C. R. Biologies 333 (2010) 424–428

Contents lists available at ScienceDirect

Comptes Rendus Biologies

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Ecology / Écologie

Expansion of green alder (*Alnus alnobetula* [Ehrh] K. Koch) in the northern French Alps: A palaeoecological point of view

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ARTICLE INFO

Article history:
Received 20 October 2009
Accepted after revision 6 January 2010
Available online 6 March 2010

Keywords:
French North-Western Alps
Holocene vegetation history
Green alder
Human impact
Deforestation
Bronze-Iron Age

ABSTRACT

Pollen analyses were undertaken on a small peat bog (Ecuelles 06° 49′ 41″E, 45° 58′ 49″N, 1855 m *asl*), located on the Anterne mountain (Upper-Arve Valley, French north-western Alps). The study highlights the role of green alder (*Alnus alnobetula* [Ehrh] K. Koch) in Holocene vegetation dynamics of the nowadays treeless subalpine belt. At this place, the onset of human perturbation caused a retreat of fir and arolla-pine stands and an expansion of green alder, which consequently dominated the landscape from 3700 up to 1965 cal. BP. After 1965 cal. BP, the clearings led to the present grasslands with few ligneous species (spruce, larch) on inaccessible cliffs or green alder on the edges of torrents or in avalanche corridors. *Picea* percentages have increased after 3900 cal. BP, but, due to human activities, spruce has never constituted large stands in the study area. The present general expansion of green alder is due to the decreasing human impact and it constitutes the first step of re-afforestation that should lead to mixed stands of spruce and arolla-pine. The study gives a new evidence of the past diversity of the vegetation cover and do not support the idea that green alder colonization at the subalpine belt constitutes a long-term risk for the vegetation diversity.

Version française abrégée

L'analyse pollinique d'une séquence tourbeuse extraite à Écuelles, (06° 49′41″E, 45° 58′ 49″N, 1855 m) sur la montagne d'Anterne (haute vallée de l'Arve, Fig. 1), met en perspective le rôle des aulnes verts dans la dynamique végétale des pelouses subalpines. Cette étude fait partie du programme de recherche pluridisciplinaire Aphrodyte 2 sur les interactions homme–climat–environnement pendant l'Holocène dans la haute vallée de l'Arve. L'aire d'étude est située dans la réserve naturelle de Passy qui illustre, sur une surface de 1800 hectares, la grande hétérogénéité géologique et écologique des Alpes du nord. Cette zone marque la limite orientale des Alpes externes d'après Ozenda [1]. Un boisement mixte de hêtres épicéas et rares sapins pousse à 1400 m *asl* sur la montagne de Pormenaz alors que quelques exemplaires de pins cembros, épicéas et mélèzes poussent en situation inaccessible sur les falaises jusqu'à 2200 m *asl*. À proximité du site, le paysage est marqué par la dominance des pelouses avec de nombreuses marques d'érosion. Les aulnes verts sont localement abondants près des torrents et des couloirs d'avalanche. Seuls quelques exemplaires de sorbiers et de bouleaux poussent rabougris en raison du pâturage de plusieurs centaines de moutons et plusieurs dizaines de vaches. Une étude précédente a montré que l'épicéa a largement colonisé l'étage subalpin de la région [4]. D'autres études ont montré également que la limite des boisements a baissé à l'époque romaine et que le couvert végétal a pu évoluer différemment sur de faibles distances [7–9].

Dans cette étude, l'accent est porté sur l'aulne vert qui s'étend actuellement aux dépens des pelouses subalpines. En raison de la fermeture du milieu qu'elle entraîne [10], cette expansion est souvent jugée indésirable car défavorable aux espèces rares inféodées aux milieux ouverts [11].

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doi:10.1016/j.crvi.2010.01.002

D'un point de vue paléoécologique basé sur la reconstitution de l'histoire Holocène de la végétation, cette expansion apparaît comme une reconquête dont les conséquences sur la biodiversité ne doivent pas être appréciées à court terme.

Un peuplement mixte de sapin et pin cembro entourait le site. Un bois de pin cembro trouvé à proximité a été daté 5950 ± 40 cal. BP (Tableau 1). Ces peuplements mixtes comprenaient également bouleaux, sorbiers et érables. Une première poussée des aulnes verts et des hêtres est enregistrée à 3908–3840 cal. BP avec le déclin des pins et sapins. Cette concordance a déjà été signalée [16–18]. Le pourcentage faible du hêtre (< 5 %) correspond à un apport pollinique provenant de l'étage inférieur. La présence actuelle du mélèze dans la même aire que les hêtres en dehors de la zone interne semble une conséquence des déboisements. L'expansion des mélézins dans l'étage subalpin des Alpes du Nord a été datée de l'époque romaine [8]. Toutefois, l'absence de pollen de mélèze dans la séquence peut être liée à sa faible représentation pollinique.

La première phase d'expansion des aulnes verts coïncide également avec l'expansion des épicéas qui ne dépassent jamais 18 % (Fig. 2, E7), même après la seconde progression des aulnes verts à 3738 ± 95 cal. BP (Fig. 2, E8). Ces taux sont faibles, comparés à ceux observés à quelques kilomètres de distance [4]. Dans la zone des Écuelles, les fourrés d'aulnes verts ont dominé le paysage de 3738 ± 95 à 1965 ± 77 cal. BP en formant un couvert dense comme le soulignent les faibles pourcentages de *Poaceae* et la présence de filicales monolètes (type athyrium). Seules les activités anthropiques peuvent expliquer ces différences d'enregistrements polliniques sur de faibles distances. La rétraction des aulnaies au début de l'ère chrétienne (1965 ± 77 cal. BP) a permis l'installation des pelouses actuelles sous l'effet de l'augmentation de la pression du pâturage comme l'indiquent les marqueurs tels *Plantago*. La persistance pendant deux mille ans de la pression anthropique permettant le maintien des pelouses subalpines masque la diversité des anciens paysages boisés. De plus, la survie d'espèces des milieux ouverts jusqu'à nos jours montre que l'expansion de l'aulne vert à l'âge du bronze n'a pas été fatale pour la biodiversité. Les études paléoécologiques rappellent que l'hétérogénéité des territoires a induit une diversification de la couverture végétale passée garante de la biodiversité et que c'est l'action humaine qui a contribué globalement à réduire cette biodiversité en réduisant les divers boisements anciens au profit d'une généralisation des pelouses pâturées [19].

1. Introduction

In temperate regions, the post-glacial dynamic processes that have built mountain ecosystems were related mainly to climate changes and/or human impact. In southwestern Europe and, particularly, in the Alpine range, the complex topography and the interaction of several climatic and anthropogenic influences have induced a great landscape heterogeneity [1,2]. This article presents the results from the palaeoecological study of the sediments of a subalpine peat bog, undertaken as a part of the Aphrodyte 2 program aiming to obtain through a multidisciplinary approach new information on the Holocene human–climate–environment interactions at high altitudes in the higher Arve Valley.

The study area (Fig. 1) is located in the natural reserve of Passy (1800 ha). It illustrates the great geological and ecological heterogeneity over a short distance in the northern French Alps [3]. It covers both the steep calacareous Fiz mountain cliffs and smoother siliceous Pormenaz Mountain that lies opposite the Aiguilles-Rouges and Mont-Blanc ranges and dominates the town of Passy in the middle section of the Higher Arve-Valley. The area marks the eastern limit of the outer Alps according to Ozenda [1]. Most eastern *Fagus* stands are observed at around 1400 m *asl* in Pormenaz Mountain whereas isolated *Picea, Larix* and *Pinus cembra* grow up to 2200 m *asl* on inaccessible cliffs. Green alders essentially grow close to a source of water or in avalanche corridors. Close to the site, *Sorbus* and *Betula* are scarse and regularly grazed. At the present time, several hundred sheep and tens of cows pasture this treeless subalpine vegetation belt and the landscape is strongly marked by erosion figures such as steep outcrops incising old peat bogs.

A previous study in neighbouring massifs sites (Fig. 1) have shown that *Picea* stands may have colonized this altitudinal belt [4]. However, according to these authors, the proposed Holocene chronology remains imprecise. We use in the following section the chronological radiocarbon-based evidences given by Beaulieu et al. [4] as they were initially published (i.e. non-calibrated) and nowadays calibrated using Calib 5.0.1 software [5] and Intcal04 calibration curve [6] as 2-sigma probability age interval. A mean age for the invasion of *Picea* has been proposed around 3000 BP. In fact, two 14C ages −3300 ± 170 BP (3980–3080 cal. BP) and 2630 ± 130 BP (3010–2350 cal. BP) bracket the increasing *Picea* percentages at La Flatière (Fig. 1, 1400 m *asl*), but *Picea* percentage increases prior to 3360 ± 180 BP (4140–3160 cal. BP) at higher elevation in the subalpine belt (Fig. 1, Prarion 1820 m *asl*). Most palaeodata in the French Alps have shown that the tree line has been broadly lowered during the Roman period, but we previously showed that close sites (few kilometres away) could have very different landscape evolution [7–9].

The case of green alder is particularly examined here. It is currently colonizing abandoned meadows in the subalpine belts, creating a dense shrub cover [10]. This colonization process is often considered undesirable since it presents a considerable risk for vegetation diversity and endangered species such as the black grouse (*Tetrao tetrix* L.) [11]. This study gives a palaeoecological point of view based on the long-term evolution of the landscapes.

2. Method

The site (a small peat bog) was cored with an 8 cm in diameter Russian peat-corer. Samples were taken for pollen profile at intervals from 2.0 to 10 cm and were prepared for pollen analysis by the standard acetylation and hydrofluoric acid method [12]. The pollen sum was at least 350 grains, excluding swamp plants and ferns. The software package Gpalwin [13] was used to construct pollen diagrams. Radiocarbon dates were carried out by LMC14 laboratory (CNRS), operating the French national

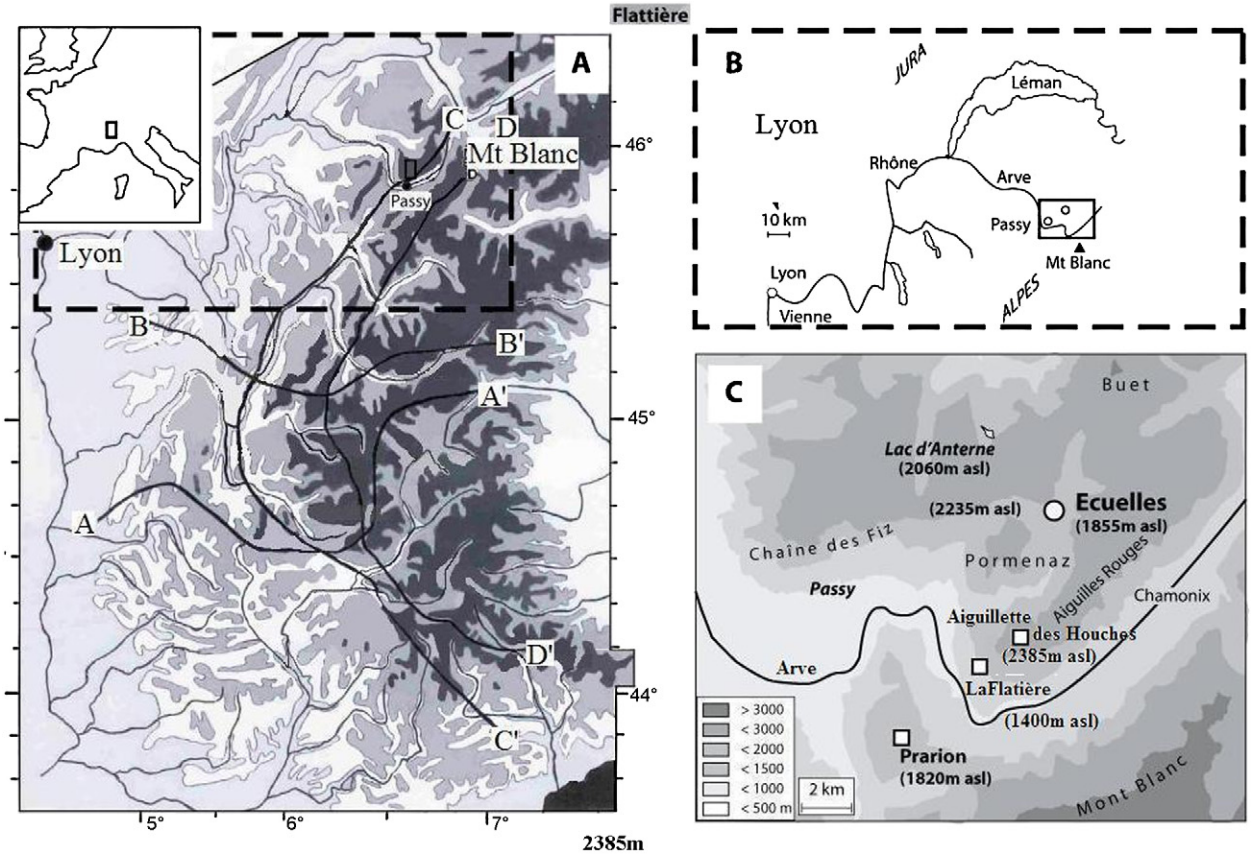

Fig. 1. A. Location and ecological zonation of the French Alps according to Ozenda [1]. The pass limit A-A′, separates the southern Alps from the northern Alps. To the North of the limit pass, a transition zone has been defined. B-B′ marks the limit between the transition zone and the unambiguous northern Alps. Eastward Increasing continentality led to distinguish the Outer Alps (to the west of C-C′), the intermediate Alps (between C-C′ and D-D′) and the inner Alps (east of D-D′). B. Sketch map of northern French showing the location of the study area. C. Sketch map of the study area showing the location of the studied peat record (white circles) as well as of lake Anterne and the peat records previously studied by Beaulieu et al. [4] (white squares).

radiocarbon device Artemis. Non-calibrated and calibrated ages are given in Table 1. Only calibrated ages are used in the text (cal. BP refers to before present, whereby convention AD 1950 is 'present'). Calibration was performed using Calib 5.0.1 software [5] and Intcal04 calibration curve [6], calibrated ages are given as 2-sigma probability age interval (Table 1).

3. Results and discussion

Pollen analysis results are shown in a summarized relative pollen diagram (Fig. 2). Discontinuous stomata occurrences are plotted on pollen diagram.

3.1. Holocene vegetation history and chronology

The pollen spectra indicate mixed stands of *Abies* and *Pinus cembra* prior to the record of the first *Picea* pollen (Fig. 2, E2-3). The presence of *Fagus* pollen is also quoted. The appearance of *Fagus* has been dated at the so-called Prarion site (1820 m *asl*), 6510–7470 cal. BP (6160 ± 220 BP) [4]. Comparison with this site gives a mid-Holocene age around 6500 cal BP for the bottom of the core.

Stomata (Fig. 2, E2, E5) indicate the presence of *Pinus* close to the site and/or litter transfer from the catchment [14]. Findings of *Pinus cembra* seeds confirm that arollapine grew close to the site. One seed from Ecuelles has been

Table 1
C14 AMS dates.

Reference	Sample	Nature	d 13C	Age 14C BP	Age cal. y. BP (2S)
SacA-8734	ECU35	Peat	−25.6	2015 ± 30	1965 ± 17
SacA-8735	ECU85	Peat	−23.6	3470 ± 30	3738 ± 95
SacA-8736	ECU105	Peat	−21.6	3600 ± 30	3908 ± 71
SacA-11731	AVECU	Seed (*P. cembra*)	–	5185 ± 30	5950 ± 40
SacA-11730	ANTCE	Wood (*P. cembra*)	–	4480 ± 30	5095 ± 55

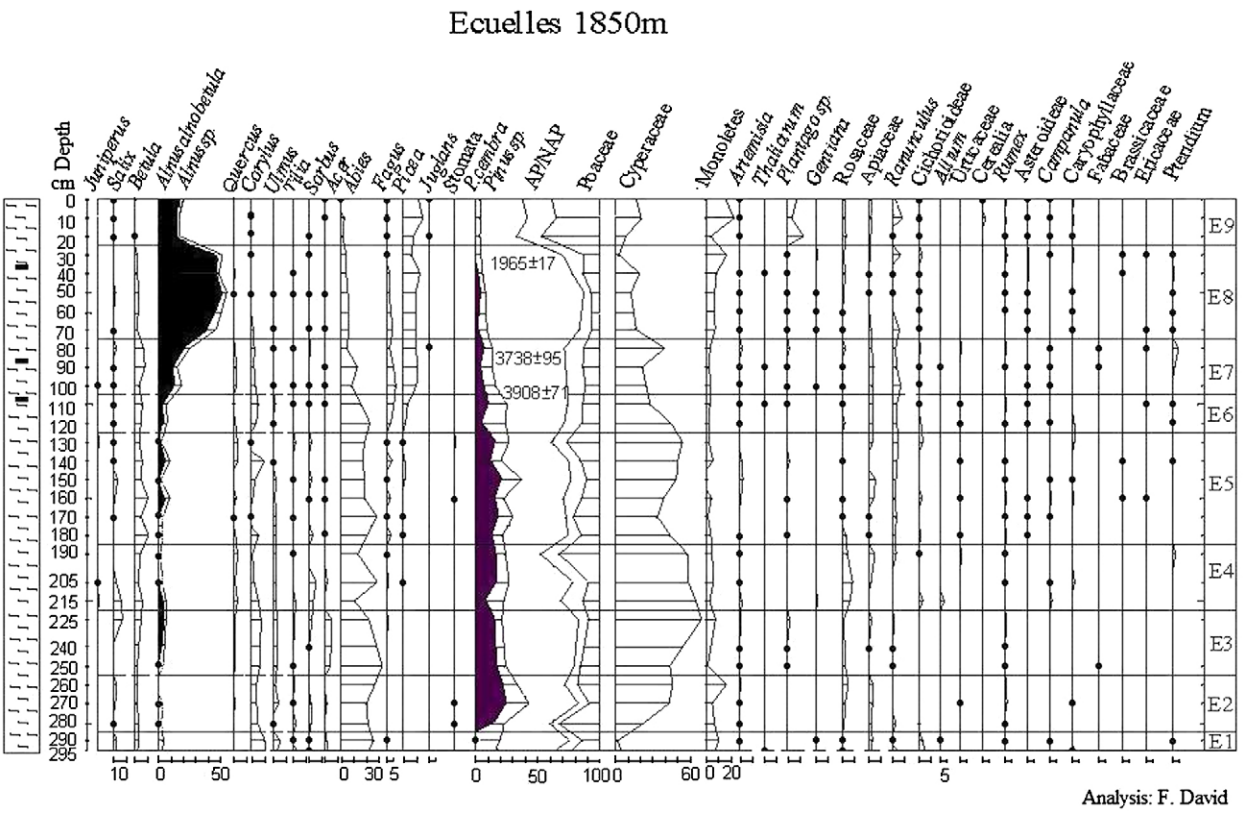

Fig. 2. Simplified relative pollen diagram.

dated 5950 ± 80 cal. BP and a piece of wood from Lake Anterne 5095 ± 55 cal. BP (Table 1). These results agree with the past and present location of *Pinus cembra* in the inner and intermediate zone of the French Alps [1,8]. Indeed, the study area (Fig. 1) is located at the transition between outer and intermediate zones and must have constituted the most western location of arolla-pine. However, *P. cembra* percentage has never exceeded 30% in pollen assemblages and thus might not have constituted a dense tree cover around the site. Since *Abies* could have developed up to 2000 m *asl*, according to altitudinal afforestation processes in the northern French Alps [14,15], fir must have grown in the vicinity of the site, constituting mixed stands with *P. cembra*. At present, *P. cembra* and *Abies* are scarse in the study area such as *Betula, Acer* and *Sorbus*. The low and regular percentages of the three last species (Fig. 2) indicate that they were components of mixed stands with *Abies* and *P. cembra*. This site (1850 m *asl*) had an intermediate position between the lower *Abies* and the higher *P. cembra* stands. We note (Fig. 2, E5) the last stomata-bearing sample prior to the beginning of pine and fir decline (Fig. 2, E6).

A *Fagus* increase is quoted at 3908 ± 71 cal. BP. But *Fagus* records remain low (5%, Fig. 2, E6-7). *Fagus* increase is due to clearings of the fir forest at lower altitude and to an opening of the vegetation cover around the site allowing a better record of long distance pollen. At present time, *Fagus* grows at 1400 m *asl*, whereas few *Larix* may be observed in surrounding cliffs. This constitutes the most western stands of *Larix*. The natural range of *Larix* is located in the inner Alps and should not grow beside *Fagus* [1]. *Larix* pollen has not been observed in our peat samples. We cannot deduce the *Larix* history in the area without a macroremain study. We already encountered a similar case in previous studies in the northern Alps, in which we reported findings of *Larix* needles whereas no pollen was found [8]. Nevertheless, this support a recent migration of *Larix* in the deforested area. The great expansion of *Larix* at the subalpine vegetation belt in the northern French Alps was related to human impact back to the Roman period [8]. Due to clearings, *Larix* can grow over the inner range of the Alps (Fig. 1).

The first expansion of green alder at 3908 ± 71 BP (Fig. 2, E7) coincided with the *Pinus* decline and *Picea* increase. This agrees with previous ecological and palaeoecological studies which have shown that the clearance of the subalpine forest have favoured the development of pioneer shrub like green alder [16,17,18]. The record of *Plantago lanceolata*, *Ranunculaceae* and *Apiaceae* gives evidence of grazing pressure. A clear second increase of green alder is quoted at 3738 ± 95 (Fig. 2, E8). It coincides with low *Picea* percentages that never exceeded 18%. These percentages are lower than those recorded at the same altitude, few kilometres away. Indeed, Beaulieu et al. [4] have recorded 70% at Prarion (1820 m) and 40% at Aiguillettes des Houches (2210 m *asl*) without any precise dating (Fig. 1). At Ecuelles, some *Picea* timbers currently grow at inaccessible stands in surrounding cliffs. Clearance in the fir and pine forest may explain this difference in the pollen records. From 3738 ± 95 to 1965 ± 17 cal. BP, the landscape was dominated by green alder bushes (Fig. 2, E8).

During this period, Poaceae showed their lowest percentages. Apiaceae and Ranunculaceae also decreased, whereas Filicales monolete (Athyrium type) increased. All this indicates a very dense above ground cover. Such changes might have strong effects on the ecosystem functioning and particularly on the maintenance of the habitat of several endangered species requiring open space such as the black grouse (*Tetrao tetrix* L.). At present time, the development of such a vegetation cover is considered by the ecologists as a threat for the maintenance of the biodiversity [11]. This consideration must be discussed. We currently observe endangered species requiring open spaces at the subalpine vegetation belt, although the landscapes have been much more forested than at present. This survival is due to the persistence of a mosaic of various environments in the past, notably during the Bronze Age expansion of the green alders. Palaeoecological studies at small sites at various expositions have shown the variety of the past subalpine landscapes [19].

At the beginning of the Christian Era (after 2040–1890 cal. BP), due to increasing grazing pressure (*Plantago*, Fig. 2, E9) the *Alnus* population severely diminished, whereas herbs conquered the subalpine vegetation. The landscape looked like the current subalpine meadows. This result agrees with the general decline of the tree-limit recorded in the northern French Alps and confirms the variety of the past subalpine landscapes, which is badly reflected by the current dominance of the subalpine meadows [19].

4. Conclusion

This study shows that human activities are responsible for the present treeless subalpine landscape. In the area, the present pasture land below 2000 m *asl* appeared at ca. 2 ka cal. BP as a result of a pressure on tree population. In the French northern Alps, the green alder is currently colonising abandoned meadows at the subalpine belt. Palaeoecological data show that it colonises territories as soon as the grazing pressure diminishes. Those territories were probably forested before the development of pastoral activities. Green alder invasion should not be considered as a threat for the maintenance of the biodiversity. The palaeoecological studies show that the heterogeneity of the territories (topography, geology) induced a great variety of the past vegetation cover that is often unsuspected. This was sufficient to permit to the endangered species to survive until the present time. Woods at the subalpine belt of the northern Alps were morphologically and specifically much more diversified than the present dominant meadows that green alder can colonise as soon as the grazing pressure diminishes.

Acknowledgements

Analytical results were acquired in the framework of the scientific programs Aphrodyte and Pygmalion, founded by the CNRS program Eclipse and the French National Research Agency (ANR), respectively. Radiocarbon dating was performed thanks to the national facility LM14C in the framework of the Insu Artemis call-for-proposal. We thank Guillaume Buchet (Cerege) for laboratory assistance in chemical treatment of pollen samples.

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