Carbon sequestration in Mediterranean ecosystems: critical aspects related to plant respiration, wildfires and nitrogen budget

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Abstract

Net primary production (NPP) in the biosphere is limited by the current low atmospheric CO_2 concentration (C_a). Hence, the increase in C_a due to anthropogenic activities, which is thought to be the main cause of climate change, is expected to result in an increase in NPP, and therefore in an increased C_a sequestration in the biomass. Increases in NPP and C_a sequestration in the biota are already detectable in boreal and tropical forests. Increased C_a results in a decrease in plant respiration –on average, about 17%–, and therefore the increase in C_a sequestration could be higher than previously assumed. This has led some authors to publish highly optimistic views about the capacity of terrestrial ecosystems to compensate for the excess of C_a. Nevertheless, increased C_a results not only in an increase in NPP (different for every plant species), but also in changes in plant morphology (also different for every plant species); these will result in changes in the patterns of space occupation by plants, which make it difficult to predict how the NPP will change in the long term, at a whole-ecosystem level. It is not clear that such optimistic views can be applied to Mediterranean terrestrial ecosystems, in which drought –the main constraint for NPP– is expected to increase in the future as a result of climate change. Increased drought is expected to lead to a greater risk of wildfires, which can generate a highly unstable situation in the ecosystem if the periodicity and intensity of fire events surpasses its capacity to recover (either by resprouting or seeding). Wildfires cause significant losses of N and P by volatilization. They also result in a strong increase in the availability of nutrients (mainly N), and hence an increase in soil fertility. Nevertheless, even though many Mediterranean plant species (in particular *Quercus ilex*) have a high capacity for the accumulation of N in basal organs, likely to support rapid resprouting, their ability to trap and take up the excess of available N released as a consequence of wildfire is often more limited. This results in the loss of these released nutrients and aggravates the impoverishment of ecosystem nutrients at each wildfire event. If the time between two fire events

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La producció primària neta (NPP) de la biosfera està limitada pels baixos nivells actuals de CO_2 atmosfèric (C_a). Per conseqüent, l'augment de C_a degut a l'activitat humana, considerat la causa principal del canvi climàtic, s'hauria de traduir en un augment de la NPP i, per tant, en un augment del segrestament de C_a a la biomassa. Els augments de NPP i del segrestament de C_a ja són detectables en boscos boreals i tropicals. L'augment de C_a produeix també una disminució de la respiració vegetal –un 17 % de mitjana–, fet que podria provocar que el segrestament de C_a fos més gran que no s'havia previst. Aquests resultats han fet que alguns autors ofereixin visions força optimistes sobre la capacitat dels ecosistemes terrestres per compensar l'excés de C_a. No obstant això, l'augment de C_a no es tradueix només en un augment de la NPP (diferent per a cada espècie), sinó també en canvis en la morfologia de la planta (també diferents per a cada espècie), que comportaran canvis en els patrons d'ocupació de l'espai, que fan difícil predir en quin sentit canviarà la NPP a llarg termini en l'ecosistema sencer. No és gens clar que aquestes previsions optimistes siguin aplicables als ecosistemes terrestres mediterranis, en els quals la sequera –principal factor limitant de la NPP– s'espera que s'agreugi en un futur, com a conseqüència del canvi climàtic. L'agreujament de la sequera es pot traduir en un augment del risc d'incendi, fet que pot conduir els ecosistemes mediterranis a una situació de gran inestabilitat, en cas que la periodicitat i la intensitat dels focs superin llur capacitat de recuperació (per germinació o rebrot). L'incendi implica pèrdues importants de N i P per volatilització; també provoca un fort augment de la disponibilitat de nutrients (sobretot N) i, doncs, un augment de la fertilitat del sòl. Moltes espècies mediterrànies, i en concret l'alzina (*Quercus ilex*), tenen una gran capacitat d'acumular N en òrgans basals, probablement per facilitar un rebrot ràpid després d'un foc, però no sempre una gran capacitat de captar l'excés momentani de N disponible. Aquest fet comporta la pèrdua d'aquests nutrients en excés, i agreuja l'empobriment en nutrients que s'esdevé a cada incendi. Si el temps entre dos focs és més curt del necessari per a la recuperació dels nutrients perduts, l'ecosistema pot entrar en una fase de degradació que pot limitar el seu paper futur com a segrestador de carboni. En conjunt, la nostra anàlisi insisteix en el fet que cal ser prudents pel que

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is shorter than the time needed to recover these nutrient losses, the ecosystem can enter a phase of degradation which could limit its future role in carbon sequestration. Overall, we advise against overconfidence in the capacity of terrestrial ecosystems to compensate fossil C emissions, especially in the case of Mediterranean plant communities.

Keywords: Climate change, carbon sequestration, plant respiration, Mediterranean, wildfires, nitrogen, resprouting

fa a la capacitat dels ecosistemes terrestres per compensar les emissions de C fòssil, especialment en el cas de les comunitats vegetals mediterrànies.

Throughout the Earth's history, the atmospheric CO_2 concentration (C_a) has undergone significant changes. An overall view of these changes [1] indicates that at the start of the Cambrian period (about 550 My BP) C_a was about 20 times its current value and then decreased to values similar to the current ones, until about 300 My BP. In the next period, C_a increased significantly such that around 175 My BP it was about five times higher than presently; subsequently C_a values decreased again. Just 15 My BP, C_a was very low, only about 200 ppmv, but it has been increasing more or less erratically ever since. The approximate value of C_a before the industrial revolution in Europe was about 280 ppmv but, in spite of the increase during the previous 15 My, it was still one of the lowest C_a values in the Earth's history.

During low C_a, the availability of CO_2 –prime matter for photosynthesis– is a limiting factor in plant production. The increase in photosynthetic activity when C_a is increased is a well-known phenomenon, widely cited in textbooks [2] and well-demonstrated by the fact that CO_2 fertilizer is sometimes applied to intensively cultivated crops. Hence, when concerns about increased C_a initially appeared, a predictable question was whether this would result in a worldwide increase in photosynthetic activity, increased organic matter production –at both the single-plant and whole-ecosystem level– and, as a consequence, an increased incorporation of C_a into terrestrial ecosystems (so-called *carbon sequestration*) that would compensate, at least partially, for the excess CO_2 released into the atmosphere by human activities.

Atmospheric CO_2 and plant production

Photosynthesis is limited by low C_a. Hence, an increase in C_a (and excluding other changes in climate) results in an intensification of photosynthesis, and therefore in an increase in plant production. In C3 species, CO_2 and O_2 are substrates that compete for the same active site of the enzyme Rubisco (ribulose 1,5-bisphosphate carboxylase): CO_2 binding leads to initiation of the photosynthetic pathway, whilst O_2 results in photorespiration [3]. Hence, a rise in C_a levels must by itself result in an enhancement of photosynthesis and a reduction in photorespiration.

Not all plant species are equally affected by increased C_a

levels. C4 species are much less affected than C3 species because of the high CO_2 concentration in the photosynthetically active cells of the former, which greatly diminishes (or even suppresses) photorespiration [3]. A classical scheme for photosynthetic activity with increasing C_a in both types of plant is given in Fig. 1. As can be seen from the figure, C4 plants are currently at or near their maximum photosynthetic capacity, and little increase in photosynthesis is expected as a result of a rise in C_a. In contrast, the productivity of C3 plants is expected to increase dramatically: their photosynthetic activity could become similar to that of C4 plants, or even higher if atmospheric CO_2 rises beyond the 750 ppm threshold. Since C4 species are mostly herbaceous, dominant in grasslands, whereas most trees and shrubs are C3 species, the postulated increase in plant productivity is expected to mainly affect forests and shrublands.

In the long term, the effect is less certain, because plants may show photosynthetic acclimation under high C_a, which consists of a reduction in photosynthetic rates, after an initial rise, to values close to the initial ones [2]. The underlying causes of this phenomenon are as yet poorly understood, but are related to the reduction in photosynthetic capacity (for example, less Rubisco [5]). Nevertheless, in most cases
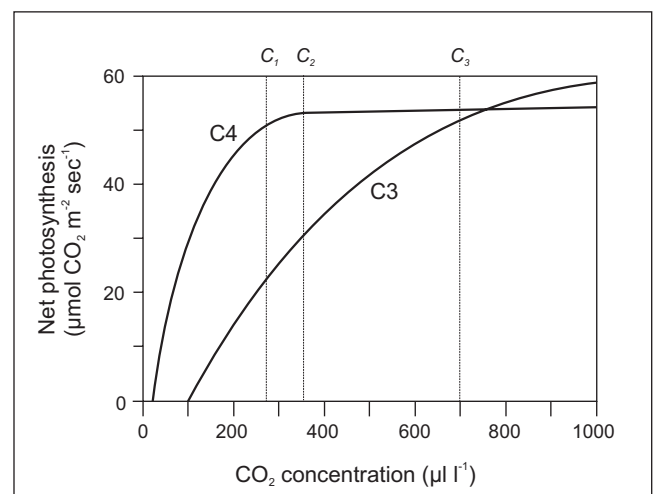

Figure 1. Typical curves for C3 and C4 plant species of net photosynthesis vs. atmospheric CO_2 concentration (C_a) values. Vertical dashed lines indicate three levels of atmospheric CO_2 concentration: that of the pre-industrial atmosphere (C_1), that of the current atmosphere (C_2), and that expected for the atmosphere around 2050 (C_3). The exact date for the third line may vary from one author to another. From [4], redrawn and slightly simplified.

the new photosynthetic rates after acclimation are still higher than those of plants maintained at normal C_a: consequently, an enhancement of photosynthetic activity is still likely, even though it would be quantitatively less spectacular than short-term experiments would suggest.

In addition to the expected increase in photosynthetic activity, other effects could enhance plant production, namely, changes in plant anatomy and morphology. Roots are the plant organ whose dry mass increases the most under CO_2 enrichment [6]. Nevertheless, whilst in agronomic plants an increase in the root:shoot ratio has been widely observed, this seems not to occur in forest species [7]. This result is important when considered in relation to plant respiration. It has been shown that increased CO_2 results in decreased plant respiration, as we will discuss below in more detail. Such a decrease in carbon loss is valid for photosynthetic organs. Per unit dry weight, root respiration is significantly higher than respiration of above-ground organs [8]; hence an increased root:shoot ratio could result in increased respiration per plant [7]. In trees, because of the maintenance of the root:shoot ratio, this effect is not expected to occur. With respect to C sequestration, this is important, since it has been calculated that in C3 plants up to 50% of the C_a fixed by photosynthesis might be lost by respiration [9].

Other important effects of increased C_a include an improvement in water use efficiency (WUE), defined as mol fixed CO_2 per unit water consumed, due to a decrease in transpiration. Both C3 and C4 plants are affected by this phenomenon, which should result in increased plant production: on average, transpiration is lowered by 34%, resulting in an increased yield of, on average, 33% [10]. This effect, mostly observed in crop plants, could be important in natural communities in dry areas, in which water availability is the most important constraint. However, the overall effect is likely to be less simple, because rising CO_2 levels result in larger plant size and increased leaf area [11]. Thus, decreased water use may be counterbalanced by an increase in plant size. Thus, although the transpiration per leaf may decrease, the transpiration per plant may increase. In intensively cultivated, irrigated crops, the predicted result would be increased plant production, with or without a decrease in total water consumption, but this may not be the case for natural, non-irrigated plant communities.

CAM (Crassulacean acid metabolism) plants are a particular case in this framework. They constitute a minor percentage of the vascular plant species (6-7%), and often show a succulent-type morphology (Cactaceae, for instance), which results in high drought resistance. In fact, dry climates favor the expansion of CAM plants [12], and CAM plants show a highly positive response to increased C_a values, comparable to that of C3 plants [13, 14]. This fact, in combination with their high drought resistance, recently led some authors [14] to predict a great expansion of CAM plants worldwide and, in those habitats in which the presence of CAM species is quantitatively significant (arid and semi-arid regions), an enhanced role of these plant species in carbon sequestration at the ecosystem level. Intentionally expand-

ing selected CAM crops could also be considered. It is noteworthy that, based on recent findings, the aforementioned photosynthetic acclimation to increased C_a is not observed in many CAM species [14].

The great capacity of CAM species to adapt themselves to increased C_a should result in an enhancement of their colonizing capacity, which is already high under current conditions [15-17]. This may be not good news, from a nature-conservationist point of view, because such colonization often results in the displacement of the native flora or, for some species, even its suppression. In Catalonia, *Opuntia ficus-indica* has become a naturalized plant and is currently expanding its area. Its colonizing potential –like that of most CAM species– could be enhanced in the future if the Earth's climate evolves towards increased drought and higher temperature.

Respiration rates under CO_2 enrichment: an optimistic view

Plant physiologists in the field of plant respiration have suggested that future rates of carbon sequestration could be higher than those of the above estimations, due to the decrease in plant respiration at high CO_2 concentrations, which had not been previously taken into account.

The decrease in plant respiration as a result of increased C_a is a well-known phenomenon, since it was observed as early as 1896 by Mangin (mentioned in [18]), but the biochemical mechanisms of this drop in respiratory activity have only recently begun to be understood [19]. As expected, the decrease is the result of many processes, some well accepted but others still somewhat speculative. They include direct effects, such as the inhibition of mitochondrial respiratory chains [20, 21]. Several respiratory enzymes have been shown to be inhibited by increased C_a or bicarbonate levels, e.g. cytochrome oxidase [20, 22, 23] and succinate dehydrogenase [24], or the enhancement of dark CO_2 uptake, through the increased activity of PEP-carboxylase in the presence of high concentrations of its substrate (bicarbonate) [19]. These direct effects are not likely to account for the observed inhibition of activity levels; hence, it is necessary to also take indirect effects into account. These are less obvious because they are based on regulatory feedback of the metabolism of the whole plant , including changes in the proportion of growth respiration/maintenance respiration, and changes in the amount and composition of available substrates for respiration. It should be noted that increased photosynthetic rates due to increased C_a often result in enhanced carbohydrate content [25] but, whilst in young plants these carbohydrates seem to be the main source for plant respiration [26], this may be not true for mature, slower growing plants [9].

The reduction in respiratory activity due to increased C_a is highly variable, as expected, and it should be noted that an increase, not a reduction, is sometimes found [25]. However, the available information [19, 27, 28] suggests that, overall, doubling C_a values will reduce plant respiration rates

by an average of 17 %, thus increasing the sequestration of C_a into the terrestrial biota.

Effects at the ecosystem level

Within the context of climate change, the decrease in respiration is a particularly important process, because C_a sequestration by terrestrial ecosystems is one of the principal ways in which to mitigate the greenhouse effect. The Kyoto protocol established that the allowed C emissions for a given country would depend, among other factors, on its capacity to compensate for these emissions through environmental policies that lead to increased C_a sequestration by the biosphere, not only by means of re-forestation, but also as a result of more rational management of agricultural ecosystems, which could enhance the role of agricultural soils as a carbon sink [29]. A decrease in plant respiration, together with a possible increase in photosynthetic rates, should result in an increased efficiency of terrestrial vegetation to act as a sink for C_a, and therefore in a surplus of *allowed* CO_2 emissions for a country having large expanses of forests and/or grasslands. The current effort made by many countries to quantify its current and potential carbon budgets must be seen in this context.

Studies of plant respiration under increased C_a have been undertaken mainly in grasslands and crops [19]. Less data is available for tree species. This is especially necessary because forest ecosystems are assumed to make a major contribution to the terrestrial carbon sink. Nevertheless, in the available studies an overall decrease has been observed in the respiratory activity of trees [30].

On a worldwide scale, it has been calculated that a reduction of 15% in plant respiration could result in a net sequestration into the terrestrial biosphere of 6-7 Gt of carbon. Such a result, obtained using the computer model GTEC 2.0, arose from considering, on the one hand, the reduction of the ratio respiration/biomass, and on the other hand, the increase in biomass and the decrease in N content also foreseen as an indirect result of increased C_a. The first one would give a net surplus in the C incorporation of 3.4 Gt C year^{-1}, and the second a surplus of 3.4-4.3 Gt C year^{-1}, both by comparison with current levels. We must be cautious in our interpretation of such a result, since it has been obtained using computer models that, as all models do, require a number of assumptions. Nevertheless, it is an optimistic result about the capacity of the biosphere to adapt itself to a climate change. It is noteworthy that the overall sequestration surplus (6-7 Gt C year^{-1}) is larger than the C emissions predicted for the USA over the next 30 years (1.5 Gt C year^{-1}) [31].

An optimistic future?

The results described above have led some institutions to release highly optimistic predictions about the capacity of forests (current and future) to compensate for fossil C emis-

sions into the atmosphere. A recent report published on the Internet by the Center for the Study of Carbon Dioxide and Global Change on C sequestration in forests [32] is a good example of this. Nearly all the data cited by that study showed an increase forest productivity, under rising C_a and/or air temperature conditions.

Care must be taken if these results are to be extrapolated to a worldwide scale, in the context of climate change. It is worth noting that most of the studies addressed the effects of increasing either C_a or temperature, but not both together. Some field studies have described increased plant production and C sequestration at an ecosystem level, which was attributed to rising temperatures. This has been seen, for instance, in Finnish forests [33] and can be explained by the fact that in boreal forests temperature (together with light availability) is the main limiting factor for plant production. However, it is unclear that such a result could be translated to warmer biosphere regions, where temperature is not the main limiting factor for plant production, for example, in Mediterranean countries, in which water deficits are the main constraint. An increment in plant biomass has also been observed in tropical forests [34], and it has been calculated that this increase could explain per se about 40% of the 'missing carbon' in the biosphere. In this case, taking into account the high temperatures of tropical ecosystems, such an increment can reasonably be attributed to rising C_a values. We must note, however, that tropical forests are currently being destroyed at an alarming rate, and probably the majority of them will have disappeared within a few decades, a fact that should be taken into account when calculating future C sequestration.

For many ecosystems, however, including Mediterranean forests, scaling up results from the single plant level to the whole community level is not just a matter of arithmetic. For instance, in a nursery experiment carried out with seven tree species typical of the northeastern USA [35], increased C_a did result in an increased biomass overall. Instead, the percentage of this surplus differed significantly, leading to the conclusion that some species will be favored over others, and changes in the community structure can be expected. Furthermore, increased C_a results not only in variations in plant biomass, but also in the morphology of affected plants. An example for Mediterranean species grown in the field under elevated C_a [36] is given in Fig. 2. Note that the change in plant production is not always positive, and is never homogeneous for the different plant parts. Of particular interest is the behavior of fine roots (Fig. 3), whose production decreased with respect to the control plots by 43 %, overall. The authors mentioned that, in the same experiment, an increase in root growth of 47 % was observed during the first few years due to the C_a increase: i.e. short-term positive results do not extrapolate to long-term periods. It was suggested that the excess root production resulted in an excessive consumption of soil nutrients, which may have become limiting in the subsequent period, a problem suggested previously [37]. This effect would not be observed in crops, where fertilizers are widely used, but in natural ecosystems it can strongly limit the positive effects of rising C_a.
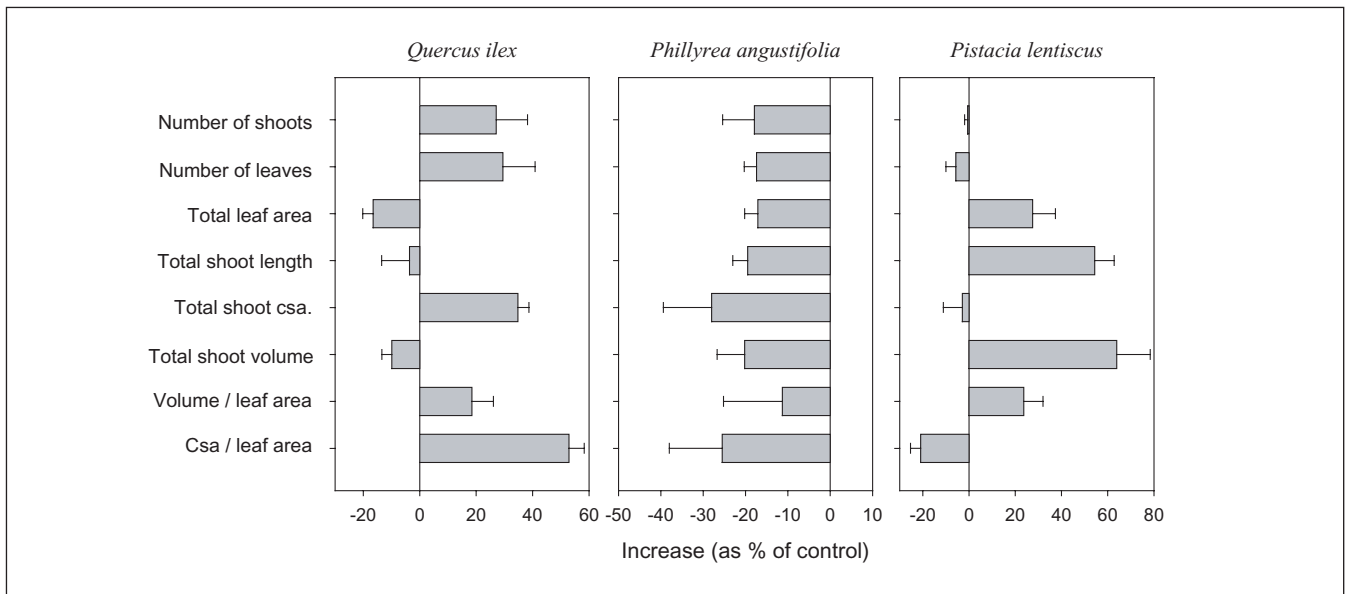
Figure 2. Quantification of changes in the morphology of the aerial part of several Mediterranean plant species as a result of increased C_a. Production of new shoots and leaves after 1 year of CO_2 enrichment. Data are given as percent of control plants; horizontal bars are standard deviations. Drawn from the numerical results of [36].
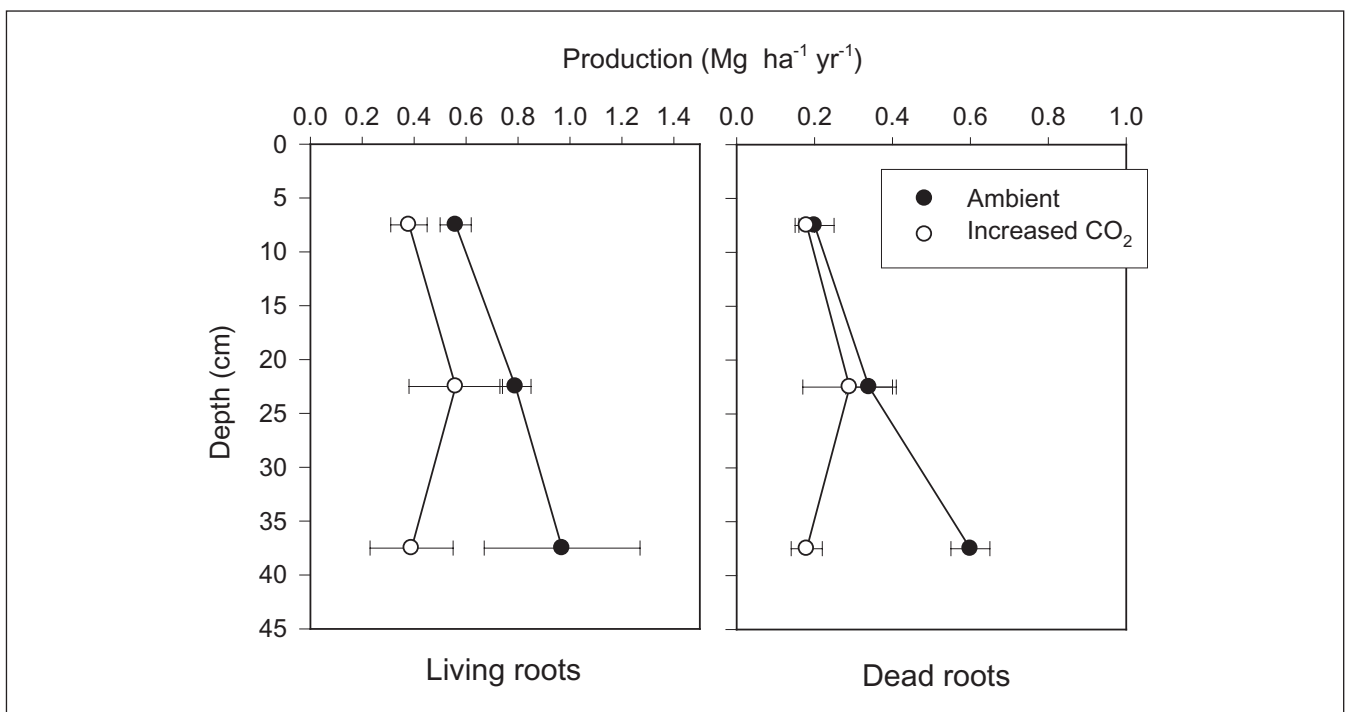

Figure 3. Quantification of changes in the production of fine roots (< 5 mm diameter) under ambient and enriched C_a conditions. Drawn from the numerical results of [36].

In general, care must be taken when data relating to fine root production are included in calculations of the entire terrestrial carbon budget, since recent results [38] suggested that the role of root production as a carbon sink may have been overestimated until now.

An interesting point for Mediterranean forests is how climate change is expected to affect the dynamics of tree leaves. Based on model simulations (GOTILWA model [39]), a decrease in the mean life of Mediterranean tree leaves (*Quercus ilex*, *Pinus halepensis*, *Pinus pinaster*) has been predicted, whilst in a deciduous, non-Mediterranean species, such as *Fagus sylvatica*, an extension of the vegetative period of leaves is expected [40]. The increased litterfall should result by itself in increased C sequestration in soils; however, since the rise in temperature results in an increased microbial activity, it is not clear that the increased C supplies are enough to compensate for the increased C loss due to soil respiration. C sequestration by trees should increase as a result of the increased C needed to replace the fallen leaves, but the validity of this prediction depends on the maintenance of the current rainfall regime and could be wrong if drought increases in the future [40].

Overall, the changes in plant morphology should result in changes in the patterns of space occupation [41], thus making it difficult to predict whether or not a (possible) increase in plant biomass at the single-plant level will result in increased biomass at the plant community level.

Carbon in soil

Currently, the forest soils of the Mediterranean zone are an efficient carbon sink, whilst those of Central Europe and Nordic countries seem less active [42], partly because of the lower respiration rate of soils in the southern latitudes, due to the summer drought, although it could also be due to the history of forest sites in Mediterranean countries. Many forests in these countries are recent; they have developed (by natural secondary succession, or through forest plantation) on abandoned agricultural lands, and as such they are in quite an early stage in the development of the organic matter profile of the soil , in which rates of carbon sequestration may be high.

A priori, it seems unlikely that increased C_a will have a direct effect on microbial activity, since the soil atmosphere is already highly enriched in CO_2 with respect to free air [43]. In an experiment aimed at studying CO_2 fertilization in Mediterranean forests [36], few effects on microbial activity were observed: these occurred mainly at the start of the experiment but were quickly buffered by the complex soil biocoenose, so that the soil system returned to control conditions within a few months. The effects of increased C_a should be mainly indirect, through (i) rising temperatures due to the greenhouse effect, and (ii) a decrease in the decomposition rate of plant residues (mainly leaf litter) due to the decrease in plant residue quality [44]. The former should result in a decrease in the soil C pool, due to the stimulation of microbial activity, whereas the latter is expected to result in an increased C accumulation in soil. A potential third cause, increased C availability due to the increased release of fine roots and/or exudates, will depend on whether or not such phenomena will really occur in the long term, as mentioned above.

The changes in litter quality are a response of plants to elevated C_a. It has been observed that such a response leads to plants with reduced protein content but increased carbohydrate content. The result of these changes is an increase in the C/N ratio of the litter, usually interpreted as a decrease in its quality for decomposition, because a higher C/N ratio implies a lower N availability for soil microflora [45]. The increase in the C/N ratio of plant litter should cause a decrease in decomposition rates [46, 47], but this is not always the case. For instance, no changes in decomposition rate were observed in a study of litters of tropical trees [48]. As a general trend, the decreases in litter quality due to rising C_a values result in no changes, or in a slight decrease in decomposition rate. In the long term, this implies a higher accumulation of C in the soils, hence in an enhancement of the role of soils as carbon sinks, provided that the lower N avail-

ability does not result in a decrease in plant production. The results obtained in the CLIMEX project (in which a boreal forest ecosystem was subjected to increased C_a) are relevant here, since they suggest that, under climate change, if no N deposition occurs, boreal forests will suffer a net loss of N to groundwaters, and become a net source of N [49].

However, it should be noted that in many industrialized countries forests are subjected (now and probably in the future) not only to increased C_a and air temperatures, but also to increased rates of nitrogen deposition. This is of particular importance because N availability is often a main constraint in stand development. The productivity of Swedish forests, for instance, greatly increases as a consequence of N fertilization [50]. Could such an extra input of N into the ecosystem compensate for the effect of the increased C/N ratio? Results at this point are inconclusive. Whilst N additions accelerate the first stages of litter decomposition, when N is limiting for the activity of the microflora, over the long term they can retard the decomposition of mature, humified organic matter, because in this case N acts as a stabilizer of humic compounds [51]. Nadelhoffer and colleagues concluded that N deposition does not have a significant effect on global C sequestration [52]. While no clear answer is available to this question, predictions about the future of the soil C budget –at least in boreal and wet temperate countries, those most affected by N deposition– will remain highly speculative.

Constraints on carbon sequestration

Photosynthesis and photorespiration, plant transpiration and plant (and microbial) respiration seem to be the only biochemical processes directly affected by C_a [5]. Other effects on the ecosystem are indirect. Nevertheless, such indirect effects can be as important as the direct ones. Climate change will not only affect C_a and air temperatures, but also the precipitation regimes of many countries.

For the Mediterranean basin, predictions from climatic models indicate that increased air temperature and potential evapotranspiration are expected, together with decreased rainfall, and hence an increased risk of drought [53]. By itself, this should result in a decrease in soil microbial activity. A European experiment of simulated climate warming showed this effect quite clearly [54]. In this experiment, forest soil samples were incubated under field conditions, each at its original location and also moved to a southern site: when a soil horizon from a northern forest was translated to a warmer but still temperate site, SOM decomposition rate increased; in contrast, when it was translated from wet-temperate to dry Mediterranean conditions, SOM decomposition rate decreased. The decreased microbial activity is expected to result in increased stability of SOM, which would enhance the role of soils as carbon sinks, provided the inputs are maintained. The latter remains speculative, since increased drought would also cause an increase in both water stress for plants and fire occurrence because of

reduced moisture of the forest biomass. In Mediterranean countries, water availability is the main limiting factor for plant production, and this problem is expected to worsen in the future. Therefore, an increase in forest biomass and C sequestration in the biomass due to rising temperature and C_a seems, a priori, unlikely.

Mediterranean ecosystems: fire as a constraint

Wildfires are a natural phenomenon, and it is accepted that they have an important role in the maintenance of biodiversity as they allow opportunistic, poorly competitive plant species to meet temporal ecological niches, thus avoiding excessive dominance of the climax ecosystems. The maintenance of shrublands against forest expansion, for instance, is thought to be due to the periodic fires that they suffer. In Mediterranean countries, wildfires at 20-50 year intervals are thought to be necessary to maintain shrubland communities [55, 56]. Even in the national park of Yellowstone, wildfires are a natural, periodic phenomenon, and in recent decades the conservation policy has included allowing small– to medium-sized wildfires to occur, although, even after the enormous fires of 1988, some forest ecologists from the USA continue to wonder whether they should be allowed [57]. However, the enhancement of the role of forests as carbon sinks would be incompatible with such a radical ecological position, as indicated by the strong carbon sequestration in North American forests resulting from the suppression of forest fires in the last century [58].

Wildfires result in a destruction of the vegetation, hence in a temporary interruption of the inputs of carbon to the soil, until vegetation is at least partially recovered. By itself, such an interruption, if repeated, decreases the role of forests as carbon sinks [59]. As expected, the shorter the gap between two wildfires, the greater the reduction (Fig. 4). Neverthe-

less, these simulated effects may be difficult to observe during short- or medium-term field research, because soil is a compartment with a significant inertia. For instance, the suppression of wildfires for 35 years in oak savannas of Minnesota resulted in a significant increase in C stored in the ecosystem: from 110 Mg ha^{-1} in control plots to 220 Mg ha^{-1} in fire-suppressed plots. Carbon increase was concentrated in woody debris, coarse roots, forest floor and especially trees; in contrast, no changes in soil and fine roots were detected [58].

The combustion of organic matter represents a return of C to the atmosphere, to a greater or lesser degree, depending on fire intensity: if not too intense, part of the pre-existing organic carbon of the biota will become charcoal, a pool of great importance in terrestrial ecosystems because of its resistance to biodegradation. The dynamics of charcoal as a carbon pool are poorly understood, partly because of the lack of reliable, routine methods to quantify it in soil samples, in spite of recent promising advances [60, 61]. Nevertheless, available data indicate that charcoal may represent a substantial proportion of total soil organic carbon: up to 35% of the total in some US agricultural soils [62], and more than 50% in some chernozemic soils in Canada [63]. Hence Fig. 3 must be taken as an oversimplification of reality, because repeated wildfires could result in a significant generation of charcoal, which could accumulate in large amounts in the soil due to its stability. Nevertheless, the data of Duguy [64] suggest that, at least in shrublands, the generation of charcoal is not enough to compensate for the effect of the interruption of C inputs to the soil. It is noteworthy that the effect can be detectable after as few as one or two wildfires (Fig. 5).
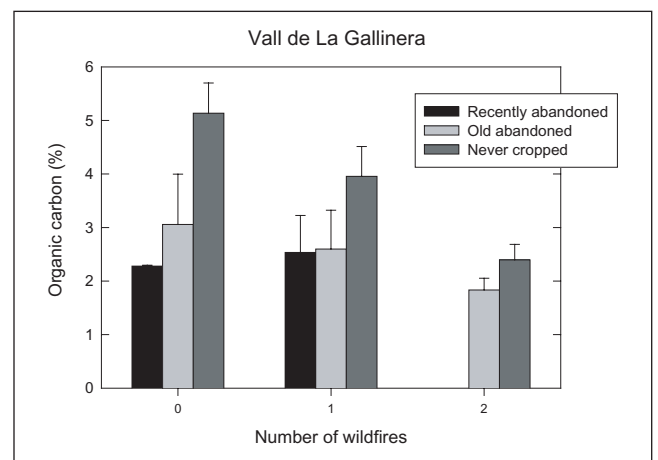
Figure 5. Concentration of organic carbon in the surface horizon of soils under shrublands, according to the fire regime and previous land use. Data obtained in La Vall de la Gallinera (Alacant). NC, Never cropped sites; OA, old abandoned crops; RA, recently abandoned crops. Data are averages of three sites; vertical bars are standard deviations. There were no available sites of RA type subjected to two recent wildfires. Data from [64].
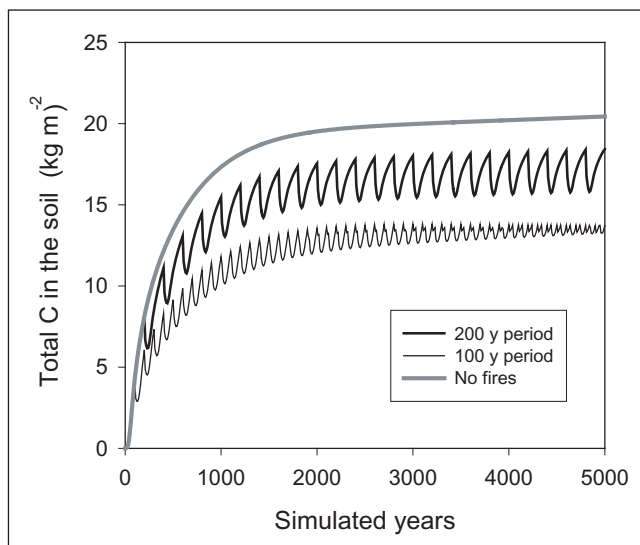

Figure 4. Simulated evolution of the total C accumulated in soil, according to three regimes of periodical wildfires: (1) no wildfires, (2) a wildfire every 200 years, and (3) a wildfire every 100 years. Results obtained using the computer model PERFIL [59].

Fire recurrence will become a crucial factor in the long-term role of forest ecosystems as carbon sinks. In forests of evergreen holm oak (*Quercus ilex* L.), resprouting is the principal means of tree recovery after a fire event, and these

forests persist irrespective of fire regime. In contrast, the persistence of pine stands is only possible when the interval between two fire events is long enough to allow the growth of pine seedlings such that a sufficient amount of cones is produced; usually, about 15 years. A recurrence of wildfires within less than 15 years can lead to the suppression of pine forest stands and their probable replacement by shrubland. In terms of carbon budget, this implies a reduction in the capacity to sequester C, since shrublands have less biomass and production than forests.

Nitrogen as a limiting factor

In addition to carbon released into the atmosphere, during a wildfire many nutrients are lost, mainly N and P [65-67]. N losses are unavoidable because of the low volatilization temperature of this nutrient under dry conditions [68, 69]. Those of P are expected to be lower: in organic soil samples P can volatilize at temperatures below 400°C, but in mineral soil samples P does not volatilize at temperatures lower than 550°C [70]. Nevertheless, these temperatures are sometimes reached in forest fires. During an experimental fire in the Prades' mountains (Catalonia, NE Spain), the temperature reached up to 200°C at 100 cm above the soil surface,

500°C at 50 cm, and up to 750°C at the soil surface. In the mineral soil, the temperature drops quickly: 370°C under the organic horizons, 240°C at 2 cm depth, and just 58°C at 7.5 cm depth [71]. Under these conditions, both N and P losses are expected to be low or non-existent in the mineral soil, but substantial in the vegetation, as confirmed by the experimental data (Fig. 6). It should be noted that the amount of lost N was about twice the amount of N remaining in the ash after fire; losses of P were lower, but also significant.

Losses of C, N and P may be restored with time: C through photosynthesis, N and P through atmospheric deposition (wet or dry), P also by weathering, and N additionally through N_2 fixation, mainly by leguminosae. In a wet forest in Tasmania, it was calculated that the N lost as a result of a wildfire could be restored by rain N inputs in about 15–20 years [73], and in northern countries, because of N deposition, losses could be also restored in a relatively short time. This is not the case in Mediterranean forests, which have a low N deposition. Actually, in the forest of Prades both water and N are the main limiting factors for tree growth [74].

Repeated wildfires may result in a significant impoverishment of the nutrient budget of the ecosystem over time. The key factor is that the time interval between wildfires must be long enough to allow the recovery of the lost nutrients. This lag is variable depending on the site and the nutrient, and
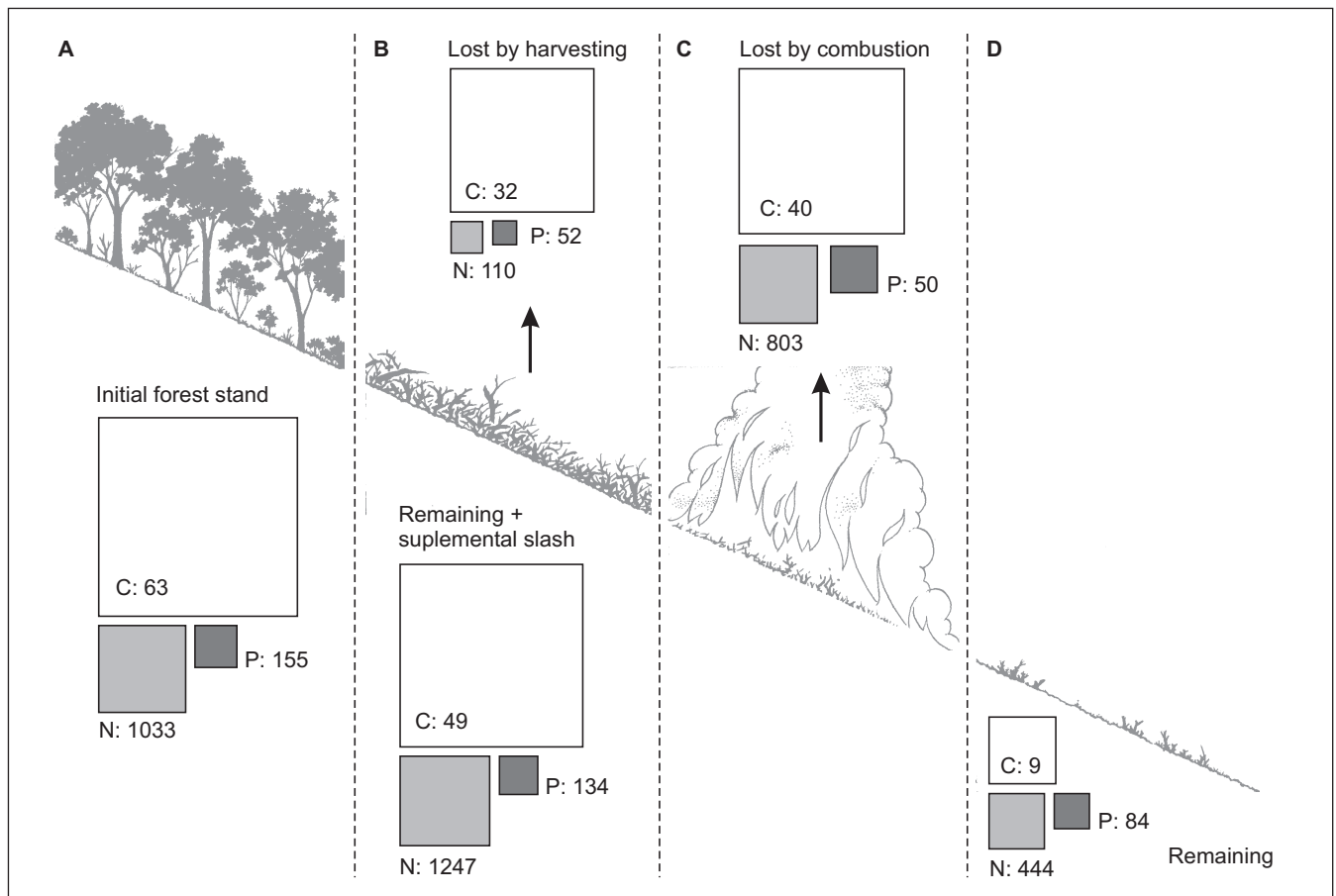

Figure 6. Changes in total C (organic), N and P in the aerial part of a *Quercus ilex* forest (including forest floor) subjected to experimental clearcutting and burning. Data for carbon in Mg ha^{-1}; data for N and P in kg ha^{-1}. A Intact forest. B The forest was clearcut: logs and branches greater than 2 cm in diameter were removed, the slash was homogeneously distributed over the plots, and the plot to be burnt received supplemental slash, in order to simulate an intense surface fire. C The remaining mass in the site was burnt. D Remaining C, N and P in the aerial part, immediately after the fire. Data from [71], redrawn and slightly simplified.

are usually longer for P than for N. Even for low-intensity fires, such as prescribed ones, a deleterious effect on soil fertility is possible due to the loss of nutrients. For prescribed fires, time intervals of about 10–12 years for N and of about 20 years for P have been mentioned [66]. For wildfires, since all the biomass is subjected to burning and not only the understory, time intervals are longer: about 100 years for P in a sclerophyllous forest of Tasmania [75]. The majority of Mediterranean forests in Catalonia have burned more frequently, and many shrubland communities burn at time intervals shorter than 20 years.

Resprouting

The nutrient impoverishment referred to above may not be significant when considering a Mediterranean forest after a wildfire, because of efficient plant re-colonization and resprouting. The germination of some Mediterranean shrub species, such as *Cistus albidus* and *Cistus salviifolius*, is favored by the high temperatures reached in wildfires [76].

The resprouting capacity of many Mediterranean plant species, and in particular *Quercus ilex*, is well-known [77], and is a key explanation of their success in fire-affected landscapes. Resprouts have a somewhat peculiar physiology, which has been extensively studied by our group, and it is worth summarizing their main features.

There is little difference between the physiology of tree resprouts from burnt and felled sites [78]: the physiological changes appear to be responses to a strong increase in available light, irrespective of the reason for such an increase. The primary effect of burning is the loss of plant cover, whilst the root systems are essentially unaffected. As a result, water and nutrient availability is greater for resprouts than for unburned plants, since the pre-existing root system is originally associated with a much larger aerial biomass [79-82]. An increasing root/shoot balance favors the stimulation of photosynthesis and rapid growth, as reported for *Quercus ilex* L. [77, 83, 84], *Quercus rubra* L. [81, 82, 85] and several chaparral species [86-88].

A crucial aspect of this adaptation is the resistance to excess irradiation. The increase in leaf carotenoids [77], for instance, should be interpreted in this context. Lower photosynthetic rates in unburned plants were the result of lower stomatal conductance and induced increased photoprotection for dissipating the excess light energy [84, 89, 90]. Both energy dissipation (as heat) and detoxification mechanisms contribute to the protective strategies of control plants and resprouts, to a different extent. In resprouts, reduced xanthophyll cycle participation (as shown by non-photochemical quenching and xanthophyll pool content) was compensated for by an increased participation of hydrophilic antioxidants [91].

The overall consequence of the resprouting capacity of many Mediterranean plant species is high ecosystem resilience, particularly in those communities dominated by broad-leaved evergreen trees and shrubs. For instance, in

the experimental forest of Prades, in 1988 [71,72], fire was of medium-high intensity, and the vegetation was completely destroyed. In about 2 years, the newly developed vegetation covered almost 70% of the soil surface: *Quercus ilex* resprouts covered almost half of this surface, 31%. In some post-fire chronosequences in Garraf (Barcelona), vegetation recovery was even more spectacular, since in some sites a plant cover of 100% (30% of which were *Quercus ilex* resprouts) was achieved in just 2 years (Fig. 7) [92].

Figure 7. Vegetation recovery after fire, in three Mediterranean ecosystem chronosequences: forests (holm oak: *Quercus ilex*), garrigue (*Quercus coccifera*) and shrublands. Data from [92]; the curve-fitting data have been re-calculated.

Short-term and long-term nitrogen limitation

It has been suggested that one of the reasons for the rapid recovery of vegetation after a wildfire is the short-term increase in soil fertility. Actually, most disturbances of forest ecosystems, and in particular clearcutting, result in a shift in soil fertility, usually N availability and nitrification increase [93]. This has been attributed to two main factors: (i) increased substrate availability; (ii) improved pedoclimatic conditions for soil microflora, mainly temperature and moisture. Temperature increases because irradiation can directly reach soil surface; moisture increases because water absorption by roots is suppressed, at least partially. These positive effects may be reversed in the medium term: if nitrate is not taken up by roots, it may be more or less completely lost by leaching [94], even though exceptions have also been noted [95].

These features also apply to burnt forests, for which an increased N mineralization has also been observed [95, 96]. An increase in the availability of nutrients is also evident. In the experimental fire of Prades mentioned above [71,72], even though nutrient losses were substantial, in ash and in the H horizon there was a short or medium term increase in available nutrients to the soil microflora and the roots. Hence, soil fertility is expected to increase in the first several months after fire. Laboratory data agree with this observation: the ash layer had an electrical conductivity of 3.13 dS m^{-1} just after fire, 82 days later it dropped to 0.84, and then decreased further to 0.45-0.35 by the end of the first year, values similar to those of the control plot. A similar result was obtained in the H horizon, a decrease from 0.89 dS cm^{-1} to 0.42, similar to the values of the control plot. This meant a

substantial loss of mineral salts, i.e. nutrients (sulphates, nitrates and phosphates of K, Na, Ca, Mg and others), which reach the mineral horizons and become more or less immediately available to roots. Similar results have been obtained by other authors [97, 98].

An important point is to what extent the recovery of vegetation after fire is due to this increased soil fertility. In the case of Prades, an increase in the amount of inorganic N in the soil was observed over the short-term. The increase was slight in the H horizon, but it was substantial in the first 5 cm of the mineral soil, and was maintained until the second year after fire [71,72]. By the end of the second year, the mineral N content had returned to values close to those of the control plot. Nevertheless, such an increase in the amount of available N may not benefit the recovering vegetation if the surplus of available N is lost by leaching. Results obtained from exchange resins suggest important losses of N in mineral form in the burnt soil compared with N amounts in control and clearcut plots (Fig. 8).
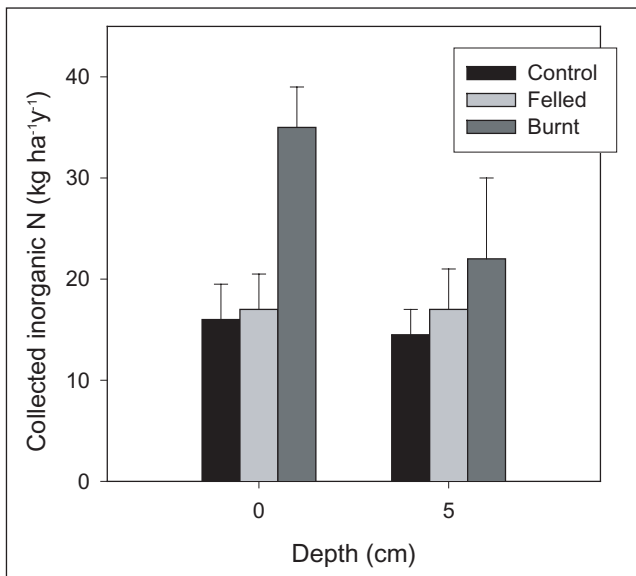

Figure 8. N leaching during the first year after fire, as collected in the field, at 0 and 5 cm depth, using exchange resins. From [71], redrawn.

As a general trend, there is increased leaching of mineral N after a wildfire has been observed [99-101], although the ecosystem has feedback regulating mechanisms to avoid dramatic losses of N, such as increased immobilization of mineral N by the soil microflora, following a wildfire [102-106].

Since a main survival strategy in response to wildfires is resprouting, a key point in our discussion will be how resprouts manage the N budget, i.e. their own reserves and the available soil N. Resprouts often have specialized organs to accumulate and maintain reserves, and these can be used to support regrowth; for example, lignotubers in *Eucalyptus* [107], basal chichi in *Ginkgo biloba* [108], burls in birch [109]. A true lignotuber has been described for *Quercus suber* seedlings [110, 111], but for 2-year-old *Quercus ilex* such a structure has not been observed [112]; instead,

the roots and the root crown seem to act as a reservoir for resprouting in this species. Such a reserve allows independence from the supply of external N to the plant, at least during the first year.

A nursery experiment carried out with *Quercus ilex* resprouts [91, 113], whose results have been summarized in Fig. 9 (a-c), illustrates this point. Three-year-old seedlings of *Quercus ilex* were provided with nutrient solutions with or without N grew equally well during the first year. After excision of the shoots, all plants were supplied with a N-containing nutrient solution. Resprouting was observed in only 30% of plants that had previously been given the N-deficient nutrient solution, but growth of the resprouts was the same in either case, that is, irrespective of the previous treatment (with or without N) (Fig. 9,a). In the non-excised plants, growth in the second year was much greater in those that had received a N-rich nutrient solution.

Excision did not alter the total N content of roots or root-crown: their N reserves, which are used to build resprouts, were replaced by N taken up from the nutrient medium. In excised plants, the previous nitrogen deprivation increased the proportion of N absorbed from the soil solution (% of total N), whereas in control, non-excised plants this proportion was higher in those that had received N in the nutrient solution. In contrast, there were no differences between N treatments with respect to absorbed N (as % of total N) in roots and the root-crown (Fig. 9, c). Over the long-term, however, the need for absorbed N is clear: in resprouts, the percent of new, absorbed N in the resprouts is always higher in the last leaf to emerge than in the first one. Nevertheless, even in the last emerged leaves the majority of the N comes from N reserves, and only 30 % from external N sources, which for young saplings is perhaps surprising.

In summary, *Quercus ilex* showed a strong capacity to accumulate N reserves, so that, even though there is a long-term dependence on external N sources –as any other plant species–, in the short or medium term these trees are able to survive or even grow independently of external N sources, which can be temporarily scarce. N reserves in the root system would probably increase with tree size. Since the N reserves are enough to start building resprouts and new organs, within several months external N will become essential to maintaining regrowth. N can become further limiting if the demands of the newly created branches and leaves cannot be adequately met. In the above experiment [91, 113], the control, non-excised plants with an adequate N supply grew considerably and also absorbed large amounts of N; but this was not the case in excised, resprouting plants, in which the biomass of newly created organs was small (compared to control plants), and did not act as a significant sink for N. Consequently, the global N demand of the plants was low, and so was the uptake of N from soil.

A strategy of 'resist, wait and see' has been successful for resprouting shrubs and trees, since it implies that they may resprout by themselves and wait for a natural recovery of the soil N reserve through atmospheric inputs. However, since plants do not efficiently take up a surplus of available N, it is
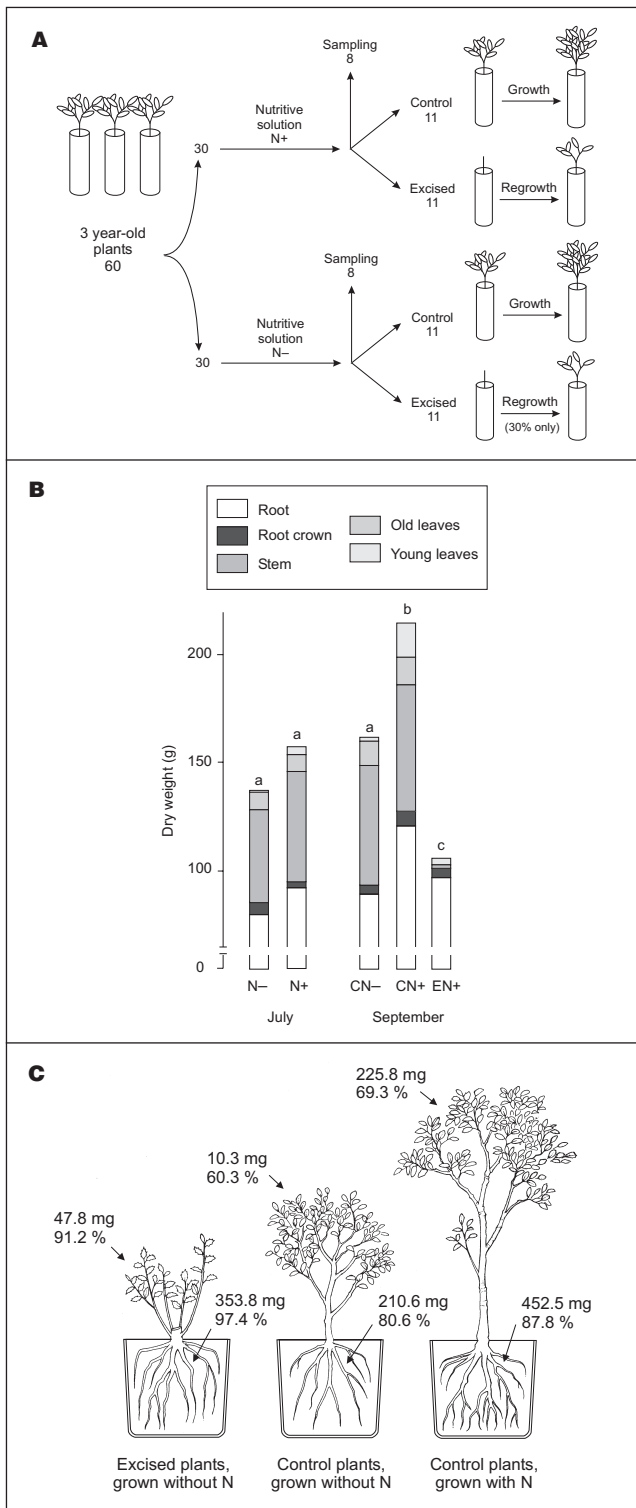
Figure 9. Growth and nitrogen use in *Quercus ilex* resprouts. From [91, 113], redrawn and slightly simplified. **A** Experimental design. Plants were initially supplied with a nutrient solution with (N+) or without (N−) nitrogen. After 1 year, some plants were sampled. Then, half of the remaining individuals were subjected to shoot excision (E), and half not (C: control plants). Both the excised and the control plants were supplied thereafter with a N-containing solution. In the case of plants previously supplied with a nutrient solution without nitrogen (EN−), only 30% resprouted. **B** Dry weight of *Quercus ilex* plants at several stages of the experiment. Different letters indicate significant differences in the dry weight of the whole plant, at $p < 0.05$. **C** Origin of the N in the *Quercus ilex* plants and resprouts, calculated from its ^{15}N signature. The data comprise the total N per individual (in mg) and the percent of this N coming from the plants own reserves.

likely to be lost. Under natural conditions, where wildfires occur at intervals long enough to allow the nutrient reserve to recover, this would be of minor importance; but in the current, humanized context, the increased wildfire frequency results in a loss of long-term ecosystem production and productivity, i.e. in the capacity of ecosystems to sequester carbon.

Are shrublands different?

The response of Mediterranean terrestrial ecosystems to the changing N budget after wildfires may be not unique. In experimental shrubland wildfires in the area of Tragó (Lleida, Catalonia), an increase in the amount of available NH_4^+ and, to a lesser extent, NO_3^-, was observed, due both to the direct effect of fire and to an increased N mineralization thereafter [114]. Nevertheless, this was followed by a period of strong immobilization, so that during the first 9 months after fire, the overall N availability in the first 5 cm of the burnt plots (mean value about 10 mg m^{-2} day^{-1}) was lower than that of control plots. Additionally, the effect of fire on the overall N budget was dependent on the site. In grasslands-shrublands dominated by resprouting species, such as *Brachypodium retusum*, the majority of the released inorganic N was retained within the soil-plant system, whereas in those dominated by the seeding species *Rosmarinus officinalis* a substantial proportion of the released N may have been lost by leaching. Of the N released after fire, a variable proportion was recovered into the vegetation: up to 100% in a mixed grassland-shrubland comprising *Brachypodium retusum* and *Genista scorpius*, about 60% in a grassland of *Brachypodium retusum* alone, and as low as 30% in a shrubland of *Rosmarinus officinalis* [114]. Note that *Brachypodium retusum* seems to be much more active than *Quercus ilex* in using external N sources when available. There is no single pattern of use of fire-generated N surplus; it may vary with plant species and, as a consequence, it may exhibit limited predictability in species-rich, complex plant communities.

A global view

Whatever the strategy employed by vegetation to utilize the available N after fire, the essential fact remains –nutritional impoverishment of ecosystems by repeated wildfires, mainly nitrogen and, to a lesser extent, phosphorus. In Catalonia, the frequency of wildfires often surpasses the capacity of atmospheric inputs to recover nutrient budgets, at least in forest ecosystems. Such a decrease in the nutrient budget of the ecosystem is expected to result in limitations to primary production and, in addition to the direct C and N losses caused by the combustion, in a decrease in the capacity of ecosystems to act as a sink for carbon. The resilience of Mediterranean ecosystems due to resprouting could minimize such an effect, but it should be noted that many resprouting

species can become exhausted by the increased fire frequency, thereby causing a decline in resprouting capacity and recovery [85, 88].

Our review of some aspects of N economy in Mediterranean ecosystems has indicated some substantial differences from boreal or wet temperate forests. For the majority of terrestrial plants, the present low C_a values are limiting for photosynthesis. Beyond this, the other limiting factors differ: the temperature increase due to climate change may result in an increased photosynthetic activity in northern forests, where plant production is limited by the cold climate, but such an effect is unlikely in Mediterranean forests, where temperature is not the main limiting factor. Rather, an increase in mean temperature, together with a decrease in precipitation, are expected to result in changes in vegetation type, particularly the replacement of forests by shrublands. This could lead current forest soils to become a source of C, because the amount of C in a soil is the result of an equilibrium between inputs and mineralization, and the input of C to the soil is usually lower in shrublands. Increased water deficits –also predicted by climate change models– and a probable increase in the frequency of wildfires would result, as discussed above, in a deterioration of Mediterranean terrestrial ecosystems, and damage to their C budget. In that context, the potential positive effects (due to decreased plant respiration or enhanced photosynthetic activity due to increased atmospheric C_a) are likely to be of minor importance.

Additionally, for many Mediterranean ecosystems, a significant drop in soil fertility is expected, due to losses of nutrients (mainly N) through wildfires. Mediterranean ecosystems are not the only ecosystems in which a low soil fertility is expected to limit carbon sequestration; such an effect has also been demonstrated in northern forests, in which an increase in C_a results in only small increases in carbon accumulation, except in fertilized forests [115]. Note also that, whereas important areas currently occupied by northern forests are subjected to N deposition, in Mediterranean countries this phenomenon is quantitatively irrelevant.

In Catalonia (as in many countries), changes in land use outweigh the possible deleterious effect of an increase in C_a and temperatures. The large-scale reduction in agriculture, especially in non-irrigated areas, has favored the substitution of ancient agricultural lands by shrubland communities, subspontaneous forests or forest plantations, sometimes of exotic species such as *Pinus radiata* or *Eucalyptus* sp. The productivity of many Mediterranean forests (especially natural forests of *Quercus ilex* or *Quercus rotundifolia*) is too low for commercial exploitation. Many of these forests are currently unmanaged, and their biomass may also accumulate. As a consequence of all of these processes, the majority of non-industrial lands in Catalonia are a net sink for carbon, and, as a result of expanding natural vegetation, many of the aforementioned constraints on the vegetation may not be apparent today. Furthermore, even though the risk of wildfires may increase due to rising temperatures and (expected) decreasing precipitation, in recent years such an effect has

been compensated for by the strong effort applied to wildfire prevention and extinction. Continuous monitoring of selected, old-forested areas is the only way to verify how rising C_a and temperatures affect Mediterranean natural communities, either positively, as according to some reports [32], or negatively (or at least unclear), as based on our discussion.

As a final remark, our analysis has pointed out the risk of being overconfident regarding the capacity of plant communities to compensate for fossil C emissions. Carbon sequestration is the result of a complex set of processes, some of which could be enhanced by climate change, but others not. Mediterranean ecosystem productivity is not expected to be favored by climate change, and the applicability to Mediterranean countries of predictions made for other areas is highly doubtful.

Acknowledgements

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