Ecophysiology of after-fire resprouts of *Arbutus unedo* L.

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Abstract. Plant-water relationships, leaf morphology and concentrations of pigments, proline, soluble sugars, anthocyans and nutrients of after wildfire resprout leaves of *Arbutus unedo* L. were compared with those of same age sprout leaves in unburned plants. In spring samples, several significant differences appear: after-fire resprouts showed some juvenile characteristics, such as high tissue elasticity, small cells, low specific leaf weight, high Chla/Chlb ratio and a high anthocyan content; on the other hand, unburned plants showed drought tolerance characteristics by osmotic adjustment and lower tissue elasticity, larger cells, higher specific leaf weight and lower Chla/Chlb ratio. In fall samples, both kind of shoots showed drought tolerance by osmotic adjustment, low tissue elasticity, large cells and high specific leaf weight. Results show that after-fire resprouts have, at the beginning of their development, higher morphological and physiological plasticity that the new sprouts of unburned plants.

Resum. *Ecofisiologia dels rebrots d'*Arbutus unedo *L. després del foc.* Es comparen les relacions hídriques, la morfologia foliar i les concentracions de pigments, prolina, sucres solubles, antocians i nutrients de les fulles de rebrots d'*Arbutus unedo* L. després d'un incendi, amb iguals característiques de les fulles de brots de plantes no cremades de la mateixa edat. A les mostres de primavera apareixen diverses diferències significatives: els rebrots, després del foc, presenten característiques juvenils, com són alta elasticitat dels teixits, cèl·lules petites, baix pes específic foliar, alta relació Chla/Chlb i un elevat contingut d'antocians; d'altra banda, les plantes no cremades presenten característiques de tolerància a l'eixut per ajustament osmòtic i baixa elasticitat dels teixits, cèl·lules més grosses, pes específic més alt i relació Chla/Chlb inferior. A les mostres de tardor els dos tipus de brots presenten tolerància a l'eixut per ajustament osmòtic, baixa elasticitat de teixits, cèl·lules grosses i pes específic foliar alt. Els resultats mostren que els rebrots després del foc tenen, a l'inici del seu desenvolupament, una plasticitat morfològica i fisiològica superior que els brots nous de les plantes no cremades.

Introduction

Evergreen sclerophyllous Mediterranean forests and shrublands are largely dominated by woody resprouters that regenerate quickly after disturbances. Anthropogenic and, to a minor extent, natural fires, are relatively frequent and fire has been considered as a major stress factor in these environments (Rundel 1982). Changes in community plant composition are of minor importance (autosuccession, Hanes 1971). Previous studies, mostly in chaparral shrubs, have found that after-fire resprout leaves are more mesophytic than leaves of mature plants. Differences have been observed between the morphology and the physiological behaviour of even aged leaves from both, resprouts and mature plants (Oechel and Hastings 1983, DeSouza et al. 1986, Hastings et al. 1989) and also between leaves of resprouts and seedlings (Saruwatari and Davis 1989, Thomas and Davis 1989).The aim of this paper is to analyze a large number of resprout features as compared to unburned plants for one perennial shrub species, *Arbutus unedo* L., a laurophyllous shrub characteristic of Mediterranean basin sclerophyllous forests and macchia ecosystems, in order to establish the relationship between the fire as an ecological factor and some resprouts physiological responses in an autosuccesion context.

Material and methods

Species and study site

Two experimental plots (400 m^2 each), burned and unburned, were selected in the Serralada Litoral Catalana, at the NE of the Iberian Peninsule. The area (31TDG 8823 and 31TDG 9620) has a subhumid Mediterranean climate, with 745 mm annual average rainfall and 16.7°C average annual temperature. The substrate consists of leucogranite, supporting soils with sandy texture. The burned plot had suffered a wildfire of severe intensity (after Wells et al. 1979 classification) that affected 105 ha on 17 July 1987. The unburned plot has remained so for at least fifty years, according to landowner's information. Measurements were carried out on *Arbutus unedo* L ., a frequently dominant shrub or small tree in the Mediterranean macchia and shrublands and in the undergrowth of *Quercus ilex, Quercus suber, Pinus halepensis* and *Pinus pinea* forests and woodlands. From a phytosociological point of view, our plots can be identified as Cistion mediomediterraneum communities (Bolòs 1983), with *Quercus suber* (cork oak) covering 80% of total soil surface.

Sampling methods

Ten randomly selected *Arbutus unedo* L. shrubs were sampled on each of the burned and unburned plots. One current-year shoot was taken from the central part

on the southern side of the crown of each sample shrub early in the morning, once in late spring (June 6th 1988) and again in autumn (November 9th 1988). We measured the elongation of one year old shoots, from the node where seasonal growth was initiated and from the point of initiation on the root crown (for unburned and burned plants respectively).We also measured the total plant height in both plant types.

Water relations

Shoots were carried in sealed plastic bags containing some water to the laboratory. These shoots were recut under water and placed in beakers containing some water, enclosed in plastic bags and stored for rehydratation in darkness and at 5°C for 48 h. Then, five water saturated unburned and afterfire shoots were used for measurements. They were weighed and then allowed to dehydrate by free transpiration for 4 h at 20°C, 60% R.H., and 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD. During dehydration, water potential was repeatedly measured with a Schollander pressure chamber (Soilmoisture 3005). From the saturated weight, fresh weights corresponding to Ψ_x (xylem water potential) measures, and dry weight, we calculated the relative water content *(RWC)*. *RWC* was plotted against $1/\Psi_x$ (type II transformation, Tyree and Richter 1981, 1982). From the graph, the osmotic potential at full turgor can be estimated. Turgor potentials (Ψ_p) were calculated from non-linear parts of the curves as the difference between actual data and the osmotic (adjusted) line. Pressure-volume curves gave the osmotic potentials at full turgor (Ψ_{p100}) and at zero turgor (Ψ_{p0}). The volumetric modulus of elasticity (ε) at 100% *RWC* (RWC_{100}) was estimated assuming linear relationship between turgor potential (Ψ_p) and *RWC*:

$$\varepsilon = \Psi_{p100} RWC_0 / RWC_{100} - RWC_0$$

where Ψ_{p100} is turgor potential at RWC_{100} and RWC_0 are *RWC* at full and zero turgor (Johnson et al. 1984).

Using the same shoots, stomatal and cuticular water loss rates were measured gravimetrically (by difference between weights at the beginning and the end of measurement periods) with a digital balance Mettler AJ 100, with 0.1 mg accuracy (Savé 1986, Sveningsson and Liljenberg 1986). Water losses were referred to dry weight (DW) and time units. We considered as stomatal or cuticular water loss rates the values obtained above and below the point of zero turgor respectively. Ratios between turgid weight TW and DW, and specific leaf weight (SLW) were also calculated on these leaves.

Leaf morphology and anatomy

The fourth leaf recently expanded from the shoot apex was excised. Pieces from a central area of the blades were then cut, preserved in a formalin-acetic acid-

ethanol mixture, cleared with chloral hydrate water solution and rinsed. Once mounted in distilled water they were used to evaluate stomatal frequency on abaxial surfaces.

Samples for light and electron transmission microscopy were prepared according to usual techniques (Parker and Ford 1982). Between-vein distances, cell perimeter and cell area were calculated from a sample of 40 mesophyll cells from each of three leaves. Measurements were performed using an Interactive Binary Analyzer System (IBAS Kontron). Mesophyll cell number, total mesophyll cell perimeter and total mesophyll cell area were referred to abaxial epidermis width. Mesophyll area/leaf area and mesophyll volume/leaf area ratios were measured according to Jurik et al. (1982). The chloroplast length and width and the adaxial and abaxial cuticle thickness were also measured. The observations were made with a Philips EM 301 transmission microscope.

Specimens for scanning microscopy were fixed in ethanol, dehydrated, transferred to amyl acetate, dried to critical point, attached to specimen stubs and coated with gold. Samples were examined under a Cambridge 20 scanning electron microscope.

X-ray microanalysis

Specimens were prepared as for SEM observation, but carbon-coated. A Jeol JSM 840 scanning electron microscope, operated at 12 Kv, forming images with a 10-10 A current intensity, was used in the observations. The multielement analyses were carried out with a SEM including an energy dispersive X-ray analyzer C6RxAN 10000 (link systems), working with $0.4\text{-}0.6 \times 10^{-9}$ A current intensity. An X-ray elemental mapping was obtained with a higher current.

Chemical solutes and pigments

Chlorophyll was extracted in dimethylphormamid and analyzed according to Inskeep and Bloom (1985). Anthocyans and other polyphenols were extracted with 3% sulphosalicylic acid and analyzed using a colorimetric method (Harborne 1984). Proline was determined according to the colorimetric method described by Torrecillas et al. (1984), soluble sugars by spectrophotometry, according to Wristler and Wolform (1962). Ca, K, Cl, S, P, Mg and Na were determined by X-ray fluorescence, with a Philips PW 1400 fluorimeter. Total nitrogen was obtained with an automatic N analyzer (Carlo Erba AWA 1500).

Results

Data obtained on water relationships, morphology and chemical composition parameters are shown in tables 1-4. Unburned plants were taller (5 m height in average) and the canopy diameter was 3 ±0.5 m, with 3 shoots per branch on avera-

ge. After-fire resprouts were 1.5 m tall and had 20 resprouts per plant in average. In the spring samples, during the early stages of the after-fire regeneration process, we assume that unburned and burned plants found a more or less similar soil water availability, because they were in very similar and neighbouring localities. Unknown differences can, nevertheless, exist due to fire-induced environmental modifications.

The new shoot length increase in June was near 10 times higher in after-fire than in unburned plants. Unburned plants in late spring showed a higher content of starch granules (Pery et al. 1989) and proline, higher values of modulus of elasticity (210% of after-fire resprouts), larger cells, 90-124% thicker cuticles on adaxial and abaxial surfaces respectively, larger chloroplast sizes, 39% more K, and higher total nutrient content (see table 4). On the other hand, Ψ_{p100} and Ψ_{p0} were lower in unburned plants and the same was true for stomatal and cuticular transpiration rates, for calcium concentration and for Chla/Chlb (10% higher in after-fire resprouts). Unburned plants showed higher SLW and lower TW/DW ratio than after-fire resprouts (see table 1).

In the November sampling, after the summer drought, hydric parameters showed similar values in the two plots. Xeromorphy was increased in after-fire resprouts: the elasticity modulus increased by 124%, osmotic values 103% and SLW 64%, whereas cell osmotic volume and TW/DW ratio decreased (see tables 1 and 2) . Mesophyll cross-section area, mesophyll cell area/leaf surface, mesophyll cell volume/leaf surface, thickness of leaf, mesophyll and abaxial cuticle, chloroplast size and nutrient concentration were all nearly the same in after-fire and unburned leaves. Adaxial cuticle was 42% thicker in after-fire than in unburned leaves. In addition, mean leaf area was 56% higher in after-fire (this difference was only 5% in June) . Chla/Chlb ratio was 18% higher in after-fire leaves and anthocyans

Table 1. Water relations (Ψ_{x100}, Ψ_{x0}, $\in$ max), stomatal and cuticular water loss rates (TRmax, TRc), proline, soluble sugars, specific leaf weight (SLW) and turgid weight/dry weight ratio (TW/DW) of leaves of *Arbutus unedo* L. in two experimental plots (burned and unburned) during late spring and autumn. Average values are given ± SD.

	Late spring (7/6/88)		Autumn (9/13/88)	
	Unburned	Burned	Unburned	Burned
$\Psi_{\pi100}$ (MPa)	−1.56 ± 0.32	−0.74 ± 0.15	−1.49 ± 0.13	−1.50 ± 0.33
$\Psi_{\pi0}$ (MPa)	−1.80 ± 0.17	−1.36 ± 0.13	−2.02 ± 0.08	−2.09 ± 0.28
$\in$ max (MPa)	14.95 ± 3.19	4.82 ± 2.28	12.64 ± 2.69	10.81 ± 1.65
TRmax (mg. g⁻¹.DW.min⁻¹)	3.08 ± 1.52	3.80 ± 2.01	3.42 ± 1.30	3.37 ± 1.10
TRcut (mg. g⁻¹.DW.min⁻¹)	1.11 ± 0.30	1.82 ± 0.33	0.97 ± 0.25	1.12 ± 0.23
Proline (mg. g⁻¹.DW)	39.60 ± 4.60	27.20 ± 4.20	108.60 ± 20.00	79.20 ± 16.00
Soluble sugars (%)	9.20 ± 0.50	8.70 ± 0.30	11.70 ± 0.50	18.20 ± 0.60
SLW (mg. cm⁻²)	14.50 ± 0.60	10.50 ± 0.44	15.04 ± 0.73	17.20 ± 0.60
TWD/DW	2.80 ± 0.09	3.90 ± 0.30	2.36 ± 0.02	2.40 ± 0.06

showed a greater increase (125%). Starch accumulation, on the contrary, was always higher in unburned plants.

Discussion

Water relationships

Differences in hydric status between after-fire resprouts and unburned plants have been noted previously in other studies: xylem water potentials have been compared on different chaparral species by Hastings et al. (1989) and Rundel (1982); stomatal conductance at midday has been also considered by DeSouza et al. (1986) and Hastings et al. (1989). Their results suggest a greater water availability to resprout leaves: resprouts have larger individual leaves but a reduced LAI (because there are less leaves), without a proportional decrease in the root system and in the capacity for water absorption. Our data support these observations. In unburned autumn plants, a higher transpiring total leaf area (LAI) can cause temporary

Table 2. Some structural characteristics of the *Arbuus unedo* L. leaves in two experimental plots (burned and unburned) during late spring and autumn. Average values are given ± SD.

| | Late spring (7/6/88) | | Autumn (9/13/88) | |
	Unburned	Burned	Unburned	Burned
Leaf area (cm^2)	9.53± 0.53	11.85± 0.72	7.67± 0.72	11.60± 1.61
Leaf thickness (μm)	219.16± 2.86	209.20± 0.72	217.68± 3.04	340.48± 4.12
Mesophyll thickness (μm)	188.44± 1.90	176.48± 0.72	177.10± 2.70	311.28± 2.87
Adaxial cuticle thickness (μm)	6.16± 0.70	3.24± 0.07	8.03± 0.16	11.39± 0.81
Abaxial cuticle thickness (μm)	7.14± 0.14	3.20± 0.46	8.18± 0.27	8.19± 0.30
Distance between veins (μm)	787.80±10.90	716.60±11.50	1138.00±16.30	722.80±14.50
Stomatal frecuency (number.mm^{-2})	321.30±18.10	570.60±25.80	—	—
Mesophyll cell cross-sectional size (μm^2)	262.80±21.80	172.28±15.30	260.51±20.14	419.00±39.60
Chloroplast length (μm)	5.23± 0.90	3.12± 0.30	5.89± 0.25	5.22± 0.40
Chloroplast width (μm)	1.92± 0.17	1.18± 0.23	2.46± 0.34	2.07± 0.40

or sustained water deficits. We can therefore expect reduced sugar translocation and an increase of starch granules (Ackerson 1981, Riazi et al. 1985). That increase of starch granules is observed in our samples (Pery et al. 1989). As a result, carbon is more available than nitrogen and proline accumulates (as observed previously by Tully et al. 1979, Aspinall and Paleg 1981, Handa et al. 1986) . The active solute accumulation and solute concentration induced by decrease in cellular volume due to starch granules (Ackerson and Hebert 1981) may promote a decline in Ψ_{p100} and Ψ_{p0} (as shown by our results on Table 1). High values of modulus of elasticity and the large cells indicate that in mature plants a small contribution from these characteristics can be expected to osmotic adjustment (Myers and Neals 1986, Robichaux et al. 1986). On the other hand, it is known that the osmotic adjustment is favoured by a high K concentration (Ford and Wilson 1981), and our unburned plants have more K than the after-fire resprouts (Table 3) .

The higher Ψ_{p100} and Ψ_{p0} of resprouts could be the result of a greater water availability per unit of transpiring surface and of a low content of osmotical solutes such as proline.This is due to lack of stress and/or lack of soluble sugars as a result of faster growth (Radosevich et al. 1977, Oechel and Hastings 1983). The low value of the modulus of elasticity and the small cells indicate that elasticity plays an important role in cellular turgor maintenance (Bradford and Hsiao 1982, Myers and Neales 1986).

Greater stomatal and cuticular water loss rate in after-fire resprouts may be explained by greater water availability (Oechel and Hastings 1983) and by morphological characteristics, such as stomatal density and cuticle thickness (Table 2) (Levitt 1980, Morgan 1984). The higher transpiration flow can promote high passive calcium absorption rates, thus explaining a larger Ca accumulation in after-fire resprouts.

High TW/DW ratio observed in spring for resprouts can be explained by low apoplastic water content and thin cell walls (Jensen and Henson 1989). The low SLW and the high transpiration rate measured (table 1) are in agreement with this interpretation. TW/DW ratios suggest that juvenile characteristics (Meseguer 1990)

Table 3. Solute concentration of *Arbuus unedo* L. leaves in two experimental plots (burned and unburned) during late spring and autumn. Average values are given ± SD.

		Late spring (7/6/88)		Autumn (9/13/88)	
		Unburned	Burned	Unburned	Burned
N	(%DW)	2.08 ± 0.07	1.49 ± 0.05	1.58 ± 0.10	1.40 ± 0.03
K	(%DW)	2.23 ± 0.04	1.60 ± 0.04	1.43 ± 0.03	1.39 ± 0.02
Ca	(%DW)	1.07 ± 0.07	1.77 ± 0.07	2.07 ± 0.00	2.47 ± 0.03
Mg	(%DW)	0.15 ± 0.00	0.15 ± 0.01	0.20 ± 0.01	0.22 ± 0.02
Na	(%DW)	0.015 ± 0.01	0.009 ± 0.00	0.15 ± 0.00	0.012 ± 0.00
Cl	(%DW)	0.008 ± 0.00	0.038 ± 0.00	0.010 ± 0.00	0.032 ± 0.03
S	(%DW)	0.190 ± 0.03	0.138 ± 0.06	0.160 ± 0.01	0.130 ± 0.03
P	(%DW)	0.28 ± 0.01	0.17 ± 0.01	0.16 ± 0.00	0.12 ± 0.01

shown in after-fire resprouts and drought stress can both play a role in the adaptation of resprouts to environmental factors.

The decrease of soil water availability and high evaporative demand during the summer drought, together with the increase in the leaf area of resprouts, can explain the change of the resprouts hydric behaviour to a water conservation behaviour more like that of mature plants. Leaves of resprouts became more xeromorphic as a result of an increase in the modulus of elasticity, the osmotic solute content and the SLW (Turner and Jones 1980, Morgan 1984, Bowman and Roberts 1985) and a decrease in cellular osmotic volume (Ackerson and Hebert 1981) and TW/DW ratio (Jensen and Henson 1989).

Structural characteristics

Smaller size of leaf mesophyll and epidermal cells, closely distributed veins and increased stomatal frequency in late spring resprouts can be related to higher photosynthetic rates (Morgan et al. 1987). Enhanced photosynthesis during the first year after the fire in *Arbutus unedo* has been described by Fleck et al. (1990). Results of mesophyll cross-sectional area show a relation between the size of leaf cells and the modulus of elasticity. Lower values of the modulus of elasticity are associated with small cells (Robichaux et al. 1986). Leaf cells and the modulus of elasticity increased in the resprouts between the two samplings to approach the mature plants values, as previously described.

Nutrient concentration

Higher total nutrient concentration (as a percentage of dry weight) found in mature plants can be related to their low Ψ_{p100} values (Morgan 1984). Whereas trends in the accumulation of solute nutrients were similar to those of total ionic concentration, Ca showed higher concentration in resprouts. Ca was located on the abaxial side of the epidermis. Solutes within the transpiration stream accumulate within or near the stomatal complex (Mansfield 1990). The accumulation of Ca could therefore be related to high transpiration rates in the resprouts.

In the fall sampling, similar nutrient concentrations were found in resprouts and mature plants. Ca and Mg increased as compared to spring samples, whereas N, P, S and K decreased. This is a result of the different mobility of the elements, and is usually observed in all leaf aging processes (Mengel and Kirby 1982).

Chlorophyll and polyphenol contents

Higher values of Chla/Chlb ratio observed in resprouts on both sampling dates (Table 4) can indicate a higher potential for photosynthetic activity (Boardman 1977, Edwards and Walker 1983). In fact, higher photosynthetic rates have always been measured in resprouts (Oechel and Hastings 1983, DeSouza 1986, Hastings et al. 1989, Fleck et al. 1990).

Table 4. Leaf chlorophyll and anthocianins content and ratio Chla/Chlb from two experimental plots (burned and unburned) of *Arbutus unedo* L. Average values are given ± SD.

	Late spring (7/6/88)		Autumn (9/13/88)	
	Unburned	Burned	Unburned	Burned
Chla ($\mu g.cm^{-2}$)	29.4 ± 4.0	13.3 ± 1.0	46.1 ± 2.6	45.4 ± 10.3
Chlb ($\mu g.cm^{-2}$)	10.0 ± 1.4	4.1 ± 0.4	12.4 ± 2.5	11.4 ± 5.0
Chl_t ($\mu g.cm^{-2}$)	39.4 ± 5.3	17.4 ± 1.1	59.1 ± 3.2	56.6 ± 14.6
Chla/Chlb	2.9 ± 0.2	3.2 ± 0.4	3.9 ± 0.9	4.6 ± 1.6
Anthocianins				
(av at 573 nm)	—	—	0.61	1.37

Under natural conditions, photosynthetic photon flux density (PPFD) is higher in most adaxial mesophylls, and decreases with the depth from the adaxial surface. Phenolic substances may serve to screen out damaging radiation from the underlying tissues (Araus et al. 1986), and this can help to explain the great tolerance of thin sun leaves to high PPFD. Anthocyan increase in resprouts can play this protective role. Further, it can be related to juvenile characteristics of lateral axillary buds in resprouts (Hacket et al. 1989, Meseguer 1990).

Conclusions

At the beginning of the growth period, resprouts showed a mechanism of drought tolerance due to tissue elasticity (Levitt 1980, Morgan 1984) . Elasticity does not influence turgor-mediated processes, such are elongative growth and photosynthesis (Bradford and Hsiao 1982), and allows a greater allocation of assimilates and nutrients to the plant growth (Munns 1988). At the same time, unburned plants showed drought tolerance by active osmotic accumulation, osmotic adjustment with osmotic concentration due to reduced cell volume caused by starch granules presence (Ackerson and Hebert 1981, Morgan 1984), together with low elasticity. This allowed lower water potential to be reached for a given change in water volume, and so continuous water uptake from drying soils was possible. Low tissue elasticity may be an important characteristic allowing low water potentials to be reached without development of detrimental water deficits (Bowman and Roberts 1985). Moreover, unburned plants have other mechanisms of drought avoidance, such as thicker cuticle and low cuticular transpiration rates (Levitt 1980).

In the fall, the two plant types showed similar mechanisms of drought tolerance, osmotic adjustment and low tissue elasticity, together with mechanisms of drought avoidance, thicker leaves and cuticles and low water loss rates. The development of these two water stress resistance mechanisms presumably resulted from summer drought stress (Morgan 1984), but differences due to leaf ontogeny

can not be discarded, as pointed by DeSouza et al. (1986): all sampled leaves have the same age, but burned resprouts show higher growth rates.

Our results show that after-fire resprouts have, at the beginning of their development, higher physiological and morphological plasticity (in the sense of Bazzaz and Carlson 1982) than the new sprouts of unburned plants. Better water and nutrient availability in resprouts, as a result of much lower shoot/root ratio, deep roots and nutrient stores in the root and root-crown (DeSouza et al. 1986) must lead to more mesophytic leaves. This interpretation fits well with our data.

It seems possible to relate these results to some generalizations on successional theory. In Mediterranean sclerophyllous evergreen communities, there is autosuccession and not a true secondary succession after a disturbance because most dominant plants resprout, and so the same individuals remain alive and retain space control. Obviously, in succession processes, changes of floristic composition are involved, whereas in autosuccession no change in an «evolutionary strategy» need to be invoked, because there are no relevant changes in communities plant composition: structural changes are mostly due to the regrowth of disturbed individuals. Bazzaz (1979) and Bazzaz and Carlson (1982) have compared species from early and late stages of secondary succession from a physiological point of view, and describe changes from high to low photosynthetic, transpiration and respiration rates, from low to high stomatal and mesophyll resistances and from more to less plasticity in resource allocation. Note that these trends are similar to those found by us during resprouts aging.

The morphological and physiological changes in resprouts reported above can be considered as a transition from mesophyllous to sclerophyllous characters. This is usually find with leaf aging, but the interesting point is that in our observations «mesophylly» of early stages is clearly more marked in resprouts than in unburned new shoots. Trying to found a mechanistic explanation for this, we hypothesize that many «adaptative» features could be only a mechanical consequence of a few simple options. Mooney (1989) has suggested that differences between mesophylly and sclerophylly between different plants can be, at least to some extent, a simple consequence of resource availability patterns. In particular, if carbon is available in excess over nitrogen, higher SLW are attained. Our results seem to indicate that Mooney's hypothesis could be tested well by experiments using resprouting plants.

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