it is one of these population characteristics which are important for the interpretation of their life-history and forecasting their future fate. In population studies the age of perennial plants is most often neglected or reduced to rough estimates, such as: stages of age (e.g. seedlings, "older seedlings", juvenile, immature, virginile, generative, senile plants, without the more precise assessment of age in years), or classes of size, which is also only certain approximate value. In case of rhododendrons this division is difficult to apply in practice. On the other hand, one may use size classes, defining for each of them the relative age of a given class, making the use of the proposals presented in this paper. The knowledge of the morphological characteristics of plants is essential for the application of the demographic theory in the plant ecology (Falińska 1996). Individual methods enabling the separation of individuals growing in natural conditions, determination of their relative or absolute age, the period of fertility, its intensity, and the same determination of the length of life of particular genetes, i.e. the big life-cycle, are still lacking. This forces us to search for other methods. Studies on the age structure and population dynamics of *Rhododendron ferrugineum*, undertaken in the north-western French Alps by Pornon and Doche (1995) were limited to the assessment of the size of an area occupied by a given class, and the size of class was identified with age. Similarly Mazyrenko (1980), investigating rhododendrons in Far East, determined their age, creating the so-called age classes and using to this aim the size of shrubs or the length of rametes. A need for evolving the more precise and reliable methods of the determination of age of perennial plants, to which belong *Rhododendron hirsutum* and *Rh. ferrugineum*, which would be useful for further population studies on these plants, was the aim of the present work. The paper presents the methods of the determination of relative and absolute age of any rhododendron shrubs which have been growing at natural localities in the Alps for many thousands of years.

The first method allows the determination of relative age of aboveground shoots, using the mathematical formula. It is relatively simple, does not demand much labor. It is particularly useful for the population-demographic studies of these plants.

The other method is a supplement to the first one. It refers to the detailed morphological analysis from the youngest annual increments of aboveground shoots, taking into account all sequences of the development and growth. Examining all development stages of individuals from seedlings to senile individuals, dying within the compass of many decades, one may obtain rather precise information. This method offers a possibility to verify the first method or may constitute an independent technique. At the assessment of age, one should also take into account the third method, which may be used for the analysis of the size of shrubs, i.e. the horizontal projection of their branches on the occupied area. To the advanced age of the genete, i.e. the length of the big life-cycle of rhododendrons testifies above all the number of branches – rametes, amounting even to 500 - 8. The more branches, the older is an individual, whose absolute age may be more than 1,000 years. The presented methods were verified in population studies on the age structure in *Rhododendron hirsutum* and *Rh. ferrugineum* in the Alps. The three described methods constitute a whole. The separate problem may be the absolute age of individuals that are older than 15 years, in which the time of the first flowering is difficult to determine. The further model studies of branching processes, based on empiric parameters and using mathematical rules and calculus of probability, may help to solve these problems (Dawidowicz and Tumidajowicz 1992; Dawidowicz *et al.* 1995).

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