Caracterització funcional d'espècies llenyoses mediterrànies amb diferents estratègies regeneratives post-incendi

(Functional traits of Mediterranean woody species with different post-fire regeneration)

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Tesi doctoral
2008

Departament de Biologia Animal, Vegetal i Ecologia
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Centre de Recerca Ecològica i Aplicacions Forestals

Director de tesi: Francisco Lloret Maya

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Memòria presentada per:

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Per optar al grau de Doctora

Amb el vist-i-plau del director de tesi:

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Bellaterra, Febrer de 2008

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Autor del quadre de la portada: **Francesc Pujol**
Maquetació de la portada: **Olga Costa**

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AGRAÏMENTS

Ara que ja han passat 4 anys, i una mica més,... vol agrair a totes les persones que l'han ajudat durant aquest temps, durant aquest viatge cap a ítaca.
Ella no sap com fer-ho, hi ha col•laborat tantíssima gent amb ella i el seu projecte,... i no voldria deixar-se a ningú,... perquè cadascuna d'aquelles persones ha estat clau en algun punt o altre del camí i totes elles han fet possible que ella arribés a aquesta ítaca.
I pensant per on començar, s'adona de dues coses: que hi ha moltíssimes persones que l'han ajudada i li ve de gust agrair-ho també per escrit; i de fet, pensa que alguns dels agraïments haurien de situar-se alguns anys enrere (i és que una és com és per haver viscut el que ha viscut i sobretot per haver-ho viscut amb qui ho a viscut).

Sovint diem els defectes a les persones, però poques vegades els parlem de les seves virtuts. Això ho vaig aprendre del Grup d'Educació per la Pau de l'Escola de Cultura de Pau de la UAB, una de les raons que ha fet possible que gaudís, d'entre moltes altres coses, del camí dur de la tesi doctoral com ho he fet. Gràcies Carles (l'únic professor a qui li vaig posar màxima puntuació de tot en l'enquesta de professorat), i també a la Marina i a la Cécile per ser tant dolces i creure en mi, igual que també a la resta del grup per fer possible que existeixi i es puguin fer projectes d'educació per a la pau. Gràcies també a l'Alba, en Carles, l'Anna, la Marta, la Roser i la Sabrina per les rialles, poemes i vetllades. Conèixer en Pepe Beunza i el grup de tambors per la pau també va carregar-me d'energia durant estones en les que estava feta pols.

Però de fet, ella creia que havia d'anar més enrere, a l'institut. Vull agrair també al meu professor de biologia fer-me descobrir el meu potencial i les meves possibilitats com a biòloga de bota, gràcies Jesús. Però de fet, allà on va descobrir la seva vocació (cosa que al final la va dur a passar-se 4 anys suant la cansalada i fent la tesi doctoral) va ser als Aiguamolls de l'Empordà, fent de participant i monitora de campaments i camps de treball. Veure ocells i natura d'aprop i dormir arran del canyís respirant a ritme de xiulets d'òliba i xot va fer que notés clar el que volia fer en un futur. Gràcies a en Jordi Martí per iniciar-me en el món de l'ornitologia i en Toni Batet en el dels mamífers. A la Mireia Vila per transmetre'm la seva il•lusió en observar una "simple" flor. A en Berto per fer-me riure sempre i per ser un gran amic. Jota: rialles a tort i a dret; Pere: corcó i tabalot entranyable; Joan: gràcies per iniciar-me en l'anellament i les teves vetllades de cançons; Edu: dedicatòries amb estil i coreografia i moltes rialles; Anna i Roser: fèiem l'equip més bo de dones monitores que ha existit mai, sens dubte!; Albert i Dani: amics i mestres ornitòlegs torroellencs claus per mi i el Montgrí. Marc: per veure que n'hi ha que també s'estressen com jo o més; Franqui: gràcies per ser com ets i per les llargues converses tranquil•les; Helan: tu i en Franqui vareu aconseguir que visqués sense rellotge, tot i que he descobert que sense rellotge també pots tenir estrés, necessito més teràpia!. Gràcies a tots i totes per les xefles, i fer que per alguns moments el món parés de rodar i pogués respirar i riure agafant aire per poder seguir treballant. Sense dubte la meva vida hagués estat molt diferent si no ens haguéssim conegut.

Els amics i amigues heu estat molt importants durant aquest camí llarg ple d'estones bones però també de malsons i estrés i jornades inacabables. Ona, Marta, Josep, Ari, Barbara, Montse, Sílvia, Marc. Benito, potser més indirectament fent costat a en Lluís, també. Neus, gràcies a tu em vaig poder emancipar en plena tesi (i en la casa més bonica i amb més colors que hagi vist mai). Toni Altaió sempre a punt per inspirar tranquil•litat o somriure tot i la serietat de l'assumpte. C.A.C (Centre Alpinista Capmany) crear tradicions com pujar al castell de St. Salvador la nit de cap d'any i veure, tan ben acompanyada, la bellesa de la plana empordanesa, sens dubte aquests instants també m'han permès seguir endavant. Olga, gràcies per ser com ets i per les estones plegades, escalant, parlant, fent galetes, el toc amb ratafia, sopant dissenyant mogudes, o bé de festa ballant, sens dubte això m'ha ajudat a poder tornar a afrontar més d'un dilluns pesat.

Gràcies a totes les persones amb qui hem compartit moments a la IAEDEN (Institució Altempordanesa per la Defensa i Estudi de la Natura), Salvem l'Empordà, Salvem el Vallès, Ecologistes de Catalunya, i l'ADENC (Associació per la Defensa i Estudi de la Natura). Les llargues hores de reunions al capvespre i ben entrada la nit, així com sortides i mogudes han fet que continuï creient que vull fer allò que penso, i que vull defensar allò que estimo encara que estigui a punt de desaparèixer. I les sortides per descobrir la natura han estat com bombolles d'aire en moments d'estrès total durant aquests 4 anys.

Fa 4 anys i una mica més ella va arribar al CREAF (Centre de Recerca Ecològica i Aplicacions Forestals). La gent i l'ambient que es respira al CREAF fan la vida més fàcil tot i la complexitat de la que està feta, i més, quan fas la tesi. Gràcies a tothom per fer-me sentir com a casa. Especialment a la Maria i en Gerard per batejar-me al CREAF, ajudar-me a l'adaptació i acabar sent amics tant importants per mi. Gràcies també a l'Ivette pel seu "toma moreno", els cops de mà, i fer-me riure sovint, a l'Esther, en Gorka, la Núria, en Roger, la Marta, en Xavier i la Paloma pels dinars i converses al Quiñonero i arreu de la UAB. A la Cristina, la Marta i la Magda per ser unes secretàries fantàstiques amb solució per tot, i també a la resta de l'equip d'administració del CREAF i del BAVE, en especial la Pilar i en J. Jeronimo. Gràcies a en Joan i en Carles per la seva eficàcia en l'informàtica i en la resolució de problemes. També a la Loles, la Patri, la Núria, en Nacho, en Roger, en

Miquel, la Marta, la Jara, en Martin, la Rebeca, en Trevor, en Lasse, Belén, Vicenç, en Josep Salvador i la resta per fer menys avorrit el pis -1 i amenitzar festes i crear moments que et queden en la ment. En Roberto, la Nacima, en Chechu, en Xavi D., Xavi A., en Rafel, la Rosor, la Charo, l'Olga, en Lluís, en Nando, en Gerardo, la Míriam, en Wilson, en Víctor, l'Anabel, l'Eduard i molts d'altres per les converses curtes, però importants per continuar, al mig del passadís o en algun despatx. A l'Imma i l'Isabel per compartir moments inoblidables i forjar una amistat durant el viatge a Califòrnia. A en Carles Palau per la confiança, també a fora del CREAF. A en Giorgio i en Trevor per la vostra companyia al despatx, ha estat molt fàcil conviure amb vosaltres.

A tots els professors/es i investigadors/es del CREAF que m'han ajudat en tot el que sempre els he demanat i a més amb celeritat, i molts d'ells, per raons diverses, són exemples i mestres per a mi. Jaume, gràcies per compartir estones amb mi i fer-me sentir especial. Josep, quina sort haver-nos conegut! Daniel, ets el millor explicant estadística. Anselm gràcies per tots els teus consells i converses. Jordi, amb la teva didàctica m'és fàcil aprendre. Romà, Joan i Jordi, moltes gràcies per resoldre qualsevol dubte plantejat durant aquests anys, i sempre al moment i atents. I és que no em voldria deixar ningú, de fet és un centre on cada formigueta que integrem el formiguer som importants, i cada formigueta millora el seu treball gràcies a l'esforç, també, de totes les altres.

Durant els primers anys al Montgrí, ella en va destacar la Solitud (definida tant bé per Víctor Català). Però ara vist amb perspectiva i després de molts més mostrejos, sovint a contra-rellotge, en destaca precisament el cantó oposat, la companyia i l'ajut d'altres persones al mig del matollar Montgrí, sense la qual, potser hagués parat boja.

I m'és imprescindible dir que la feina de cadascuna de les persones que m'han ajudat al camp i al laboratori ha estat clau per a poder arribar a aquesta meta amb el temps amb que ho he fet. Gràcies a tots i totes, la majoria estudiants de pràctiques en empreses (la majoria també, ara, fent tesis doctorals o treballant en el món de l'ecologia, cosa que celebro de tot cor): Montse, Marta, Albert, Jose i Mercè. També a l'Anna per la seva ajuda tècnica i paciència amb les imatges d'arrels, i a la Gemma per ajudar-me a sobreviure el mostreig d'arrels, amb robatori inclòs. Gràcies també a la Lucía i la Míriam, que han passat de ser estudiants de pràctiques en empreses a unes amigues increïbles. Gràcies també a l'Anna Saperas, que m'ha ajudat al camp, i també sovint al tornar del camp.

I parlant de treball de camp i Montgrí, em queda la gent que m'ha facilitat el treball al massís, gràcies Bep per tots els permisos sense problemes, i a tu Mapi per totes les facilitats, bona predisposició i converses sobre gestió. Tan de bo tots els massissos i zones naturals del nostre país es gestionessin amb tantes ganes i interès. Edu, quina sort que coincidíssim aquella època al Montgrí, ha estat genial saber que si tenia qualsevol

problema (com ara plegar el cotxe en una pista) estaves a prop per donar-me un cop de mà. Joan Font, gràcies també per explicar-me tants secrets com t'he demanat de la flora i els racons del Montgrí.
I gràcies a la música en general per fer-me companyia al tornar del camp sola cap al CREAF, o ben entrada la nit sortint del laboratori. No sé si ho heu provat mai, però a mi, cantar (els Pets, Gossos, Sopa de Cabra, en Pau Riba) ja sigui a dins del cotxe, o amb un micròfon fent garrotins i nyacres m'ha ajudat sempre a revifar en moments en que pensava que ja no era possible. Gràcies també, als colors, sobretot al taronja, el verd, el lila i el blau.

Gràcies a l'Ignasi del servei d'anàlisi química de la UAB pel seu interès per les meves mostres i per oferir un bon servei. Gràcies també a l'AGAUR (Agència de Gestió d'Ajuts Universitaris i de Recerca) i als seus administratius que han fet possible que ser becària fos menys dramàtic. Gràcies també a la Generalitat de Catalunya per deixar-me gaudir de la beca pre-doctoral sense la qual no m'hagués estat possible començar i acabar aquest camí doctoral. I gràcies pel finançament econòmic dels projectes REN 2003-07198 and CGL2006-01293/BOS I l'"European research group (GDRE) Mediterranean and mountain ecosystems in a changing world".
A en Juli P. i la Susana P. pel treball fet en col•laboració. Gràcies per la teva proximitat, Fernando V., i pels teus consells personals i professionals. Sara P. gràcies per ajudar-me en tot el que has pogut sempre. Gràcies a tots els membres del tribunal (i revisors externs) per acceptar formar-ne part: Eric Garnier, Fernando Valladares, Josep Peñuelas, Anselm Rodrigo, Josep Maria Espelta, Sara Palacio i Jordi Martinez-Vilalta, Juli Pausas, M. Pilar Castro.

De les meves estades a l'estranger, vull agrair sobretot a en Bill Shipley que m'ensenyés els secrets del món de la causalitat durant la meva estada a Sherbrooke, Québec. En Josep Escarré, i la gent del pis de dalt del CNRS, gràcies per la cordialitat i el bon tracte rebut. Gràcies també a l'Eric Garnier per comentar parts de la tesi i compartir opinions. Gràcies a la Sandra Lavorel i la gent del GDRE pels debats sobre ecologia funcional. A Austràlia, gràcies a tota la gent del MEDECOS, on vaig aprendre un munt de coses sobre els ecosistemes mediterranis d'arreu del món. I encara que la vaig conèixer durant una estada abans de començar la tesi, també vull agrair a la Michelle D. Boone (abans a Missouri, ara a Ohio), els seus ànims fins avui mateix, sempre ha estat pendent de què n'és de mi, i encara ens escrivim cartes i ànims creuant el "gran bassal".

I el que sens dubte m'ha permès arribar a fer aquest camí a estat en Paco Lloret. Gràcies a tu, Paco, se'm va brindar l'oportunitat de començar aquest projecte al CREAF. Amb tot el coneixement que tinc del món doctoral, sé que sóc afortunada d'haver-te tingut de director de tesi. Sempre m'has ajudat a solucionar qualsevol tipus de problema o dubte per petit o gros que fos, sempre tant ràpidament com has pogut i si ha pogut ser, acompanyat també d'algun somriure. I és que a més d'ajudar-me a aconseguir fer la tesi, també m'has format, crec que el període pre-doctoral és una etapa de formació científica i personal, i com a gran professor que ets, crec que has aconseguit que l'acabi tenint la sensació que he après un munt de coses. Sempre he tingut la sensació que has confiat en mi, i això per mi ha estat clau per aconseguir tot el que he aconseguit. Escriuria moltes més coses, però quan penso en la cara que faràs quan veuràs la llargada dels agraïments..... Gràcies per tantíssimes coses (incloses totes les revisions que has fet d'aquesta tesi), i bé, com diuen en aquella pel.lícula: "sempre ens quedarà el Western Australia"... amb el karri, el kwongan, els cangurs… i les paparres!... Gràcies per donar-me tantes oportunitats.

La família és clau, gràcies per fer-me costat. Mare i Toni, se que és difícil pensar que una filla es pugui guanyar la vida traient arrels amb un compressor d'aire al mig d'un matollar, o bé comptant fulles i escanejant-les,... però tot i amb això, sempre heu cregut en mi i heu deixat que fés el que més m'agrada fent-me costat. Gràcies també mare, per aguantar-me en els moments més difícils, a més d'una mare sempre has estat una de les meves millors amigues (fins i tot has vingut al camp algun dia a disfrutar de les carícies a les cames dels garrics,... ☺). Xavi gràcies per fer-me costat i a la Montse també. Al meu avi i la meva iaia i tots els tiets, tietes i cosins, gràcies també per creure en mi. Iaia, m'havies ensenyat boixets (puntes al coixí) i punt de cadeneta, però encara no a fer servir la màquina de cosir, gràcies, ara ja podem dir que en sé (simesno a cosir bossetes de nylon... tinc "fondo", eh! en vaig fer unes 700!). Maria, Josep i Joan gràcies per fer-me sentir com si fos una filla més (no gaire gent diu això dels sogres,... ☺), i per interessar-vos sempre per totes les meves coses (tan bones com maldecaps), i per vetllar per fer-me una vida més fàcil, tot això sempre ha estat molt important per mi. A la resta de la família d'en Lluís també moltes gràcies per tot i per fer-me sentir com a casa, a Figueres.

Lluís, em quedes tu, t'he deixat pel final, com els postres de xocolata, que ja saps que m'encanten. Ja portem molts anys junts, i espero que amb el temps, veurem aquests període de 4 anys com una anècdota. Però ara que encara hi sóc al mig me'n faig creus de com hem aguantat tanta pressió, viatges a l'estranger, i també entre el Vallès i l'Empordà, sempre encaixant a la perfecció com dos motlles fets a mida. M'has aguantat nervis, neures, inseguretats i desfetes, i sempre m'has ajudat a seguir endavant i no deixar mai que em desfés del tot. Ara que ho veig amb una mica de perspectiva, em pregunto si hagués arribat a aquesta meta sense tu,.... Sí, potser sí, però, dubto que hagués arribat fins on ho he fet amb un gran somrís per dins i per fora tal i com ho faig avui. Gràcies per la paciència i pels bocins de tu: el teu somrís al mig d'un matollar en cap de setmana, al laboratori algun vespre, a casa alçant-me des de ben avall després d'un dia de camp, intentant desenganxar-me de l'ordinador abstreta per la pantalla, i sobretot per intentar fer-me riure a l'arribar a casa, o a través de la web-cam des de l'altra punta del món, arronsats damunt una manta en un prat, o fent la migdiada. Estar i viure amb tu sí que és un camí cap a ítaca, i que espero que no s'acabi mai. Gràcies per tot altre cop, sobretot per fer-me sentir SEMPRE única, bona, amb potencial i tant especial.

I un cop va haver fet aquell repàs de totes les persones que li havien fet possible que ella fes aquell camí i arribés a aquella meta, ho va escriure, demanant disculpes per si s'havia deixat a algú, i els hi va dir:

"Un llapis mai no dibuixa sense una mà, gràcies a totes i tots!"

Sandra

P.d. Per últim vull agrair a en Francesc Pujol que em cedís el seu quadre per la portada, i a l'Olga que m'ajudés en el foto-muntatge. A en Joan pel disseny de les "sub-portades" interiors. I a la Fundació per la Pau per realitzar la campanya "Prou investigació militar" a la que convido que tots els científics i científiques que llegeixin aquesta tesi s'hi sumin (www.prouinvestigaciomilitar.org).

ÍNDEX

FUNCTIONAL TRAITS OF MEDITERRANEAN WOODY SPECIES WITH DIFFERENT POST-FIRE REGENERATION

I. INTRODUCCIÓ

CONTEXT GENERAL DEL TREBALL

Hi ha una llarga tradició de classificar els tipus biològics de plantes segons criteris fisiognòmics o bé segons criteris funcionals. Els criteris funcionals són bàsics per entendre i definir com i quines plantes afecten al funcionament de l'ecosistema (Pugnaire & Valladares, 1999; Terradas, 2001). Durant anys s'ha fet un esforç significatiu per entendre el paper de les plantes en la dinàmica i el funcionament de les comunitats i ecosistemes (Woodward & Cramer, 1996; Smith *et al.*, 1997; Lavorel & Cramer, 1999), i en conseqüència s'han desenvolupat diferents esquemes de grups funcionals (Noble & Slatyer, 1980; Westoby, 1998; Weiher *et al.*, 1999). Per tal de clarificar la terminologia, Lavorel *et al.* (1997) van diferenciar entre 4 tipus principals de classificacions funcionals. Aquests són: els *grups emergents*, les *estratègies, els grups funcionals estrictes* (o *d'efecte*) i els *grups específics de resposta*. Els *grups emergents* són grups d'espècies que reflecteixen correlacions naturals d'atributs biològics, però no estan directament relacionats amb les funcions de l'ecosistema. Les *estratègies* determinen una classificació segons els patrons adaptatius relacionats amb l'ús i la disponibilitat de recursos. Les altres dues classificacions funcionals són les que recentment han demostrat avanços conceptuals estimulats per la recerca relacionada amb predir els efectes del canvi global en la dinàmica de la vegetació (Woodward & Cramer, 1996; Smith *et al.*, 1997). Així doncs, ja que un dels objectius principals d'aquest treball és aproximar-se a predir els efectes dels incendis en els ecosistemes mediterranis, en aquest treball es parlarà només dels grups funcionals (d'efecte i de resposta). Per tant, els *grups funcionals de plantes*[1] es defineixen com agrupacions d'espècies que tenen un rol semblant en un ecosistema basat en un conjunt d'atributs biològics, i que responen de maneres semblants a múltiples factors ambientals (Gitay & Noble, 1997). Els grups funcionals poden definir tan en relació a la seva contribució en els processos de l'ecosistema (com ara el cicle del carboni i l'aigua) com en la resposta a variables de canvis ambientals, com per exemple una pertorbació. Així, els *grups específics de resposta* a una pertorbació contenen espècies que responen de manera similar a aquesta alteració sobtada del medi.

Alguns models conceptuals de vegetació a gran escala (Woodward & Cramer, 1996; Smith *et al.*, 1997) assumeixen que l'agrupació de plantes basada en el coneixement *a priori* de la seva funció, o en correlacions entre els seus atributs, faria possible predir directament els canvis en els processos de l'ecosistema a partir dels canvis projectats en la composició de plantes en resposta al canvi global. Aquestes assumpcions, reflecteixen la idea que "els grups funcionals d'efecte" (espècies amb efectes similars en una o vàries

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[1] També anomenats "Plant functional types - PFTs"

funcions de l'ecosistema) (Gitay & Noble, 1997; Walker *et al.*, 1999) i "els grups funcionals de resposta" (grups d'espècies amb respostes similars a un factor ambiental particular com ara la regeneració després d'un incendi) (Gitay & Noble, 1997; Lavorel *et al.*, 1997) haurien de coincidir. Així, s'han fet diversos estudis sobre la relació entre les pertorbacions (com per exemple l'herbivoria) i els grups funcionals (Díaz & Cabido, 1997; McIntyre *et al.*, 1999; McIntyre & Lavorel, 2001). Lavorel & Garnier (2002) van fer una revisió sobre els estudis fets sobre aquesta temàtica a partir d'experiments on es documenta els efectes de la diversitat funcional de plantes en el funcionament dels ecosistemes (Díaz & Cabido, 2001; Díaz *et al.*, 2003). Chapin *et al.* (2000) va proposar un model conceptual on les modificacions en la composició d'espècies resultant de canvis ambientals es traduïa en modificacions en el funcionament de l'ecosistema via canvis en la representació dels trets de les espècies. El marc conceptual en el que es basa l'estudi que es presenta és el suggerit per Lavorel & Garnier (2002) que articula les respostes ambientals i els efectes en l'ecosistema a través de la variació dels graus de solapament entre els trets rellevants (Figura 1).

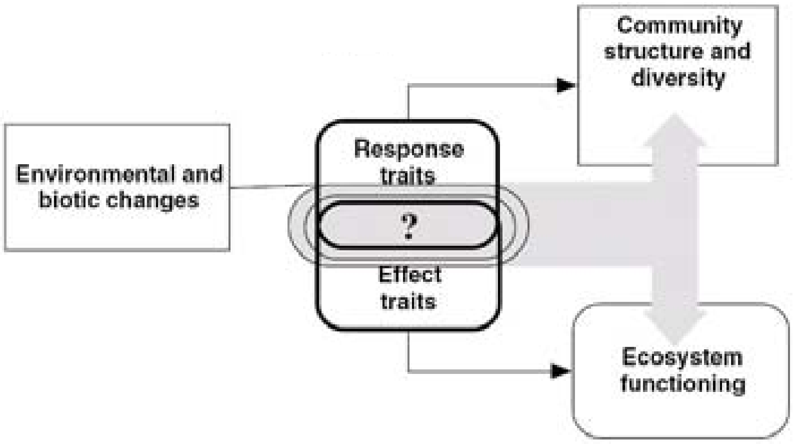

Figura 1. Il·lustració del marc conceptual de relacions entre els canvis ambientals i el funcionament dels ecosistemes. Font: Lavorel & Garnier, 2002. [2]

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[2] "Trait" del gràfic està traduit com a "tret" en el text.

En el moment de canvi global en el que ens trobem, l'estudi dels efectes de les pertorbacions sobre el funcionament dels ecosistemes és un dels camps de l'ecologia de més rellevància. Pel que fa a estudis de casos concrets relacionant els grups funcionals de resposta i els grups funcionals d'efecte, n'hi ha varis, sobretot en relació a l'ús de recursos. Per exemple, s'ha comprovat en comunitats de prats, que trets que confereixen resistència a un estrès ambiental com l'herbivoria, i que determinen grups específics de resposta, també determinen taxes de descomposició i un reciclatge de nutrients més lents. Per tant poden considerar-se grups funcionals d'efecte (Aerts, 1995; Díaz & Cabido, 2001). També s'han fet aproximacions i models per tal d'estudiar els grups funcionals en ecosistemes pertorbats per incendis (Pausas & Lavorel, 2003; Müller *et al.*, 2007; Pausas & Lloret, 2007), i en concret s'han comparat alguns trets de les plantes en relació a la seva resposta als incendis en ecosistemes mediterranis d'arreu del món (Ackerly, 2004; Pausas *et al.*, 2004). Però són pocs els estudis fets a la conca mediterrània per tal de definir si els diferents grups regeneratius post-incendi d'espècies llenyoses són també grups funcionals diferents. Així doncs, a partir d'aquest objectiu genèric, aquest estudi pretén estimar els efectes dels incendis sobre el funcionament de l'ecosistema a la conca mediterrània.

Hi ha molts estudis que demostren que els incendis són una pertorbació important en l'evolució i la dinàmica de la majoria d'ecosistemes mediterranis (Mutch, 1970; Vallejo & Alloza, 1998; Keeley & Fotheringham, 2000; Minnich, 2001; Lloret *et al.*, 2002; Espelta *et al.*, 2003; Bond *et al.*, 2005). De bracet amb les transformacions dels usos del sòl, els incendis són probablement la pertorbació més important en aquests ecosistemes (Whelan, 1995; Rundel, 1998). Els canvis recents en els usos del sòl han portat cap a un abandonament progressiu de les terres agrícoles, cap a una important fragmentació d'hàbitats, i cap a una sobre-explotació dels recursos terrestres (Moreno & Oechel, 1995; Peñuelas & Boada, 2003; Peñuelas *et al.*, 2004). A més, el canvi global que està tenint lloc a la conca mediterrània (els canvis dels usos del sòl amb la conseqüent acumulació de combustible, l'homogeneïtzació dels paisatge en certes zones, i l'increment de la sobre-freqüentació humana) han estat factors importants dels canvis en el règim d'incendis incrementant-ne la seva abundància (Papió, 1994; Folch, 1996; Lavorel *et al.*, 1998; Lloret, 2004; Lloret *et al.*, 2008). Cal tenir en compte que, actualment, un altre factor important relacionat amb els canvis en el règim d'incendis és l'escalfament del clima ja que està generant un clima més àrid a la conca mediterrània i per tant un major risc d'incendis (Moreno & Oechel, 1995; Peñuelas, 1996; Piñol *et al.*, 1998; Flannigan *et al.*, 2000; Pausas, 2004).

La història dels incendis a la conca mediterrània ha estat tan lligada a les activitats humanes i a les comunitats vegetals que és difícil estimar el règim natural d'incendis. Hi ha alguns estudis que demostren que els incendis eren presents a les regions costaneres mediterrànies de la península ibèrica abans del període de la romanització (Riera-Mora & Esteban-Amat, 1994; Carrión & Van Geel, 1999; Scott, 2000; Scott, 2002). Més tard, hi va haver un important nombre d'incendis, durant l'edat mitjana, degut a l'expansió de la ramaderia i a d'altres activitats humanes. Més recentment, els incendis han tingut un impacte especialment dramàtic a la península ibèrica a partir del segle XX. Actualment, els incendis forestals es consideren com a un dels principals problemes ambientals el qual afecta l'estructura, la dinàmica i la composició de boscos i matollars, i constitueix un factor de risc per a les persones que viuen a prop de medis forestals. Fins la segona meitat del segle XX, el foc es considerava un element destructiu de les àrees forestals promogut pels humans. La visió del foc com un component dels ecosistemes naturals és relativament recent i coincideix amb el descobriment de que la majoria d'aquests sistemes són resilients, és a dir, que recuperen l'estructura i la composició d'espècies relativament ràpid (Hanes, 1971; Trabaud & Lepart, 1980). En concret, alguns estudis assenyalen que els matollars són més resilients que els boscos (Díaz-Delgado *et al.*, 2002; Lloret *et al.*, 2002). Tot i així, el procés de regeneració pot ser sensible als diferents règims d'incendis depenent de les característiques demogràfiques de les espècies i les seves estratègies regeneratives post-incendi (Zedler *et al.*, 1983; Pausas, 1999).

Els canvis en el règim d'incendis tenen un impacte sobre la composició de les espècies que pot ser particularment rellevant en les regions mediterrànies (Franklin *et al.*, 2001; Delitti *et al.*, 2005; Franklin *et al.*, 2005; Eugenio & Lloret, 2006; Syphard *et al.*, 2006). Aquestes regions tenen una remarcable riquesa d'espècies respecte a la petita àrea que ocupen (el 16 % de les plantes vasculars són presents en el 2.25 % de l'àrea total mundial, inclosa en les regions mediterrànies) (Cowling *et al.*, 1996; Hopper, 2007). Aquesta biodiversitat ha portat a incloure les cinc àrees geogràfiques mediterrànies dins dels 25 "hotspots" de biodiversitat a nivell mundial, definides bàsicament pels seus elevats nivells d'endemismes de plantes i pels elevats nivells de pertorbació humana (Rundel, 2004). Tanmateix, Rodrigo *et al.* (2004) van mostrar evidències que no totes les espècies de plantes sobreviuen als incendis en qualsevol situació. Com a resultat, un incendi pot afectar a la composició d'espècies de les següents maneres: (1) permetent l'entrada de noves espècies a l'ecosistema pertorbat, (2) eliminant altres espècies que no es regeneren després del foc (Vilà *et al.*, 2001; Lloret *et al.*, 2003; Rodrigo *et al.*, 2004), i/o (3) canviant els patrons d'abundància relativa (Vilà *et al.*, 2001; Eugenio & Lloret, 2004; Grigulis *et al.*, 2005).

Aquest estudi es basa en aquest últim punt, és a dir, en el fet que els incendis poden canviar els patrons d'abundància relativa, depenent de les capacitats regeneratives post-incendi de les plantes. *A priori*, els efectes principals dels incendis en les espècies vegetals són la combustió del material i la mort d'individus. Però d'altra banda, la majoria d'espècies llenyoses mediterrànies tenen mecanismes de regeneració post-incendi. D'aquesta manera, la pèrdua d'individus després dels incendis es minimitza, ja que algunes espècies tenen òrgans protegits de les altes temperatures que els hi permeten la rebrotada (espècies rebrotadores). Per tant, les plantes rebrotadores persisteixen vegetativament a nivell individual . Altres espècies poden compensar la pèrdua d'individus immediatament després de l'incendi amb llavors que poden resistir les condicions d'aquesta pertorbació (espècies germinadores) (Trabaud, 1987; Trabaud, 1991; Keeley, 1995; Lloret, 2004). Sovint tenen un banc de llavors persistent i el reclutament de nous individus és afavorit pel foc, per exemple trencant la dormància de les llavors (Pausas *et al.*, 2004). Hi ha algunes espècies que mostren ambdues estratègies (espècies germinadores-rebrotadores), alhora que hi ha algunes espècies que no poden regenerar-se després d'un incendi. Clarament, es pot trobar una important variabilitat en aquests grups, d'acord amb el grau de vulnerabilitat respecte a la intensitat de l'incendi, i el tipus d'estructures promotores de la rebrotada (com per exemple lignotubers, arrels, rizomes o bulbs) (Vesk *et al.*, 2004; Vesk & Westoby, 2004). Les germinadores i les rebrotadores sovint es consideren els dos grans grups funcionals de resposta als incendis perquè representen els dos tipus bàsics de regeneració post-incendi (Zedler *et al.*, 1983; Pausas, 2001; Pausas *et al.*, 2004; Pausas & Verdú, 2005).

Bellingham & Sparrow (2000) van suggerir que la clau d'èxit per a una estratègia o altra és simplement si aquesta estratègia li permet a la planta reocupar el lloc abans de la propera pertorbació. En el cas de les rebrotadores, quan els fenòmens de pertorbació succeeixen successivament al mateix individu, la planta hauria de ser capaç de recuperar les parts aèries. Però després d'unes quantes pèrdues de la part aèria, la planta pot arribar a perdre la seva capacitat per recuperar els teixits productius degut a l'esgotament dels seus òrgans d'emmagatzemamament que li permeten la rebrotada (Vilà & Terradas, 1995; Iwasa & Kubo, 1997). Pel que fa a les plantes germinadores, aquestes germinen de manera abundant després d'una pertorbació, però després d'una sèrie consecutiva d'incendis, el banc de llavors pot davallar degut a la impossibilitat de produir noves llavors viables (Lloret *et al.*, 2003). Vila *et al.* (*personal observation*) suggereixen que a altes freqüències d'incendis, la proporció de rebrotadores i germinadores davalla mentre que la de les espècies que tenen ambdues estratègies regeneratives es manté. De totes maneres, quan la freqüència d'incendis és tan alta que no dona temps a refer les poblacions d'espècies que omés germinen, les rebrotadores passen a sre més abundants.

D'altra banda, aquests patrons d'abundàncies relatives de grups regeneratius post-incendi poden variar en funció de la intensitat de l'incendi, la recurrència, el lloc, i les espècies afectades (Pausas, 1999; Pausas & Lloret, 2007).

A la conca mediterrània, el grup de rebrotadores està majoritàriament constituït per espècies de vida llarga que mostren un elevat percentatge d'individus cremats que sobreviuen i rebroten després d'un incendi, però no mostren un reclutament significatiu després d'un incendi, mentre que les germinadores són espècies de cicle de vida més curt (Pate *et al.*, 1990; Verdaguer & Ojeda, 2002; Knox & Clarke, 2005; Schwilk & Ackerley, 2005). De fet, Herrera (1987) va mostrar que la mitjana de la producció de fruits era significativament major en les espècies no-rebrotadores que en les espècies rebrotadores. En els matollars, moltes rebrotadores es troben típicament en estadis tardans de la successió. Les germinadores,però, poden reclutar immediatament després o entre incendis, i també després d'altres pertorbacions que eliminin la part aèria com l'estassada. Lloret (1998) va demostrar que, després d'un incendi, les germinadores podien produir plançons amb més supervivència i taxes de creixement més altes que en períodes anteriors a l'incendi. De totes maneres, com ja s'ha mencionat, hi ha suport per a la hipòtesi de que la proporció d'aquests grups regeneratius en comunitats de plantes poden ser sensibles al règim d'incendis, particularment, a la intensitat del foc i la recurrència (Pausas, 1999; Pausas & Lloret, 2007; Lloret *et al.*, 2008).

Així doncs, partint de la recerca feta fins al moment, podem establir que:

(a) el règim d'incendis afecta a la dinàmica, composició i evolució dels ecosistemes mediterranis, i aquests canvis dependran principalment de la capacitat regenerativa post-incendi que tinguin les plantes afectades.

(b) Depenent de la capacitat regenerativa post-incendi, les plantes es poden classificar com a grups funcionals de diferent resposta als incendis

L'objectiu principal d'aquest treball és verificar si els grups funcionals de resposta (grups regeneratius post-incendi) són també grups funcionals respecte a l'ús de recursos i la inflamabilitat. De manera que si els diferents grups funcionals de resposta als incendis tenen diferents funcions en l'ecosistema, es podria concloure que els incendis poden afectar al funcionament dels ecosistemes a través dels canvis en la composició i proporcions de les estratègies regeneratives post-incendi.

CARACTERITZACIÓ FUNCIONAL DE LES ESPÈCIES LLENYOSES DEL MONTGRÍ

Els grups funcionals de plantes, es poden definir com a grups d'espècies que comparteixen funcionaments, respostes o rols semblants. Aquestes similituds es basen en el fet que tendeixen a compartir un conjunt de trets funcionals clau (Brzeziecki & Kienast, 1994; Chapin *et al.*, 1996; Noble & Gitay, 1996; Thompson *et al.*, 1996; Grime *et al.*, 1997; Westoby, 1998; Weiher *et al.*, 1999; Lavorel & Garnier, 2002; Pausas & Lavorel, 2003). Seguint la terminologia proposada per Violle *et al.* (2007), considerem els trets funcionals de les plantes com a qualsevol tret o atribut que afecti indirectament la seva *fitness* a través dels seus efectes en la reproducció, creixement o supervivència. La major part dels trets funcionals mesurats en aquest treball estan descrits com a tal i s'han mesurat seguint els procediments proposats per Cornelissen *et al.* (2003) per permetre la seva comparació amb altres estudis. S'han mesurat trets funcionals foliars que estan relacionats amb els recursos com ara els nutrients o l'aigua i també trets del sistema radicular. També s'han estudiat trets funcionals relacionats amb la inflamabilitat, per tal de relacionar els grups funcionals amb el règim d'incendis. Per últim també s'han considerat trets funcionals de descomposició de la fullaraca per tal de tenir més informació sobre el retorn dels nutrients al sòl.

El conjunt dels resultats obtinguts s'han integrat a través d'anàlisis de causalitat i anàlisis multivariables en la mesura que ha estat possible (depenent dels requeriments de les diferents tècniques estadístiques utilitzades) per tal de cercar relacions entre els trets. Les relacions de causalitat entre els trets foliars i els grups funcionals post-incendi estan explicades en el capítol IV. Els anàlisis multivariables es poden trobar, en alguns capítols i en el resum que es presenta al capítol final de síntesi.

Segons el vist fins ara, es poden considerar quatre grups generals de plantes depenent de la seva estratègia regenerativa: germinadores (S+ R-), rebrotadores (S- R+), germinadores-rebrotadores (S+ R+) i les que no es regeneren després d'un incendi (S- R-) (*sensu* Pausas, 2004; Pausas & Verdú, 2005) (Figura 2). Les germinadores i rebrotadores són espècies que només germinen o només rebroten després d'un incendi, i les germinadores-rebrotadores són el grup d'espècies que té facultat per fer ambdues coses, mentre que el grup que no fa cap de les dues coses no s'estudia en aquest treball, perquè no hi havia cap espècie amb aquests trets a l'àrea d'estudi.

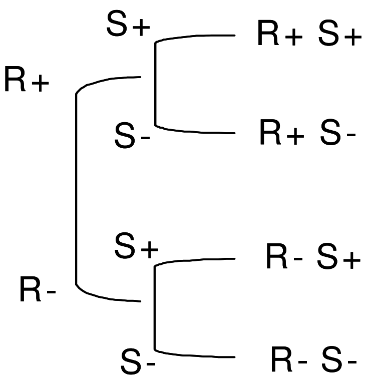

Figura 2. Classificació dels quatre tipus bàsics de resposta als incendis. Les abreviacions són: R+, rebroten; R-, no rebroten; S+, germinen (propàguls persistents); S-, no germinen (no tenen propàguls persistents). Les dues dicotomies són: primer, si els individus persisteixen després de l'incendi a través de la rebrotada, i en segon lloc si la població de l'espècie persisteix després de l'incendi a través de propàguls. Els quatre grups són: R+ S+, espècies germinadores-rebrotadores (espècies facultatives que tan poden germinar com rebrotar); R+ S, espècies rebrotadores (en alguna bibliografia se'n diuen "rebrotadores obligades" ja que només poden persistir a través de la capacitat de rebrotar; R- S+, espècies germinadores (sovint se'n diuen "germinadores obligades" ja que només poden persistir a través de la capacitat de les seves llavors o propàguls per sobreviure al foc); R- S-, són les espècies que no persisteixen després del foc. Font: (Pausas *et al.*, 2004).

Recentment es tendeix a tractar les capacitats regeneratives com a capacitats separades, és a dir: tenir o no el caràcter rebrotador, o ser capaç o no de produir propàguls que persisteixin després del foc. Aquesta classificació és una simplificació donada la variabilitat de respostes dins del caràcter rebrotador i el germinador. Les espècies que poden tenir ambdues respostes després d'un incendi, es poden tractar com a rebrotadores, com a germinadores o bé com a un grup a part. Per aquesta raó, segons el tipus de tret mesurat i l'hipòtesi considerada en els diferents capítols, el grup germinador-rebrotador (S+ R+) s'ha considerat com a germinador o com a rebrotador, de manera que durant el treball es parla de[3]:

"Germinadores" (S+ R-, S+ R+) i "no-germinadores" (S- R+) quan s'ha inclòs el grup de plantes germinadores-rebrotadores en el grup de les germinadores.

"Rebrotadores" (S+ R-) i "no-rebrotadores" (S- R+, S+ R+) quan s'ha considerat el grup germinadores-rebrotadores en el grup de les rebrotadores.

"Germinadores" (S+ R-), "Rebrotadores" (S- R+) i "Germinador-rebrotador" (S+ R+) classificació que s'ha utilitzat quan no hi havia cap hipòtesi inicial per incloure'l en un grup o l'altre.

S'han considerat una trentena[4] d'espècies llenyoses representatives dels matollars calcaris de la zona Mediterrània de la península ibèrica. Això permet la caracterització a nivell de comunitat a partir de les abundàncies relatives de les diferents espècies. Es van agafar el

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[3] A la resta de capítols, en anglès: "germinadora" és "seeder", "no-germinadora" és "non-seeder", "rebrotatora" és "resprouter", "no-rebrotadora" és "non-resprouter" i "germinadora-rebrotadora" és "seeder-resprouter".

[4] El nombre d'espècies ha variat entre un mínim de 8 en el cas de les arrels i un màxim de 30 en el cas dels trets foliars.

màxim de mesures possibles en el mateix lloc, el massís del Montgrí, al nord-est de Catalunya (42.16ºN, 3.24ºW) per intentar minimitzar la variabilitat espacial que potencialment pot influenciar significativament en la plasticitat fenotípica de molts dels trets estudiats.

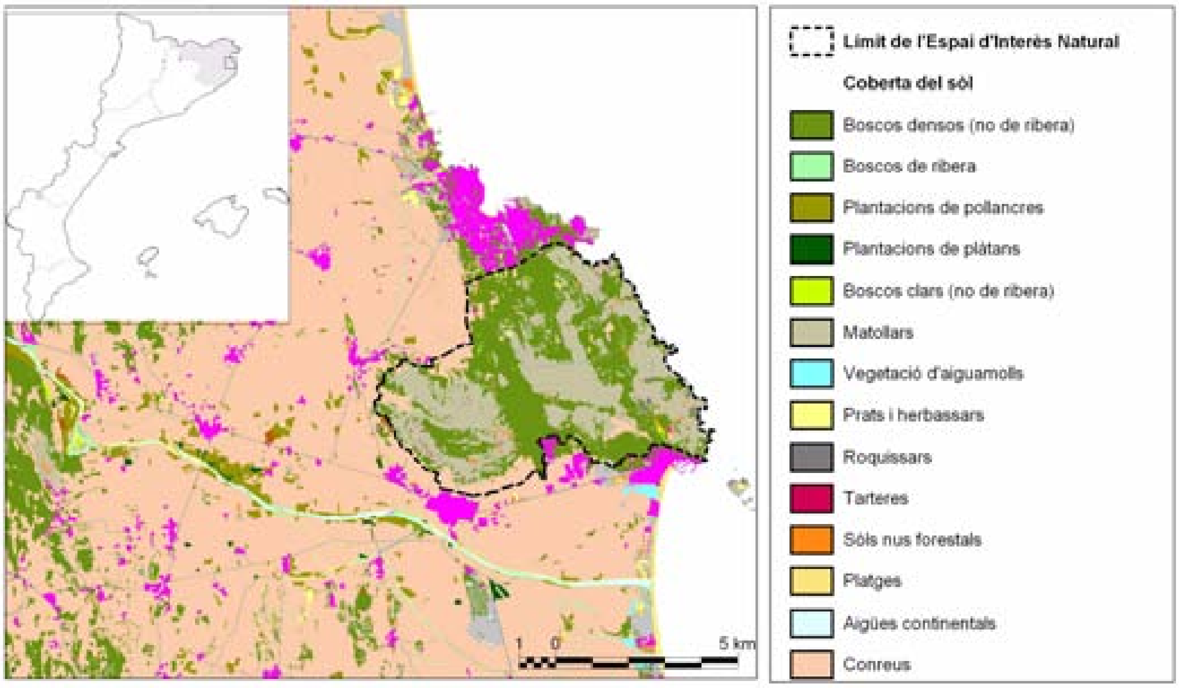

Figura 3. Situació i cobertes del sòl del Massís del Montgrí, l'àrea d'estudi. Font: Mapa de cobertes del sòl de Catalunya (http://www.creaf.uab.cat/mcsc).

En el cas de l'estudi d'inflamabilitat es va comparar la inflamabilitat en dos llocs distants al llarg del litoral mediterrani:Murta a València, i Montgrí a Catalunya[5]. En el cas de l'estudi de descomposició es van recollir les mostres de fullaraca al Montgrí per tal de mantenir el mateix origen que en la resta de trets, però l'experiment es va desenvolupar al Garraf. El Garraf té un clima i un substrat molt semblants als del Montgrí, i és on estan instal·lats els equipaments de l'experiment de simulació de canvi climàtic[6].

A més dels trets ecològics, almenys a la conca mediterrània, les rebrotadores i les germinadores també tenen diferències evolutives degudes a la història biogeogràfica de la flora mediterrània. Mentre la majoria dels taxons rebrotadors van evolucionar al Terciari

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[5] Aquest estudi es va fer en col.laboració amb Pausas, J., G. i Paula, S., en el marc del projecte"Síndromes de respuesta regenerativa y propiedades funcionales de comunidades vegetales mediterráneas con relación al régimen de incendios". Ministerio de Ciencia y Tecnología, Programa Nacional de Recursos Naturales. REN2003-07198-C02-01.

[6] Aquest estudi es va fer en col.laboració amb Peñuelas, J. i Estiarte, M. en el marc del projecte:"Vulnerability assessment of shrubland ecosystems in Europe under climatic changes –VULCAN–EVK–2000-22108".

(Pre-Pliocè) (Herrera 1992) abans de l'establiment del clima mediterrani (Suc, 1984; Jalut *et al.*, 2000), la majoria de taxons germinadors van aparèixer durant el Quaternari (Verdú, 2000; Pausas & Verdú, 2005). Alguns estudis indiquen que, en aquesta regió, els atributs ecològics convergents entre espècies amb les mateixes estratègies regeneratives post-incendi (grups funcionals de resposta) poden ser deguts a constriccions filogenètiques (Pausas & Verdú, 2005; Paula & Pausas, 2006). A més, les mesures presents en espècies relacionades filogenèticament poden estar auto-correlacionades (Blackburn & Duncan, 2001; Garland *et al.*, 2005; Sol *et al.*, 2007). D'altra banda hi ha estudis que han intentat esbrinar si el règim d'incendis ha tingut un paper important a l'hora de modelar l'estructura filogenètica de les comunitats de la conca mediterrània (Verdú & Pausas, 2007), però encara no s'ha aconseguit discernir els efectes del règim d'incendis dels efectes deguts al clima, ja que van molt lligats. Verdú *et al.* (2007) han fet un estudi a més gran escala comparant espècies del mateix gènere però amb diferents estratègies regeneratives post-incendi i una de les conclusions que han tret és que el foc no és un factor determinant en la diversificació d'espècies d'ecosistemes mediterranis propensos a patir incendis. Així doncs, la relació entre la filogènia i els incendis és encara objecte d'estudi i per això durant aquest treball, a l'estudiar els trets de les plantes s'ha volgut considerar el paper de la filogènia en la relació entre els grups funcionals post-incendi i els trets estudiats. En alguns casos també s'han considerat com a covariable els tipus biològics de les espècies donada la seva relació potencial amb aquests trets[7].

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[7] Els tipus biològics segons **Raunkiaer C. 1934.** *The life form of plants and statistical plant geography*. Oxford, UK: Oxford University Press.

OBJECTIUS

Tenint en compte l'objectiu principal (esmentat anteriorment) de la tesi, els **objectius** concrets dels **diferents capítols** són:

- Capítol I. INTRODUCCIÓ. Es fa una introducció general sobre la temàtica de l'estudi de la tesi, així com aclariments generals sobre la metodologia emprada i els sistemes de classificació de les espècies estudiades.

- Capítol II. LEAF AND SHOOT WATER CONTENT AND LEAF DRY MATTER CONTENT. S'estudia en els diferents grups regeneratius post-incendi el contingut d'aigua (en fulles i branquillons) al llarg de les estacions de l'any així com també el contingut de matèria seca de les fulles. Així aquest capítol es centra en trets funcionals relacionats amb l'ús de l'aigua i l'acumulació de matèria seca de la fulla.

- Capítol III. LEAF NUTRIENT CONTENTRATION. Es verifica si les diferents estratègies regeneratives post-incendi tenen també diferències en el contingut de nutrients (carboni, nitrogen, fòsfor, potassi, calci, magnesi i sodi) de les fulles. I per tant, s'intenta saber si actuen com a dos grups funcionals diferents en relació als nutrients.

- Capítol IV. TESTING CAUSALITY ON LEAF TRADE-OFFS IN MEDITERRANEAN WOODY SPECIES: POST-FIRE REGENERATIVE STRATEGY LINKS WATER REGULATION AND LEAF DRY MATTER CONTENT. S'analitza si els trets estudiats als capítols II i III (així com també l'Area Específica Foliar) segueixen les mateixes relacions de causalitat entre ells que les descrites en altres ecosistemes del món. També s'estudia si les diferències de trets regeneratius post-incendi estan relacionades amb els "trade-offs" de la fulla i per tant podrien influenciar les propietats funcionals dels ecosistemes subjectes al règim d'incendis.

- Capítol V. FOLIAR STABLE CARBON AND NITROGEN ISOTOPES. A partir de tècniques de discriminació isotòpica, s'estudien les diferències entre grups regeneratius post-incendi i la seva eficiència en l'ús de l'aigua així com també en el tipus de font de nitrogen que utilitzen.

- Capítol VI. FUEL LOADING AND FLAMMABILITY. S'exploren les característiques d'inflamabilitat i de càrrega de combustible en espècies amb diferent estratègia regenerativa post-incendi en dos llocs d'estudi. D'aquesta manera es consideren trets lligats als incendis i que potencialment poden ser rellevants a l'hora de l'establiment de retroalimentacions entre règim d'incendis i vegetació.

- Capítol VII. LEAF LITTER DECOMPOSITION: RESPONES TO CLIMATE CHANGE. En aquest capítol els dos objectius principals són: determinar la descomposició de fullaraca per les espècies amb diferents estratègies regeneratives, i explorar les conseqüències del canvi climàtic sobre la descomposició de fullaraca en matollars de la conca mediterrània. Òbviament també s'estudia la interacció entre aquests dos factors (canvi climàtic i regeneració post-incendi). Les propietats relacionades amb la descomposició determinen les diferències en el retorn de nutrients i la matèria orgànica i són un punt cabdal en el funcionament dels ecosistemes terrestres.

- Capítol VIII. ROOT SYSTEM TOPOLOGY AND MORPHOLOGY. Aquest capítol es centra en els atributs del sistema radicular de les diferents estratègies regeneratives post-incendi i que fan referència a la seva topologia i/o morfologia. Òbviament aquests trets estan íntimament lligats a l'adquisició d'aigua i nutrients per la planta i afecten a la seva dinàmica en el sòl.

- Capítol IX. SÍNTESI. En aquesta part de la tesi es fa una síntesi de les principals conclusions i patrons obtinguts durant el desenvolupament del treball.

- Capítol X. CONCLUSIONS. S'exposen de manera breu les principals conclusions de cada capítol i del conjunt de la tesi..

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GALERIA D'IMATGES DE LES ESPÈCIES D'ESTUDI

Fotografies: Sandra Saura Mas

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GERMINADORES (S+ R-)

Ononis minutissima

Cistus albidus

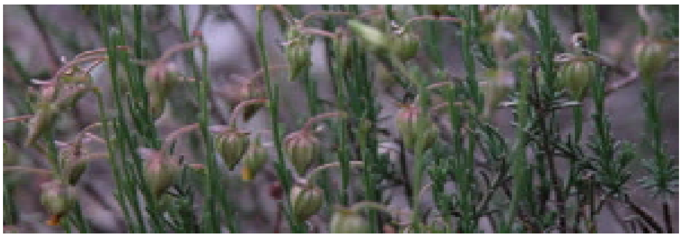
Cistus monspeliensis

Fumana thymifolia

GERMINADORES (S+ R-)

Helianthemum appeninum

Helichrysum stoechas



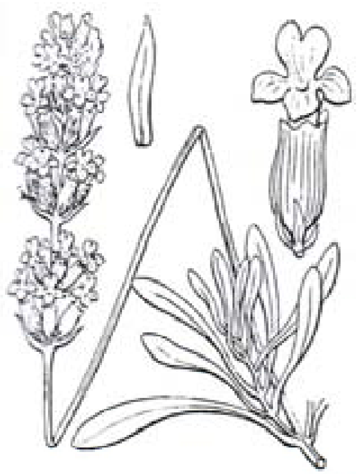
Fumana ericoides

Rosmarinus officinalis

GERMINADORES (S+ R-)

*Cistus crispus**

*Fumana laevipes**



*Lavandula latifolia**

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REBROTADORES (S- R+)

Lonicera implexa

Clematis flammula

Erica arborea

Crataegus monogyna

REBROTADORES (S- R+)

Smilax aspera

Olea europaea

Daphne gnidium

Pistacia lentiscus

REBROTADORES (S- R+)

Quercus coccifera

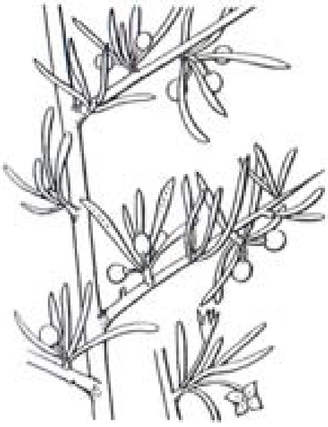
Phillyrea angustifolia

Quercus ilex

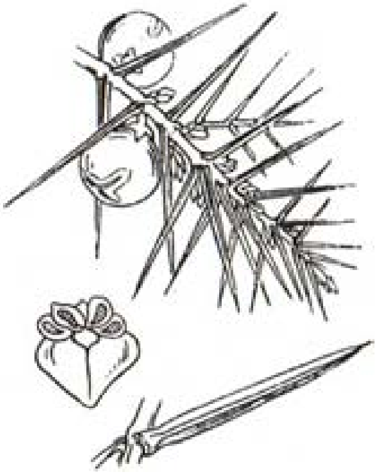
Rhamnus alaternus

REBROTADORES (S- R+)

Arbutus unedo+



*Rhamnus lycioides**



*Juniperus oxycedrus**

Osyris alba+

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GERMINADORES-REBROTADORES (S+ R+)

Dorycnium hirsutum

Dorycnium pentaphyllum

Staehelina dubia

Coronilla minima

GERMINADORES-REBROTADORES (S+ R+)

Thymus vulgaris

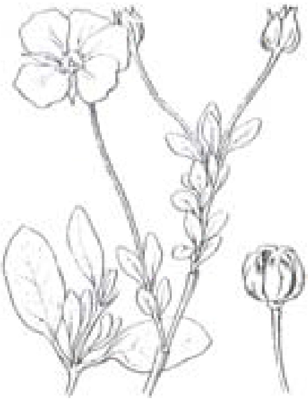
Teucrium polium

Globularia alypum

GERMINADORES-REBROTADORES (S+ R+)

Argyrolobium zanonii

Calicotome spinosa



*Cistus salviifolius**

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II. LEAF AND SHOOT WATER CONTENT AND LEAF DRY MATTER CONTENT

Main contents of this chapter have been published as: Saura-Mas, S., Lloret, F. 2007. Leaf and Shoot Water Content and Leaf Dry Matter Content of Mediterranean woody species with different post-fire regenerative strategies. Annals of Botany 99(3): 545-554.

ABSTRACT

- Post-fire regeneration is a key process in Mediterranean shrubland dynamics, strongly determining functional properties of the community. In this study, I test if there is a co-variation between species regenerative types and functional attributes related to water use.

- The seasonal variations in Leaf Relative Water Content (RWC), Leaf Dry Matter Content (LDMC), Leaf Moisture (LM) and Live Fine Fuel Moisture (LFFM) were analyzed in 30 woody species of a coastal shrubland, with different post-fire regenerative strategies (seeding, resprouting, or both).

- RWC results suggest that the studied resprouters have more efficient mechanisms to reduce water losses and maintain water supply between seasons. In contrast, seeders are more drought tolerant. LDMC is higher in resprouters over the course of the year, suggesting a more efficient conservation of nutrients. The weight of the phylogenetic constraint to understand differences between regenerative strategies tends to be important for LDMC, while it is not the case for variables such as RWC.

- Groups of species with different post-fire regenerative strategy (seeders and resprouters) have different functional traits related to water use. In addition to the role of phylogenetical constraints, these differences are also likely to be related to the respective life-history characteristics. Therefore, the presence and abundance of species with different post-fire regenerative response, as a result of disturbance regime, influence the functional properties of the communities.

Keywords: functional traits, Leaf Dry Matter Content, Mediterranean plants, post-fire, regenerative strategy, Relative Water Content, resprouter, seeder, woody species.

INTRODUCTION

Many studies have demonstrated that wildfires are an important disturbance in the evolution and dynamics of most Mediterranean-type ecosystems (Hanes, 1971; Whelan, 1995; Lloret *et al.*, 2002). Accordingly, most Mediterranean woody species display post-fire regenerative mechanisms. Some species (resprouters) have organs that are protected from high temperatures to permit resprouting, and other species (seeders) can compensate for the loss of individuals immediately after wildfires with seeds that resist high temperatures and germinate by taking advantage of the increased space and resources available after a fire (Trabaud, 1987, 1991; Keeley, 1995). There is also a third group of species that use both post-fire regenerative strategies (seeder-resprouters group). Finally, in the Mediterranean ecosystems there are a few species that can not regenerate after a wildfire. Of course, a significant variability can be found within these groups, according to the degree of vulnerability to fire intensity, and the type of structures promoting regrowth (such as lignotubers, crown roots, rhizomes or bulbs) (Lloret, 2004). However, seeders and resprouters are often considered the two main groups, since they represent the two basic types of post-fire regeneration (Zedler *et al.*, 1983; Pausas *et al.,* 2004; Pausas & Verdú, 2005).

Apart from their ecological features, species with resprouting or seeding capacity in the Mediterranean basin also have distinct evolutionary characteristics, due to their biogeographical history. While most seeders taxa evolved in the Quaternary (Post-Pliocene), most of the resprouter taxa were already present in the Tertiary (pre-Pliocene) (Herrera, 1992) before the establishment of the typical Mediterranean climate (Suc, 1984; Jalut *et al.,* 2000). Thus, some studies indicate that, in this region, post-fire regenerative attributes may be due to phylogenetical constraints and not necessarily to adaptation to environmental disturbances like fire regimes (Verdú, 2000; Verdú *et al.,* 2003; Pausas & Verdú, 2005).

Fire might affect species composition by (1) eliminating other species that cannot regenerate after fire (Vilà *et al.,* 2001; Lloret & Vilà, 2003; Rodrigo *et al.*, 2004), (2) changing the patterns of relative abundance (Eugenio & Lloret, 2004), according to the way their life history fits to a fire regime, or (3) allowing the establishment of species new to the disturbed ecosystem. More specifically, the high recurrence of fires might drive a community dominated by resprouters into a community with high abundance of seeders (Lloret *et al.,* 2003; Pausas, 2001; Bellingham & Sparrow, 2000). Functional ecosystem properties may differ according to the relationship between species composition and disturbance regime. Under similar climatic conditions, successional studies show that species composition largely determines ecosystem functional properties, which in turn can be explained by species' functional attributes (Garnier *et al.,* 2004; Polley *et al*., 2005). In this context, functional plant classification aims to group species according to functional similarities, thereby giving us a more comprehensive description of community functions (Lavorel *et al.,* 1999; Díaz & Cabido, 2001). Thus, models of ecosystem behavior may be elaborated on species' functional properties under a variety of different circumstances, such as fire regime (Keane *et al*., 2004).

In a Mediterranean context, functional attributes related to water economy or fire behavior are a priori good candidates to explore the hypothesis that changes in species composition due to fire regime may promote changes in the functional properties of the whole community. Leaf Relative Water Content (RWC) is an outstanding indicator that is used to evaluate plant water status (Larcher, 1995; Teulat *et al*., 1997). Peñuelas *et al*. (2004) described how photosynthetic rates and stomatal conductances decreased as Leaf Relative Water Content diminished in non-irrigated *Phyllirea angustifolia* plants. Leaf Dry Matter Content (LDMC) has also been proposed as an indicator of plant resource use (Garnier *et al.,* 2001a). This trait is related to leaf lifespan and it is involved in a fundamental trade-off between rapid production of biomass and an efficient conservation of nutrients (Grime *et al*., 1997; Poorter & Garnier, 1999; Ryser & Urbas, 2000). Finally, living fuel moisture content, which is determined by Leaf Moisture (LM) and Live Fine Fuel Moisture (LFFM), is used in various fire model systems (Andrews & Bevins, 2003; Piñol *et al*., 2005) as a determining factor for the ignition and propagation of fire (Chandler, 1983).

The purpose of this study is to characterize a set of coexisting woody species with different post-fire regenerative strategies (resprouter, seeder and seeder-resprouter), according to various attributes related to their resource use, particularly, water economy, nutrient conservation and combustibility. Thus, I analyze the seasonal variation of the Leaf Relative Water Content, the Leaf Dry Matter Content, the Leaf Moisture and the Live Fine Fuel Moisture in 30 woody species from coastal shrublands of Catalonia.

The main aim is to verify whether there is a co-variation between regenerative groups and functional groups. This hypothesis is based on the different biogeographical origin of the taxa coexisting in Mediterranean communities and in the role that these species play during the course of the succession. Since both regenerative and functional attributes are constrained by phylogenetic history, phylogenetical distances between taxa were also considered in the analyses.

More specifically, the following questions are addressed: (a) Does seasonality determine different Leaf Relative Water Content and Leaf Dry Matter Content in plants with different post-fire regenerative strategies? (b) Do different post-fire regenerative strategies have different moisture contents in live fine fuel (leaves and shoots)?

MATERIAL AND METHODS

Study site, species and general sampling procedure

The study area was located on the Massís del Montgrí, a Mediterranean protected coastal area located in the NE of Catalonia**,** (North-East Iberian Peninsula, (UTM 31T X_{min}: 510766.6, Y_{min}: 4655228.4; X_{max}: 515098.8, Y_{max}: 4661482.5)). Vegetation grows on limestone and is mainly dominated by open pine forests and also by Mediterranean shrublands, dominated by *Quercus coccifera, Cistus albidus, Cistus monspeliensis,* and *Rosmarinus officinalis* (Polo & Masip, 1987). Sampling was conducted in 1-2-m-high mature shrublands that had been untouched by wildfire for over 10 years.

The area's climate is sub-humid Mediterranean, according to the Emberger classification (Emberger, 1942). The mean annual precipitation is 654.6 mm, with cool winters (mean minimum annual temperature: 4.1ºC) and warm summers (mean maximum annual temperature: 26.8ºC) (Ninyerola *et al.*, 2000, 2003).

The study was carried out on a subset of 30 woody plant species growing in the study region and representative of the studied community and belonging to as many different families and regenerative strategies as possible in this type of community. They were classified into three groups depending on their post-fire regenerative strategies (Cucó, 1987; Papió, 1988; Lloret & Vilà, 1997; Verdú, 2000; Alberdi & Cavero 2003; Lloret & Vilà, 2003), and after direct field observations in a close area that burned in September 2004: Seeders (S), Resprouters (R) and Seeder-resprouters (SR). Seeders are species that germinate after fire but do not resprout (S+ R-, *sensu* Pausas & Verdú, 2005); Resprouters are considered to resprout but not to germinate (S- R+); and Seeder-resprouters can germinate and resprout after fire (S+ R+).

Seven species were considered seeders (S), 14 resprouters (R) and nine seeder-resprouters (SR). Seeders belonged to two families, resprouters to 13 families, and Seeder-Resprouters to four families (Table 1). Species that neither germinate nor neither resprout were not considered since there is not anyone present in the studied community.

Table 1. List of study species including their family, regenerative strategy and life-form according to Raunkiaer classification (Raunkiaer 1934). Chamaephyte = C, Nano-Phanerophyte = NP, Macro-Phanerophyte = MP, Phanerophyte = P, Phanerophyte-Vine = PV.

Study Species	**Family**	**Regenerative Strategy**	**Life-form**
Argyrolobium zanonii (Turra) P. W. Ball	Leguminosae	Seeder-Resprouter (SR)	C
Calicotome spinosa (L.) LK	Leguminosae	Seeder-Resprouter (SR)	NP
Cistus albidus L.	Cistaceae	Seeder (S)	NP
Cistus monspeliensis L.	Cistaceae	Seeder (S)	NP
Cistus salviifolius L.	Cistaceae	Seeder (S)	NP
Clematis flammula L.	Ranunculaceae	Resprouter (R)	PV
Coronilla minima (L.)	Leguminosae	Resprouter (R)	C
Crataegus monogyna Jacq.	Rosaceae	Resprouter (R)	MP
Daphne gnidium L.	Thymelaeaceae	Resprouter (R)	NP
Dorycnium hirsutum (L.) ser. In DC.	Leguminosae	Seeder-Resprouter (SR)	C
Dorycnium pentaphyllum Scop.	Leguminosae	Seeder-Resprouter (SR)	C
Erica arborea L.	Ericaceae	Resprouter (R)	MP
Fumana ericoides (Caav.) Gandg.	Cistaceae	Seeder (S)	C
Fumana thymifolia (L.)	Cistaceae	Seeder (S)	C
Globularia alypum L.	Globulariaceae	Seeder-Resprouter (SR)	NP
Helianthemum nummularium (L.) Miller	Cistaceae	Seeder (S)	C
Lavandula latifolia Med.	Labiatae	Seeder-Resprouter (SR)	C
Lonicera implexa Aiton	Caprifoliaceae	Resprouter (R)	PV
Olea europaea L.	Oleaceae	Resprouter (R)	MP
Osyris alba L.	Santalaceae	Resprouter (R)	NP
Phillyrea angustifolia L.	Oleaceae	Resprouter (R)	NP
Pistacia lentiscus L.	Anacardiaceae	Resprouter (R)	MP
Quercus coccifera L.	Fagaceae	Resprouter (R)	NP
Quercus ilex L.	Fagaceae	Resprouter (R)	MP
Rhamnus alaternus L.	Rhamnaceae	Resprouter (R)	P
Rosmarinus officinalis L.	Labiatae	Seeder (S)	NP
Smilax aspera L.	Liliaceae	Resprouter (R)	PV
Staehelina dubia L.	Compositae	Seeder-Resprouter (SR)	C
Teucrium polium L.	Labiatae	Seeder-Resprouter (SR)	C
Thymus vulgaris L.	Labiatae	Seeder-Resprouter (SR)	C

Sampling and measurements of traits

For each species, replicate samples were collected from ten different plants, in each season: spring (May 2004), summer (August 2004), autumn (November 2004) and winter (February 2005). Individuals of the same species were collected throughout the year, on the same site and under similar conditions (on limestones without forest canopy).

Three leaf variables were estimated through all over the year: Leaf Relative Water Content (hereafter RWC in the text and W in the equations), Leaf Dry Matter Content (hereafter LDMC in the text and D in the equations) and Leaf Moisture (hereafter LM in the text and M in the equations). Moreover Live Fine Fuel Moisture (hereafter LFFM in the text and F in the equations) was also measured from shoots (< 6 mm diameter).

The Relative Water Content (W) (%) was determined as

$$W = 100 \times ((M_f - M_d) / (M_t - M_d))$$

where M_f is the fresh mass, M_t is the turgid mass after re-hydrating the leaves, and M_d is the dry mass after drying the leaves in an oven. The Leaf Relative Water Content takes into account the turgid mass of leaves, and so it is the proportion of the leaf water content related to the maximum water content that can potentially be achieved by the leaf.

The Leaf Dry Matter Content (D) (mg/g) was determined as

$$D = M_d / M_t$$

Thus, LDMC is the proportion of the leaf matter content without water related to the mass of the leaf with the maximum water content.

Leaf moisture (M) (%) and Live Fine Fuels Moisture (F) (%) of leaves and shoots, respectively, were determined as

$$M = F = 100 \times ((M_f - M_d) / M_d)$$

They indicate the water content of leaves (M) and shoots (F) under field conditions in relation to its dry mass.

Leaf and shoot samples were collected from well–grown plants and they were taken from the part of the canopy exposed to direct sunlight at the time of sampling. Fully-expanded leaves free from herbivore or pathogen damage were severed from a stem or twig, and the petioles were removed (Garnier *et al.,* 2001b). The number of leaves sampled from each individual varied according to the size and the weight of the leaves of each species. In all species (except *Calicotome spinosa* in summer, autumn and winter; *Crataegus monogyna* in winter, because there were no available leaves), the leaves were collected at noon (between noon and 2 pm). RWC was determined following an adaptation of the method used by Munné-Bosch and Peñuelas (2004). Leaves were stored in ice-box conditions, inside plastic jars filled with water to saturate the leaves (a previously weighed plastic jar filled with water was used for each individual). They were stored for 6 to 9 hours, i.e. the period needed to reach water saturation (Espelta, 1996 unpubl. res.). After saturation was achieved, the fresh weight of leaves was obtained weighting the plastic jar filled with the water used for saturation and the leaves. Plastic jars closed hermetically and were conserved in ice-box conditions so that there were no looses of water. Then, the leaves were weighed outside the jar, in order to obtain their saturated weight (with a precision of

10^{-5} g). Finally, they were oven-dried for 48 h at 70ºC and weighed. LDMC and LM were obtained with the same procedure as RWC.

To determine LFFM, ten shoots (< 6 mm diameter) from ten different individuals were collected for each species (except for *Cistus salviifolius* in spring). Each shoot was closed in a hermetic plastic bag and stored in ice-box conditions so that the water lost occurring during journeys between the field and the laboratory remained inside the plastic bag (Viegas *et al.,* 2001). Then they were weighed. Finally, they were oven-dried for 48 h at 70ºC and weighed again (f wt and d wt, with a precision of 0.01 g).

Data analyses

The dependent variables for leaf data analyses were RWC, LM and LDMC. In the case of shoots, the dependent variable was LFFM. The differences between the species belonging to the three regenerative strategies during the seasons of the year were tested by using repeated-measures ANOVA analyses, where the within-subject factor was season and the between-subject factor was regenerative strategy (S, SR, R). In these analyses the replicates were the mean values of each species obtained from the ten sampled individuals. For shoot data analyses, the within-subject factor had four levels (spring, summer, autumn, winter), while for leaves there were three levels (summer, autumn, winter). I failed to obtain RWC, LM and LDMC values for spring leaves in several study species. Consequently, spring was excluded from these repeated-measures ANOVA analyses of RWC, LM and LDMC to avoid too many missing values. All species, except *Calicotome spinosa* and *Crataegus monogyna* (because they lack leaves in some seasons), were included in the repeated measurement ANOVA analyses of leaf parameters. In the case of LFFM, all species, except *Cistus salviifolius* (no data from spring were available), were included in the analyses.

The Relative Seasonal Variations of RWC, LM and LFFM were estimated as: (winter values – summer values) / (winter values). Accordingly, One-Factor ANOVA analyses were performed to test differences between regenerative strategies.

Since spring season could not be included in the previous repeated-measures ANOVA analyses that considered the seasonal variation of some variables, a nested ANOVA analysis was performed separately for each one of the four seasons, and for each of the dependent variables (RWC, LM, LDMC and LFFM). Species was considered a random factor nested within strategy.

Post-hoc comparisons between the different regenerative strategies were carried out using Fisher LSD-test for all tests with significant ANOVA results. To better approximate normality, RWC and LDMC were transformed into their log-odds (i.e. in [LDMC / (1 - LDMC)]), since they are proportions. LM and LFFM were not transformed as they accomplished the requirements for parametric analyses.

As the set of studied species were not equally independent units and phylogenetic constraints influence species traits, I tested the hypothesis that differences between species in leaf and shoot variables are higher when the phylogenetic distance between species increases. First, following Pausas and Verdú (2005), a phylogenetic tree was assembled for the whole set of species by pruning the Hilu *et al*. (2003) Angiosperm tree to the family level, where the respective species were grafted. Thus, a phylogenetic tree was obtained, where the distances between the closest branches were assumed to be the unit (Figure 1). The phylogenetic distance matrix between species considered, for each pair of species, the sum of the respective number of steps until a common bifurcation. I considered that the distance between species belonging to the same family was one, and the minimal distance between species belonging to different families was two. In this way I considered that the distance between families was higher than between species of the same family, even when these species belong to different genus. Similarly, the values of the leaf or shoot variable distance matrix between species were calculated as $(x_i - x_j)^2$, x_i and x_j being the values of a given variable x (RWC, LDMC, LM, LFFM) for the species i and j.

Then, three-way Partial Mantel-tests was performed, in which the correlation between the variables and the regenerative type distances (A and B, respectively) were analyzed when the effects of phylogenetic distance (C) are kept constant (Smouse et al., 1986; Fortin and Gurevitch, 1993). For these analyses, a “regeneration distance matrix” was obtained from the absolute differences of the values given to each regenerative type: resprouters (0), seeder-resprouters (1) and seeders (2). This code was selected because seeder-resprouters share traits of both seeders and resprouters and there is not any a priori reason to assume that seeder-resprouters are closer to any of the two other categories. The statistics resulting from this partial test are regression coefficients ($b_{AB.C}$) corresponding to the partial linear correlation of two distance matrices (A,B) after controlling for the linear effect of a third matrix (C). Significant differences from zero in these coefficients were assessed by comparing reference distributions obtained after 999 iterations that permuted the arrangement of the elements of one of the distance matrices. The test for each variable was performed for each one of the four seasons, and when data were unavailable for some species it was dropped from the analysis and the matrices were modified accordingly.

The Statistica 6 (Statsoft) program was used for the computation of statistical analyses. The Passage 1.0 program (Rosenberg, 2002) was used for Mantel-tests to analyze the effects of phylogeny.

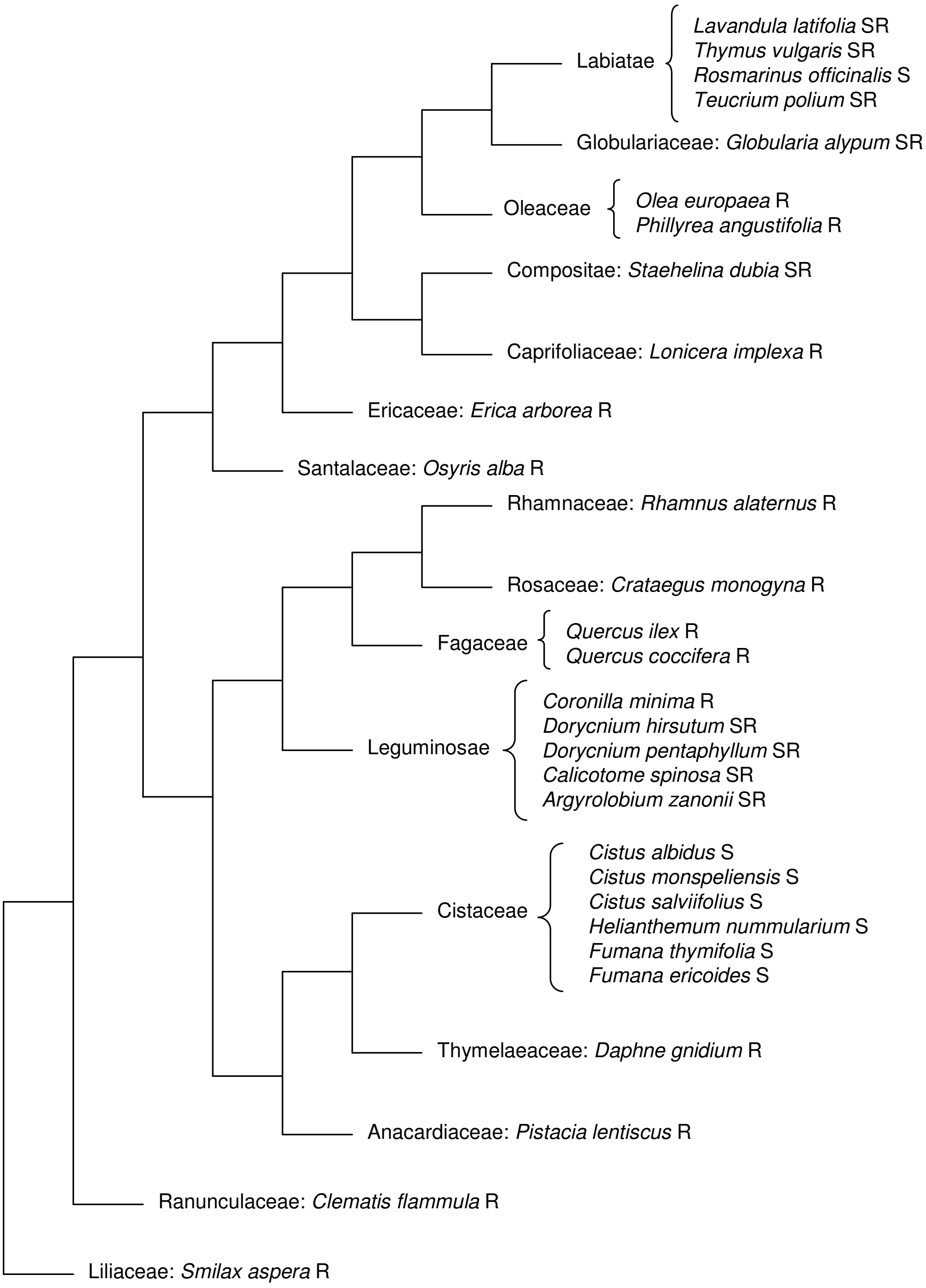

Figure 1. Phylogenetic tree assembled using information from Hilu et al 2003. R = Resprouter, S = Seeder, SR = Seeder-Resprouter

RESULTS

Leaf Relative Water Content (RWC)

Overall, RWC was significantly higher in resprouters than in seeder-resprouters and seeder species ($F_{2,25} = 5.73$, $p = 0.009$). No significant differences between seeder-resprouters and seeders were found (Figure 2). As expected, RWC significantly increased from summer to winter ($F_{2,50} = 44.66$, $p < 0.001$). Although this seasonal variation in RWC was less intense in resprouters than in the other two strategies, the interaction between season and strategy was only marginally significant ($F_{4,50} = 2.47$, $p = 0.056$) (Figure 2). Accordingly, the Relative Seasonal Variation was lower for resprouters than for the other two types (Table 2). In fact, when analyzing each season separately, significant differences between regenerative strategies were only observed in spring ($F_{2,149} = 6.22$, $p = 0.008$) and summer ($F_{2,233} = 12.04$, $p < 0.001$). Post-hoc analyses demonstrated that, in both spring and summer, resprouters had a significantly higher RWC than seeders and seeder-resprouters. The same pattern was observed when correlating differences in RWC between species and regenerative type, keeping the phylogenetic distance constant (Table 3).

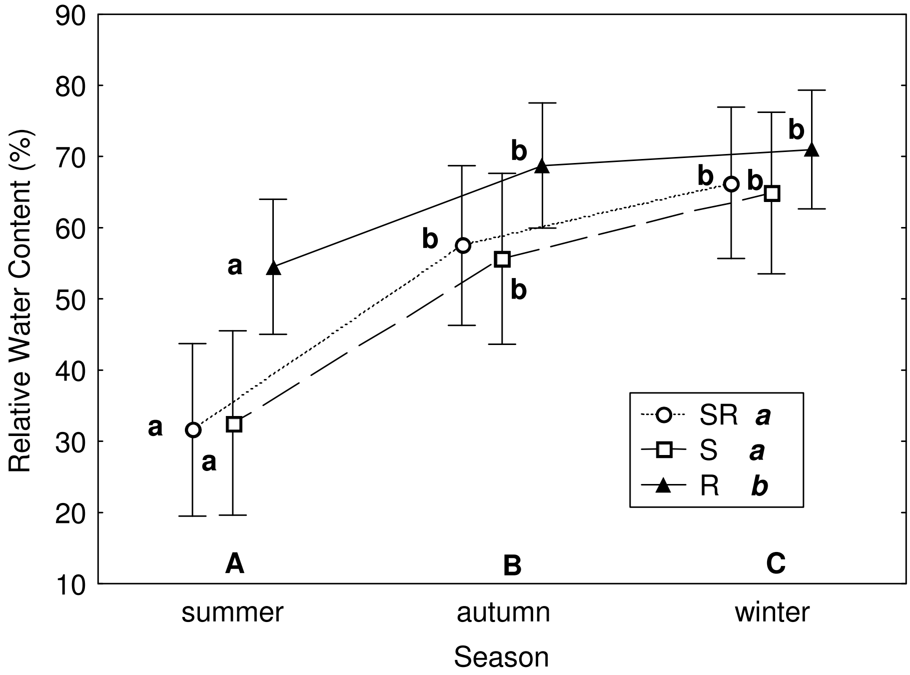

Figure 2. Mean Leaf Relative Water Content (RWC) (%) of the three regenerative strategies (Seeder (S), Resprouter (R) and Seeder-Resprouter (SR)), in summer, autumn and winter.
Vertical bars denote 0.95 confidence intervals.
Post-hoc Fisher-LSD significant differences (p<0.05) are indicated with different letters: capital letters indicate differences between seasons, italic lower-case letters in the legend indicate differences between strategies, and plain lower-case letters indicate differences between seasons for a given strategy. All the species (except *C. spinosa* and *C. monogyna*) are included.

Table 2. One-way ANOVA for the relative seasonal variation of the three water-related variables for the three different regenerative strategies. Values of the relative seasonal variation are the result of: [variable (winter) — variable (summer)] / variable (winter)]. Post hoc Fisher's L.s.d. Significant differences (P , 0.05) are shown in the third column. RWC, relative water content; LM, leaf moisture, LFFM, leaf fine fuel moisture; R, resprouter, S, seeder; SR, seeder–resprouter.

	n	F	p-value	Fisher LSD Post-hoc
RWC	28	9.35	<0.001	R < S, SR
LM	28	8.48	0.002	R < S, SR
LFFM	30	4.43	0.021	R, SR < S

Table 3. Summary of results of the Partial Mantel-Test between the RWC, LDMC, LM and LFFM matrices and the Regeneration distance matrix for each season, when the effect of phylogenetic distance was kept constant. RWC and LDMC data were transformed into their log-odds. *The Partial Mantel-Test shows significant differences between regenerative strategies, which were also observed in the results of the Nested-Anova for each season, without taking into account phylogeny. nsThe Partial Mantel-Test does not show any significant differences between regenerative strategies, but significant differences were found in the results of the Nested-Anova for each season, without taking into account phylogeny.

		spring	summer	autumn	winter
RWC	b	0.251	0.173	0.027	-0.067
	p-value	0.017*	0.010*	0.728	0.214
LDMC	b	0.045	0.001	0.118	0.063
	p-value	0.700	0.978^{ns}	0.052^{ns}	0.246
LM	b	-0.099	-0.010	0.064	-0.007
	p-value	0.339	0.881	0.327	0.902
LFFM	b	-0.100	0.016	-0.077	0.141
	p-value	0.171	0.874	0.235	0.033*

Leaf Dry Matter Content (LDMC)

Overall, LDMC was significantly higher in resprouters than in the other two regenerative strategies ($F_{2,25}$ = 4.50, p = 0.021) (Figure 3), but no significant differences between seasons were found ($F_{2,50}$ = 1.34, p = 0.269). The interaction between regenerative strategy and season was not significant ($F_{2,50}$ = 1.82, p = 0.140). When analyzing each season separately, significant differences between strategies were found in summer ($F_{2,233}$ = 5.16, p = 0.013) and autumn ($F_{2,248}$ = 5.65, p = 0.009). Post-hoc analyses demonstrated that in summer, resprouters had a higher LDMC than seeders, and seeders had a higher LDMC than seeder-resprouters, while in autumn resprouters had a higher LDMC than the other two strategies that showed similar values. These differences between regenerative strategies can be attributed to phylogenetic constraints, since no significant correlation between differences in LDMC and regenerative type were found when keeping constant the effect of phylogenetic distance in Partial Mantel-tests (Table 3).

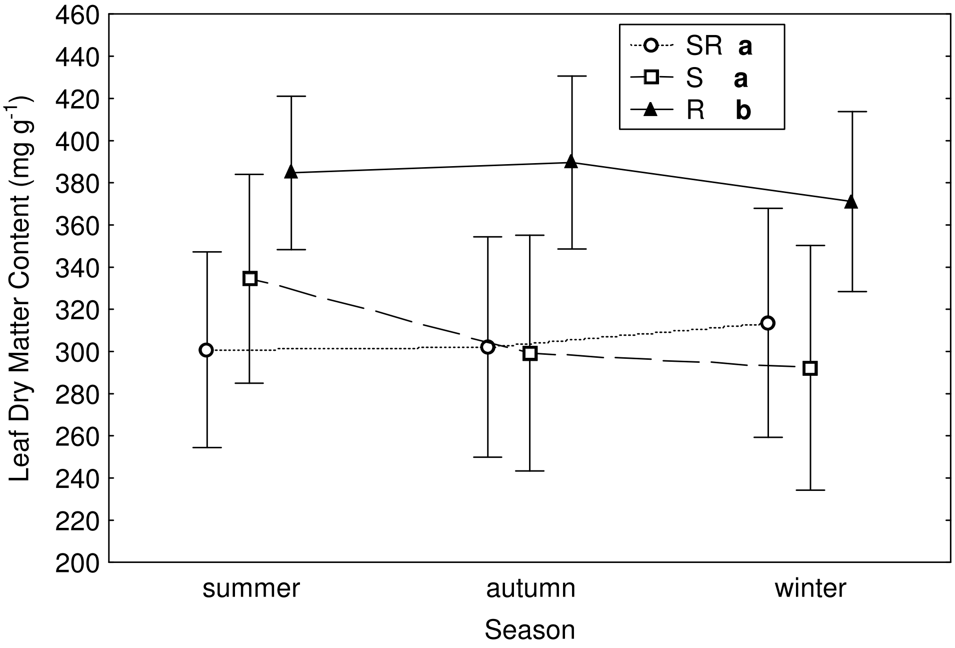

Figure 3. Mean Leaf Dry Matter Content (LDMC) (mg g-1) of the three regenerative strategies (Seeder (S), Resprouter (R) and Seeder-Resprouter (SR)), in summer, autumn and winter. Vertical bars denote 0.95 confidence intervals. Lower-case letters indicate Post-hoc Fisher-LSD significant differences (p<0.05) between strategies. All the species (except *C. spinosa* and *C. monogyna*) are included.

Leaf Moisture (LM)

There was a significant increase in LM from summer to winter ($F_{2,50}$ = 46.01, $p < 0.001$), but the seasonal pattern of variation changed according to the regenerative strategies (season×strategy interaction: $F_{4,50}$ = 4.05, p = 0.006) (Figure 4). Although there were no significant differences between regenerative strategies in a given season, seeders varied the most between summer and winter, while seeder-resprouters varied less and resprouters presented the most constant pattern across the seasons (Table 2). Thus, in winter, the LM of seeders was higher than in autumn, while the other two strategies did not display any significant differences between autumn and winter. As a result, of the three strategies, the seeders presented the lowest LM in summer, but their values were the highest in winter (Figure 4). No significant correlations were observed between LM and regenerative type when keeping constant the effect of the phylogenetic distance (Table 3).

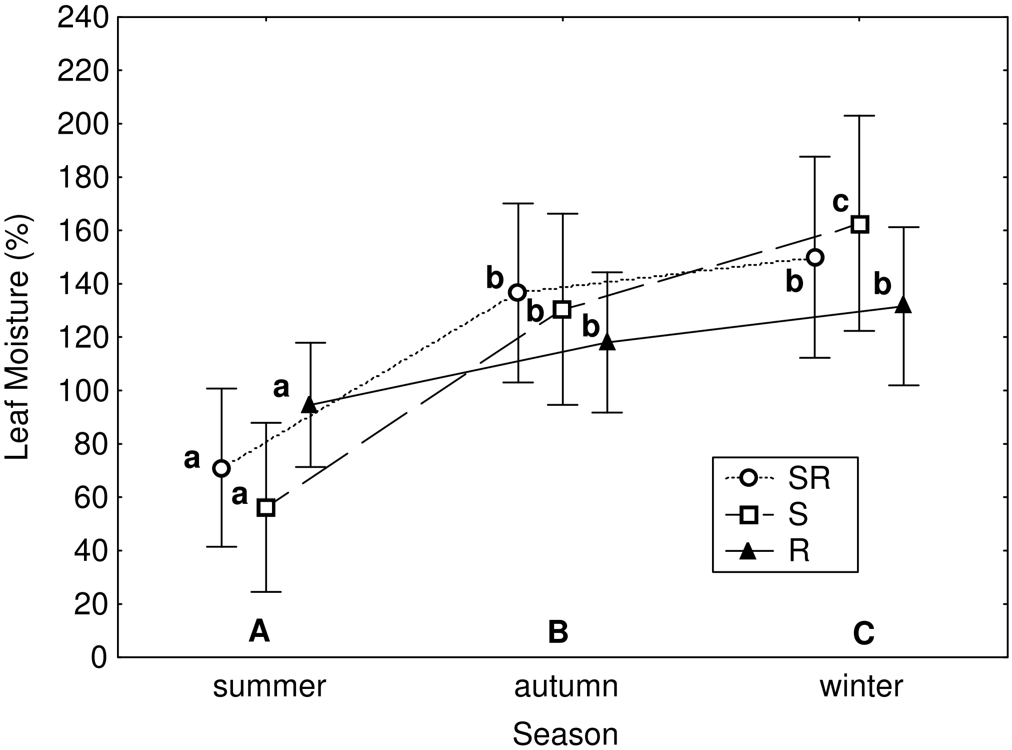

Figure 4. Leaf Moisture (LM) (%) means of the three regenerative strategies (Seeder (S), Resprouter (R) and Seeder-Resprouter (SR)), in summer, autumn and winter. Vertical bars denote 0.95 confidence intervals. Post-hoc Fisher-LSD comparisons are represented with letters, significant differences (p<0.05) are indicated with different letters. Capital letters indicate significant differences between seasons, and lower case letters indicate post-hoc differences between seasons for a given strategy. All the species (except *C. spinosa* and *C. monogyna*) are included.

Live Fine Fuel Moisture (LFFM)

As expected, LFFM was significantly lower in summer than in autumn, winter and spring, the latter being the season with the highest values ($F_{3,78}$ = 52.93, $p < 0.001$) (Figure 5). Overall, differences between regenerative strategies were not significantly different ($F_{2,26}$ = 0.88, p = 0.426), although seeders tended to attain higher LFFM values than the other regenerative strategies in autumn and winter (season×strategy interaction: $F_{6,78}$ = 2.39, p = 0.036). Thus, the seasonal pattern of seeders differed from the other regenerative strategies, since the LFFM of seeders varied the most between summer and winter, while those of seeder-resprouters and resprouters varied the least over this period (Table 2). Accordingly, Nested ANOVA showed significant differences between strategies in winter ($F_{2,259}$ = 5.71, p = 0.009), when seeders attained their highest values, followed by resprouters and seeder-resprouters (Fisher LSD post-hoc test).

The same pattern was observed when correlating differences between species in LFFM (winter) and regenerative type when keeping the phylogenetic distance constant (Table 3).

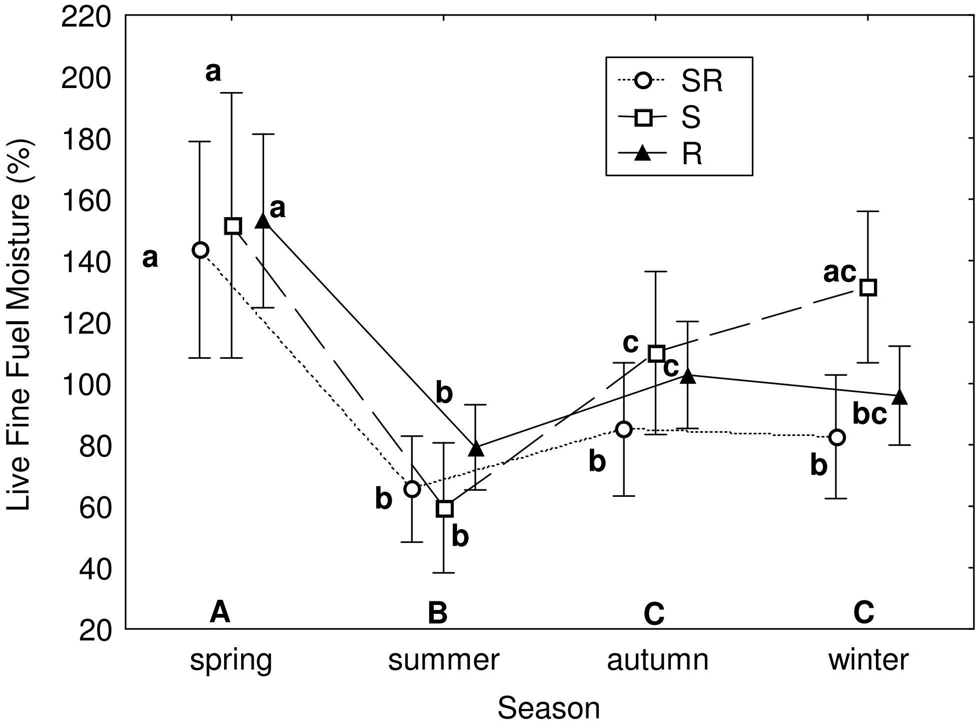

Figure 5. Mean Live Fine Fuel Moisture (LFFM) (%) of the three regenerative strategies (Seeder (S), Resprouter (R) and Seeder-Resprouter (SR)), in spring, summer, autumn and winter. Vertical bars denote 0.95 confidence. Post-hoc Fisher-LSD significant differences ($p<0.05$) are indicated with different letters. Capital letters indicate differences between seasons: lower case letters indicate differences between seasons for a given strategy. All the species (except *C. salviifolius*) are included.

DISCUSSION

Although in areas with a Mediterranean-type climate, all plant species are expected to endure Mediterranean summer drought, this study demonstrates that the species with resprouting syndrome show different behavior in the face of seasonal drought when compared to seeders. Thus, species with different post-fire regenerative strategies exhibit different functional properties within the ecosystem (Paula & Pausas in press). RWC results suggest that resprouters exhibit higher and more stable water conservation than seeders from summer to winter. Accordingly, Correia & Catarino (1994) described very negative values of leaf water potential for the seeder *Cistus* species, with high variations throughout the year, while the resprouter *Pistacia lentiscus* sustained fewer variations and less water deficits over the course of the year. Therefore, morphological drought-avoiding traits are more common in resprouters, while non-resprouters should be physiologically more drought-tolerant (Pausas *et al*. 2004), allowing them to survive on drier sites. Results are complementary with findings in similar communities (Paula & Pausas, 2006) and suggest that the resprouters under study have more mechanisms to reduce water losses and maintain water supply between seasons, so they tend to avoid dehydration. In contrast, seeders would tolerate lower leaf water contents in their tissues during drought periods. As a result, seeders tend to lose and take water more easily than resprouters do, and these differences may be due to traits such as cell characteristics that permit elasticity and osmotic adjustments (Medrano & Flexas, 2004).

In addition, plant water stress varies according to the depth and extension of root systems (Pereira & Chaves, 1993). Dawson & Pate (1996) described different root morphology for Australian woody species with different resistance to fire: the most sensitive species had a single main root and a number of shallow lateral roots while fire-resistant species had multiple lateral and main roots arising from a lignotuber. Similar descriptions are available of woody species from the Mediterranean basin: *Cistus* seedlings have shallow root systems while some resprouter species such as *Pistacea lentiscus* have deeper rooted seedlings (Kummerow, 1981; Clemente *et al.*, 2005). Thus, it is highly feasible that species belonging to different post-fire regenerative strategies also differ in respect to the depth and extension of their root systems, and this factor could be involved in leaf-water and nutrient conservation strategies. The extension of root systems is also related to above-ground plant size. In this case, most of the resprouters are bigger than the seeders, and they could develop deeper root systems, allowing more stable RWC throughout the year.

One important reason for the co-variation between post-fire regenerative traits and water-use-related traits may be that these two groups of taxa (resprouters and seeders) originally evolved under different environments. Most of the resprouters under study are species that have evolved from ancient taxa present in the Tertiary (pre-Pliocene), before the establishment of the Mediterranean climate, while most seeders appeared later, contemporary to the Mediterranean climate, and they comprise less families. This difference in evolutionary context may, therefore, have contributed to the emergence of different strategies to tackle seasonal water deficit: relatively stable leaf water content and drought-avoiding traits in resprouters, and drought-tolerance traits and poiquilohydric tendencies in seeders, appearing under conditions of great variability in available water.

Seasonal variation is shown to be present in all the three variables related to water. The general pattern is that the lowest water content is found in summer, while it tends to increase between autumn and winter. As it was expected according to Garnier et al 2001a, results suggest that Leaf Dry Matter Content is a parameter that does not vary so much between seasons, since this parameter relies on the dry mass of the leaf and the maximum of water that it can be stored. However, there are some interesting differences in LDMC in species with different regenerative strategies. I found that resprouters have a consistently higher LDMC than seeders throughout the year. This means that the leaves of resprouters, when compared to those of seeders, have a structure with a greater proportion of dry matter in relation to saturated weight. This suggests a slower production of biomass, a longer leaf lifespan, and a more efficient conservation of nutrients (Grime *et al*., 1997). Ryser & Urbas (2000) reported that differences in behavior after disturbances are more closely related to the leaf lifespan and conservation of nutrients than to the availability of nutrients. In contrast seeders, which often correspond to early successional species, would invest more resources in fast growth and reproduction, with a less efficient use of nutrients and water (Terradas, 1979; Nogueira *et al.,* 2004).

LM and LFFM are often used as indicators of combustibility (Piñol *et al.,* 1998; Viegas *et al*., 2001; Andrews & Bevins 2003; Castro *et al*., 2003). The results of LM and LFFM indicate that seeders have more leaf and shoot moisture and that they rehydrate more in winter. Moreover, seasonal variation is higher in leaves than in shoots, in both strategies. Despite the tendencies observed in some species, the statistical analyses do not support the hypothesis that seeder species foment a greater risk of fires in summer, at least with respect to this parameter related to combustibility. Further exploration of structural traits is needed to form a more complete picture of differences in combustibility and inflammability in the different regenerative strategies.

An important number of species in the Mediterranean basin display both post-fire regenerative strategies (seeding and resprouting (SR)). Results suggest that this group tends to follow a similar strategy for water and nutrient use as drought-tolerant seeders. This concurs with the evolutionary history of these species, which involves only four families (Leguminosae, Labiatae, Compositae and Globulariaceae) that mostly evolved in the Quaternary (Post-Pliocene). However the relatively stable seasonal pattern of LFFM in seeder-resprouters tends to be more similar to that of resprouters than that of seeders, indicating that they cannot rehydrate shoots to the same extent as seeders during autumn and winter.

Species belonging to the same family can be expected to display more similar traits than distant taxa. This may be relevant for an evolutive explanation of the traits occurrence, but it is not particularly important when describing the pattern of changes of the functional attributes in the community in relation to the disturbance regime. Thus, the observed differences between regenerative types may be influenced by the fact that some of them are represented by few families (seeders), and the phylogenetical and the regenerative effects are hardly distinguished. The partial linear correlations and the randomisation of the Mantel tests circumvents at certain extent this problem. Accordingly, when the phylogenetic distance is kept constant, the differences between regenerative groups tend to disappear, suggesting that attributes related to leaf nutrient conservation and leaf structure are more likely to be determined by phylogenetic constraints. This is not the case with LFFM (in winter) and RWC, where differences between regenerative groups exist even when the weight of the phylogenetic distance is kept constant. RWC would appear as a plastic trait indicating leaf water status. It would quickly respond to water environmental conditions with a similar behavior in phylogenetically distant taxa. Finally, LM and LFFM do not show any dependence on phylogenetic constraints, although, overall, there are no significant differences between the regenerative groups.

Overall, this study reveals important differences in the leaf properties (water and matter content) of species that present distinct post-fire regeneration strategies throughout the various seasons. This supports the hypothesis that changes in the relative abundance of post-fire regenerative groups due to fire regime would promote changes in functional properties at the community level. These differences between regenerative types can be interpreted under the classical “r – K” syndromes gradient. It is worth noting that this gradient of syndromes is determined by the evolutionary context. On the “r” side there are species that emerged within the typical Mediterranean climate and that belong to a few families (Cistaceae, Labiatae), while on the “K” side there is a number of Tertiary (Pre-Pliocene) taxa belonging to a larger variety of families. This finding concurs with the observation in Mediterranean forests of the impact of drought episodes on these groups of species (Peñuelas *et al.,* 2001). This suggests that the irregular water availability of the Mediterranean climate would have favored the radiation of woody taxa with a relatively shorter lifespan, with a lesser ability to regulate water use (drought tolerance strategies) and produce a large number of seeds that can be stored in the soil seed bank until the appropriate conditions for establishment arise. Clearly, these traits closely correspond not only to the conditions found after wildfires, but also, generically, to the early stages of the succession that can be initiated by other disturbances (fire, clearing or drought episodes).

ACKNOWLEDGEMENTS

I would like to thank R. Ogaya, J. Piñol and J. Terradas and two anonymous referees for fruitful suggestions and advice. Ll. Benejam, A. Burgas, M. Jané, M. Sallent, A. Saperas, A. Vilà, and M. Del Cacho helped in the field work. This study was funded by the Department of Universities, Research and Information Society of the Generalitat de Catalunya and the European social funds, and the Spanish MCYT project REN 2003-07198.

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III. LEAF NUTRIENT CONCENTRATION

The main contents of this chapter have been submitted to Perspectives in Plant Ecology, Evolution and Systematics as:
Saura-Mas, S., Lloret, F. Linking post-fire regenerative strategy and leaf nutrients in Mediterranean woody plants.

ABSTRACT

- The main purpose of this paper is to explore the differences between the leaf nutrient concentration in species from Mediterranean shrublands showing the ability to resprout after disturbances such as fire (resprouters) and others without this capacity (non-resprouters). Since resprouting capacity is expected to be related to a more conservative use of nutrients, I hypothesize that relevant functional properties of these communities can be determined by the relative abundance of this type of species as a result of particular fire regimes.

- The following leaf traits were measured: leaf carbon concentration (LCC), leaf nitrogen concentration (LNC), leaf phosphorous concentration (LPC), leaf potassium concentration (LKC), leaf calcium concentration (LCaC), leaf magnesium concentration (LMgC) and leaf sodium concentration (LNaC), in 30 woody species coexisting on a coastal shrubland. The weight of species' taxonomic affiliation was also considered in the analyses.

- Non-resprouters showed higher LPC and LCaC than species with a resprouter syndrome. However, non-resprouters displayed lower LCC, which could be related to their cell and life-history properties. Furthermore, the relationship between LNC and LPC is weaker in resprouter species, which suggests that P is a major nutrient limitation on plant growth in this group of species.

- Overall, differences between leaf nutrient concentrations suggest that shifts in the proportion of resprouter and non-resprouter species resulting from fire regime changes may cause modifications in the fluxes of relevant elements such as P, C and Ca.

Keywords: fire, leaf traits, nutrient, plant functional groups, regenerative traits, resprouter

INTRODUCTION

Functional plant classification aims to group species according to functional similarities, thereby providing a more comprehensive description of the community functions subjected to a given disturbance regime (Lavorel *et al.*, 1999; Díaz & Cabido, 2001; Keane *et al.*, 2004; Violle *et al.*, 2007). The functional role of the species may be highly determined by their response to environmental constraints, such as disturbance regime (Lavorel *et al.*, 1997; Lavorel *et al.*, 1999). Accordingly, post-disturbance regenerative strategies can define groups of species with similar response in front of disturbances (PFRG, plant functional response groups (*sensu* Lavorel *et al.*, 1997)). Thus, we can establish the hypothesis that changes in species composition due to disturbance regime may promote modifications in the properties of the whole community (Carreira & Niell, 1992; Sardans *et al.*, 2005). This hypothesis will be sustained by a correlation between attributes defining functional (for instance, leaf nutrients concentrations) and response groups (for instance, post-disturbance regeneration attributes) (Díaz & Cabido, 2001; Lavorel & Garnier, 2002; Violle *et al.*, 2007).

Among functional traits, leaf nutrient concentration provide valuable insights about ecosystem's functioning and as been used to describe patterns of productivity, litter decomposition and total soil carbon and nitrogen in relation to secondary succession (Garnier *et al.*, 2004) and land use management (Quetier *et al.*, 2007). In particular, leaf carbon concentration correlates with the amount of CO_2 assimilated by the ecosystem and consequently with net primary production (Schulze, 2000; Chapin *et al.*, 2006). It is also related with carbon fluxes within the ecosystem since most of this carbon will rapidly return to the soil. Leaf nitrogen concentration is also considered an important functional trait, being positively associated with the net photosynthetic rate per unit mass (Reich *et al.*, 1997; Garnier *et al.*, 1999; Garnier *et al.*, 2001) and the relative growth rate (Cornelissen *et al.*, 1997). Leaf phosphorous concentration plays an important role in bioenergetic molecules such as ATP (Cebrián, 1996; Schulze et al., 2005). In fact, leaf nitrogen and phosphorous concentration have been described as an index of soil nutrient limitation being related to plant growth strategies, (Koerselman & Meuleman, 1996; Aerts & Chapin, 2000; Sterner & Elser, 2002). There are some other nutrients – such as K, Mg, Ca and Na – that being present in the leaves at lower concentrations nevertheless serve important functions in cells' structural and metabolic properties, such as the regulation of cytoplasmic volume which can be related to other leaf and plant traits such as growth rate (Reich *et al.*, 1997; Taiz, 1998; Reich *et al.*, 2003; Wright *et al.*, 2004; Shipley *et al.*, 2006).

According to their ability to regenerate after fire, two large groups of species can be considered: resprouters (species that can regenerate by resprouting, including those that also present new seedlings after fire) and non-resprouters (species that only regenerate after fire by seedling establishment, also named “seeders” in the literature) (Pausas *et al.*, 2004; Pausas & Verdú, 2005; Saura-Mas & Lloret, 2007).
Fire regime is likely to determine the relative abundance of the different post-fire regenerative types. Thus, regional and local surveys have reported an increase of the relative abundance of non-resprouters in burned areas (Bellingham & Sparrow, 2000; Franklin *et al.*, 2004; Lloret *et al.*, 2005). These empirical observations have been supported by long-term simulations under different fire regimes (Lloret *et al.*, 2003; Pausas & Lloret, 2007).

Post-disturbance regenerative strategies are based on life-history attributes, which in turn are likely to be related to resources uptake, storage and use. In the Mediterranean basin, the group of resprouters is mostly constituted by long-lived species, typically found in late successional shrublands that often show a high percentage of individuals that survive and resprout after fire, while they do not show significant recruitment of new individuals shortly after wildfire. In contrast, non-resprouters show a shorter life cycle and a higher recruitment after disturbances such as fire or drought (Pate *et al.*, 1990; Verdaguer & Ojeda, 2002; Knox & Clarke, 2005; Schwilk & Ackerley, 2005). Lloret (1998) also showed that, after wildfires, non-resprouters produce seedlings with higher survival and growth rates than in the period before fire. Thus, long-lived resprouters are expected to show a higher resource allocation to underground organs in order to sustain plant re-growth (Knox & Clarke, 2005), while short-lived non-resprouters would have shorter leaf life span, high specific leaf area and higher photosynthetic rates (Bell, 2001; Ackerly, 2004), similarly to early successional species of mesic forests (Bazzaz, 1979). These traits are expected to be reflected on the leaf nutrient concentration of these groups of species.

Convergent ecological attributes between species of the Mediterranean basin with the same post-fire regenerative strategies may also be influenced by historical and phylogenetical constraints (Verdú, 2000; Verdú *et al.*, 2003; Pausas & Verdú, 2005). While most non-resprouter taxa diversified in the Quaternary (Post-Pliocene), when the Mediterranean climate was established, many resprouters evolved in the Tertiary (Pre-

Pliocene) (Herrera, 1992; Verdú, 2000; Pausas & Verdú, 2005), before the occurrence of the typical Mediterranean conditions (Jalut *et al.,* 2000). Therefore, differences in leaf nutrients concentrations at species level may have been at some extent influenced by different evolutive, climatic contexts.

Here, the main hypothesis is that the two post-fire regenerative groups (resprouters and non-resprouters) show differences in leaf nutrient concentrations (carbon, nitrogen, phosphorous, potassium, calcium, magnesium, sodium). Therefore, they act as two different functional groups in relation to community's nutrients functioning. Since both regenerative and functional attributes are constrained by phylogenetic history, taxonomic affiliations of species were also considered in the analyses. Moreover, the following additional objectives were addressed: (a) to characterize the leaf nutrient concentration in thirty of the most common woody species on western Mediterranean limestone shrublands; (b) to analyze of the relationship between LNC and LPC and other leaf nutrient concentration.

MATERIALS AND METHODS

Study area and species

The study area was located on the Massís del Montgrí, a protected Mediterranean coastal area located in the NE of Catalonia (north-east Iberian Peninsula, 42.16ºN, 3.24ºW). The vegetation is mainly dominated by open pine forests and also by Mediterranean shrublands with a prevalence of *Quercus coccifera*, *Cistus albidus*, *Cistus monspeliensis*, and *Rosmarinus officinalis* (Polo & Masip, 1987). The soil is *Terra rossa*, a calcareous soil in which carbonates have been extensively lost through lixiviation but a great richness of Ca has been preserved (Table 1). High levels of the C:N relationship indicate that organic matter is very little transformed and that the soil is relatively poor in N. The texture of the soil is mostly clay-loam, and P concentrations are high in the first 5 cm of soil but become poor at depths of 5-20 cm. The Mg and K concentrations are high, but Na is not very abundant in this soil (Klute, 1986).

Sampling was conducted in mature shrubland vegetation (1-2 m high shrubs) that had been untouched by wildfire for over 10 years. The area's climate is sub-humid Mediterranean, according to the Emberger classification (Emberger, 1942). The mean annual precipitation is 654.6 mm, with cool winters (mean minimum annual temperature: 4.1ºC) and warm summers (mean maximum annual temperature: 26.8ºC) (Ninyerola *et al.*, 2000; Ninyerola *et al.*, 2003).

Table 1. Chemical and physical properties of soil in the study area, at 0-5 cm and 5 – 20 cm depth intervals. Soil characteristics were obtained from seven compound samples (collected in 25 m transects).

Soil chemical and physical characteristics		
	0 - 5 cm	**5 - 20 cm**
Ph (water)	7,05	7,90
Conductivity (dS/m)	0,51	0,33
Carbonates	4,50	5,00
Organic Carbon (%)	20,70	4,10
Total N (%)	1,43	0,25
C : N	14,47	16,40
Available P (ppm)	37,17	5,17
K (ppm)	493,83	303,67
Mg (ppm)	643,50	168,67
Ca (ppm)	11501,17	5194,83
Na (ppm)	87,00	44,17
Sand (%)	35,75	49,87
Thick Silt (%)	18,32	4,43
Fine Silt) (%)	12,73	15,83
Clay (%)	33,08	29,87

The study was carried out on a subset of 30 woody plant species growing in the study region, representative of the studied community and belonging to as many different families and regenerative strategies as possible in this type of community. They were classified into two groups, according to their post-fire regenerative strategies: resprouters (R) and non-resprouters (NR). The resprouter group is formed by species that only resprout (S- R+, *sensu* Pausas & Verdú, 2005) and species that both germinate and resprout after fire (S+ R+). Non-resprouters are species that germinate after fire but do not resprout (S+ R-). Species were assigned to one of these two groups according to information from the literature (Cucó, 1987; Papió, 1988; Lloret &

Vilà, 1997; Verdú, 2000; Alberdi & Cavero, 2003; Lloret *et al.*, 2003), and after direct field observations in a nearby area that burned in September 2004. Twenty species were classified as resprouters (R) and 10 as non-resprouters (NR). The resprouters belonged to 13 families and the non-resprouters to four families (Table 2). Species that neither germinate nor resprout after fire (S- R-) were not considered as none were present in the studied community.

Table 2. Study species, post-fire regenerative strategies (PFRS: resprouter = R, non-resprouter = NR) and life-form (according to Raunkiaer classification). Chamaephyte = C, Nano-Phanerophyte = NP, Macro-Phanerophyte = MP, Phanerophyte = P, Phanerophyte-Vine = PV.

Study Species	Family	PFRS	Life-form
Argyrolobium zanonii (Turra) P. W. Ball	Leguminosae	R	C
Calicotome spinosa (L.) LK	Leguminosae	R	NP
Cistus albidus L.	Cistaceae	NR	NP
Cistus monspeliensis L.	Cistaceae	NR	NP
Cistus salviifolius L.	Cistaceae	R	NP
Coronilla minima (L.)	Leguminosae	R	C
Daphne gnidium L.	Thymelaeaceae	R	NP
Dorycnium hirsutum (L.) ser. In DC.	Leguminosae	R	C
Dorycnium pentaphyllum Scop.	Leguminosae	R	C
Erica arborea L.	Ericaceae	R	NP
Fumana ericoides (Caav.) Gandg.	Cistaceae	NR	C
Fumana laevipes (L.) Spach.	Cistaceae	NR	C
Fumana thymifolia (L.)	Cistaceae	NR	C
Globularia alypum L.	Globulariaceae	R	NP
Helianthemum appeninum (L.) Miller	Cistaceae	NR	C
Helichrysum stoechas (L.) Moench.	Compositae	NR	C
Lavandula latifolia Med.	Labiatae	NR	C
Lonicera implexa Aiton.	Caprifoliaceae	R	PV
Olea europaea L.	Oleaceae	R	MP
Ononis minutissima L.	Leguminosae	NR	C
Phillyrea angustifolia L.	Oleaceae	R	NP
Pistacia lentiscus L.	Anacardiaceae	R	MP
Quercus coccifera L.	Fagaceae	R	NP
Quercus ilex L.	Fagaceae	R	MP
Rhamnus alaternus L.	Rhamnaceae	R	P
Rosmarinus officinalis L.	Labiatae	NR	NP
Smilax aspera L.	Liliaceae	R	PV
Staehelina dubia L.	Compositae	R	C
Teucrium polium L.	Labiatae	R	C
Thymus vulgaris L.	Labiatae	R	C

Sampling and measurements

Since the main objective of this study was to test differences in leaf nutrient concentration among coexisting species belonging to the two post-fire regenerative groups, I estimated the following 7 leaf variables: leaf carbon concentration (hereafter LCC), leaf nitrogen concentration (LNC), leaf phosphorous concentration (LPC), leaf potassium concentration (LKC), leaf calcium concentration (LCaC), leaf magnesium concentration (LMgC) and leaf sodium concentration (LNaC). All of them indicate the proportion of each nutrient relative to the dry weight of the leaf.

For each species, replicate samples were collected from ten different plants, and individuals from the same species were collected on the same site. Samples were collected in February 2006, when the studied species were likely to be in a very similar phenological state, before the spring growth season (Floret *et al.*, 1989; Milla *et al.*, 2006). Leaf samples were collected from well–grown plants and they were harvested from branches with a maximum age of 1 year sited in the canopy and exposed to direct sunlight. They were fully-expanded leaves, free of herbivore or pathogen damage (Garnier *et al.*, 1999). The number of leaves sampled from each individual varied according to the size and weight of the leaves of each species; the dry weight of each sample was approximately 2 g, the minimum necessary for chemical analyses. Finally, the leaves were oven-dried for 48 h at 60ºC and subsequently ground. The LPC, LKC, LCaC, LMgC and LNaC analyses were undertaken using ICP-OES (Optical Emission Spectroscopy with Inductively Coupled Plasma) in a PERKIN ELMER, Optima 4300 (Shelton, Maryland, USA), while LNC and LCC were measured with an elemental analyzer NA 2100 (Thermofisher Scientific, Milan, Italy).

Statistical analysis

The differences in the leaf nutrient concentrations between the species belonging to the two regenerative strategies were tested by using general linear mixed models (GLMM), where the fixed-effect was regenerative strategy (resprouters (R) and non-resprouters (NR)) and the dependent variables for leaf data analyses were LNC, LCC, LPC, LNaC, LKC, LCaC and LMgC. In these analyses, the replicates were the ten sampled individuals of each species, and species was considered a random factor in all the analyses.

First of all, I tested the differences between the two post-fire regenerative strategies for each of the seven variables and considering species as a random factor in a general linear mixed model (GLMM).

One difficulty in population level analyses is the need to deal with the autocorrelation that may exist in parameter measures within the same taxa (Blackburn & Duncan, 2001; Garland *et al.*, 2005; Sol *et al.*, 2007). GLMM was used to test whether there was any autocorrelation on account of the higher taxonomical level "family" for the seven variables by considering a hierarchical nested design of species among families. Since this autocorrelation existed, I created an additional GLMM that considered the post-fire regenerative strategy as the fixed effect, and species as the random factor nested within a family to control the effect of taxonomic affiliations. Order was not considered, as there was nearly the same number of orders as families. This approach ensured that the significance tests for the fixed-effect predictors were not biased by taxonomical affiliations. To better approximate normality, LNC, LCC, LPC, LNaC, LKC, LCaC and LMgC were transformed into their Log_e (i.e. in Log_e (LPC)), and I implemented models with the error structure defined as normal.

I analyzed the differences in LNC with respect to post-fire regenerative strategies, considering LPC as a co-variable, in order to discover the relationship between the two nutrient concentrations in the two different regenerative groups. The effect of taxonomic affiliations was also considered in this analysis. I obtained a linear regression between LNC and LPC for resprouters and another for non-resprouters by considering the mean of each species (mean from the 10 measured individuals of each species). Linear regression was performed with the Log_e of the two variables to better approximate normality.

The overall relationship pattern of the leaf concentration of the seven nutrients, in the 30 species, was analysed through a principal components analysis (PCA), considering the mean of each species for each of the seven leaf nutrient concentrations that were Log_e -transformed before analysis. PCA was carried out by scaling inter-sample distances (i.e. inter-study species), and finally centered and standardized by nutrient concentration variables.

Analyses were performed using Statistica 6.0 (Statsoft) and SPSS 13.0 (SPSS), except for the principal components analysis, which was undertaken with Canoco 4.5 program.

RESULTS

Without considering the possible taxonomical affiliation effects, there was a significant difference between resprouters and non-resprouters in three of the seven leaf nutrient concentrations (Table 3): LPC (Figure 1), LCC (Figure 2) and LCaC (Figure 3). Non-resprouters have higher LPC, and LCaC, while they have lower LCC. As expected, species (random factor) was significant in all statistical tests. *Erica arborea* is the resprouter shrub with the least LPC, while *Helianthemum appeninum* is the species with the highest LPC. Figure 2 shows that the resprouter with the highest LCC is *Erica arborea*, while the three species belonging to the *Fumana* genus (*F. ericoides*, *F. laevipes* and *F. thymifolia*) have the lowest LCCs. Finally, the non-resprouter species with the highest LCaC is *Ononis minutissima*, while the non-resprouters with lower values are *Quercus ilex* and *Erica arborea*.

Table 3. Summary of results of generalized linear mixed model (GLMM) accounting for variation in LNC, LPC, LCC, LKC, LCaC, LMgC and LNaC. Significance of the fixed effect (regenerative strategy) is tested without taxonomical affiliations effects (left columns) and with taxonomical affiliations (right columns). LNC, LPC, LCC, LKC, LCaC, LMgC and LNaC were transformed to its Log$_e$.

	Without taxonomic affiliations			**With taxonomic affiliations**	
Variable	**Effects**	**F**	**p-value**	**F**	**p-value**
LNC	PFRS	0,352	0,558	0,205	0,660
	Family			2,326	0,058
	Species	52.178	< 0,001	33,269	< 0,001
LPC	PFRS	6,740	0,015	4,170	0,070
	Family			2,055	0,089
	Species	35,044	< 0,001	24,129	< 0,001
LCC	PFRS	4,214	0,048	2,665	0,135
	Family			1,970	0,103
	Species	92,725	< 0,001	65,507	< 0,001
LNaC	PFRS	1,777	0,193	1,487	0,257
	Family			1,255	0,330
	Species	20,274	< 0,001	18,275	< 0,001
LKC	PFRS	1,018	0,322	0,509	0,491
	Family			3,388	0,012
	Species	37,679	< 0,001	18,620	< 0,001
LCaC	PFRS	5,748	0,023	6,755	0,039
	Family			0,836	0,617
	Species	49.695	< 0,001	53,440	< 0,001
LMgC	PFRS	1,619	0,214	0,979	0,347
	Family			2,151	0,077
	Species	32,433	< 0,001	21,717	< 0,001

Autocorrelation associated with taxonomical affiliation was observed for each of the seven variables (LNC: p = 0.044, LPC: p = 0.029, LCC: p = 0.043, LKC: p = 0.008; LMgC: p = 0.043), with the exception of LNaC and LCaC, where family did not have any significant effect. The GLMM results, including species nested within family as a random factor, showed that taxonomical affiliation explained the differences between post-fire regenerative groups while it is not as important in LPC (p = 0.07). Due to the lack of taxonomical autocorrelation, LCaC continues being significantly higher in non-resprouters (Table 3). Furthermore, taxonomical affiliation shows a significant effect in LKC, and marginally significant differences in LMgC and LNC (Table 3). LNaC is the nutrient that is least explained by the studied variables, since there are no differences between families or regenerative strategies.

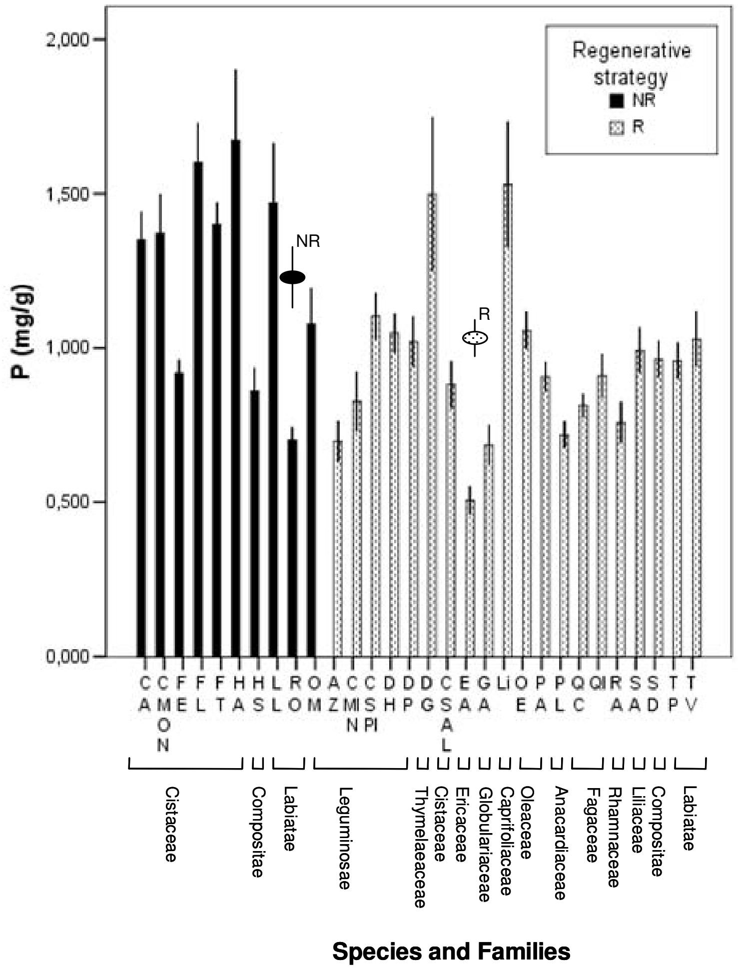

Figure 1. Leaf Phosphorus content: P (mg g^{-1}) means for each of the 30 study species. Values are grouped in resprouters (R) and non-resprouters (NR). Vertical bars denote +/- 2 s.e. Each species is abbreviated with two letters (the first one indicates genus and the second indicates species). *Coronilla minima*, *Cistus monspeliensis* and *Calicotome spinosa* are abbreviated as CMIN, CMON and CSPI, respectively. The ovoid symbol indicates the mean of each of the regenerative strategies.

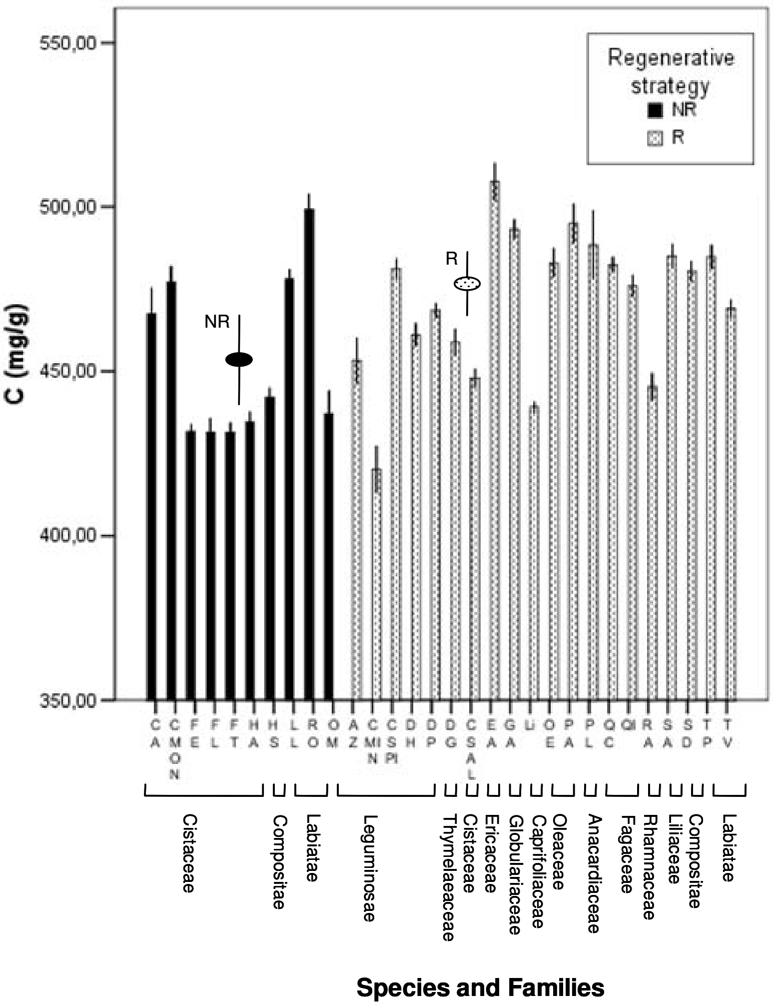

Figure 2. Leaf carbon content: C (mg g^{-1}) means for each of the 30 study species. Values are grouped in resprouters (R) and non-resprouters (NR). Vertical bars denote +/- 2 s.e. Each species is abbreviated with two letters (the first one indicates genus and the second indicates species). *Coronilla minima, Cistus monspeliensis* and *Calicotome spinosa* are abbreviated as CMIN, CMON and CSPI, respectively. The ovoid symbol indicates the mean of each of the regenerative strategies.

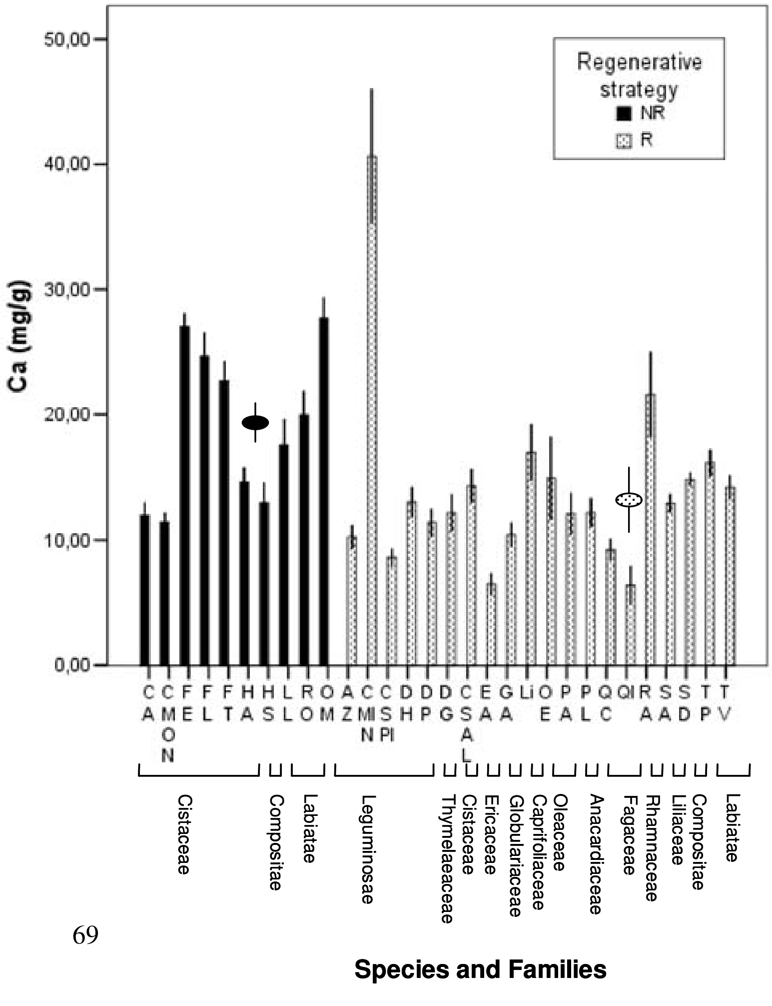

Figure 3. Leaf calcium content: Ca (mg g^{-1}) means for each of the 30 study species. Values are grouped in resprouters (R) and non-resprouters (NR). Vertical bars denote +/- 2 s.e. Each species is abbreviated with two letters (the first one indicates genus and the second indicates species). *Coronilla minima, Cistus monspeliensis* and *Calicotome spinosa* are abbreviated as CMIN, CMON and CSPI, respectively. The ovoid symbol indicates the mean of each of the regenerative strategies.

Although there are no differences between resprouters and non-resprouters with respect to LNC, when LPC was included as a co-variable in the model analysing LNC without taxonomic affiliation, significant differences between post-fire regenerative groups were obtained (Table 4, Figure 4), indicating that the regenerative strategy has an effect on the relationship between LNC and LPC. In non-resprouters, R^2 is higher, indicating a stronger relationship between LNC and LPC than in resprouter species. This effect disappeared when taxonomic affiliation was considered (Table 4).

Table 4. Summary of results of generalized linear mixed model (GLMM) accounting for variation in LNC considering LPC as a co-variable. Significance of the co-variable (LPC) fixed effect (regenerative strategy) is tested without taxonomical affiliations effects and with taxonomical affiliations. LNC and LPC were transformed into their Log_e.

		Without taxonomic affiliations		**With taxonomic affiliations**	
Variable	Effects	F	p-value	F	p-value
LNC	LPC	9,833	0,004	6,128	0,028
	PFRS	4,029	0,054	2,446	0,143
	Species	58,974	< 0,001	25,625	< 0,001
	Family			3,956	0,006

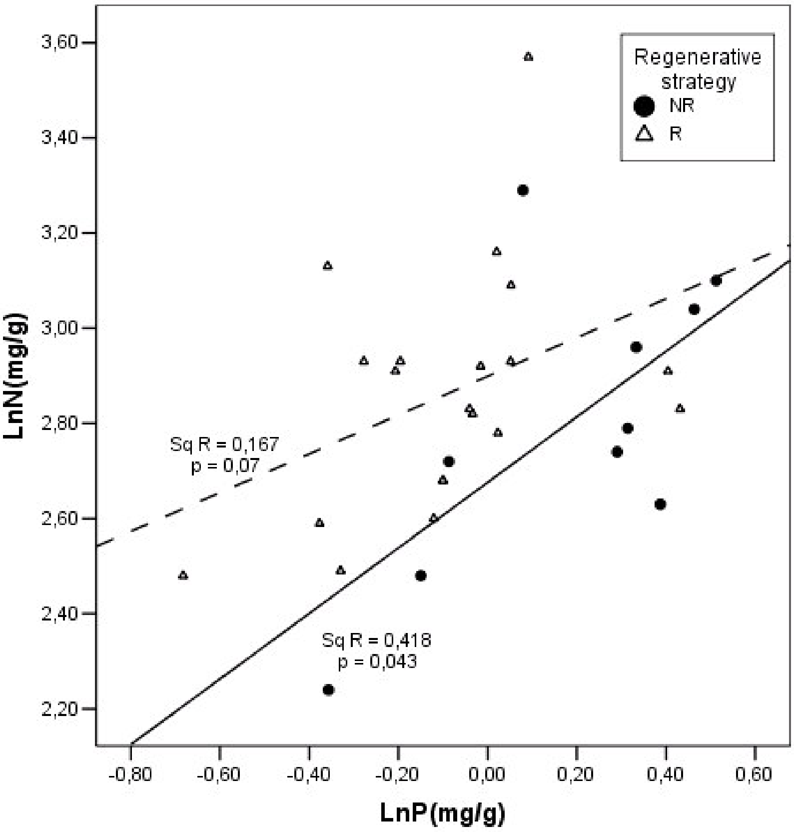

Figure 4. Two simple linear regressions, one for resprouter species and one for non-resprouter species, with LNC (mg g^{-1}) as the dependent variable and LPC (mg g^{-1}) as the independent variable. Sq R = R2. Resprouters: Log_e (LNC) = 2.899 + 0.407 (Log_e (LPC)) . Non-resprouters: Log_e (LNC) = 2.676 + 0.689 (Log_e (LPC)).

Finally, when the overall relationship between the leaf nutrient concentrations was explored, the main axis or component explained 42% of the variation in the total data set (Figure 5). LCC and LNaC are positively correlated with this primary axis of variation, while the other variables are negatively correlated.

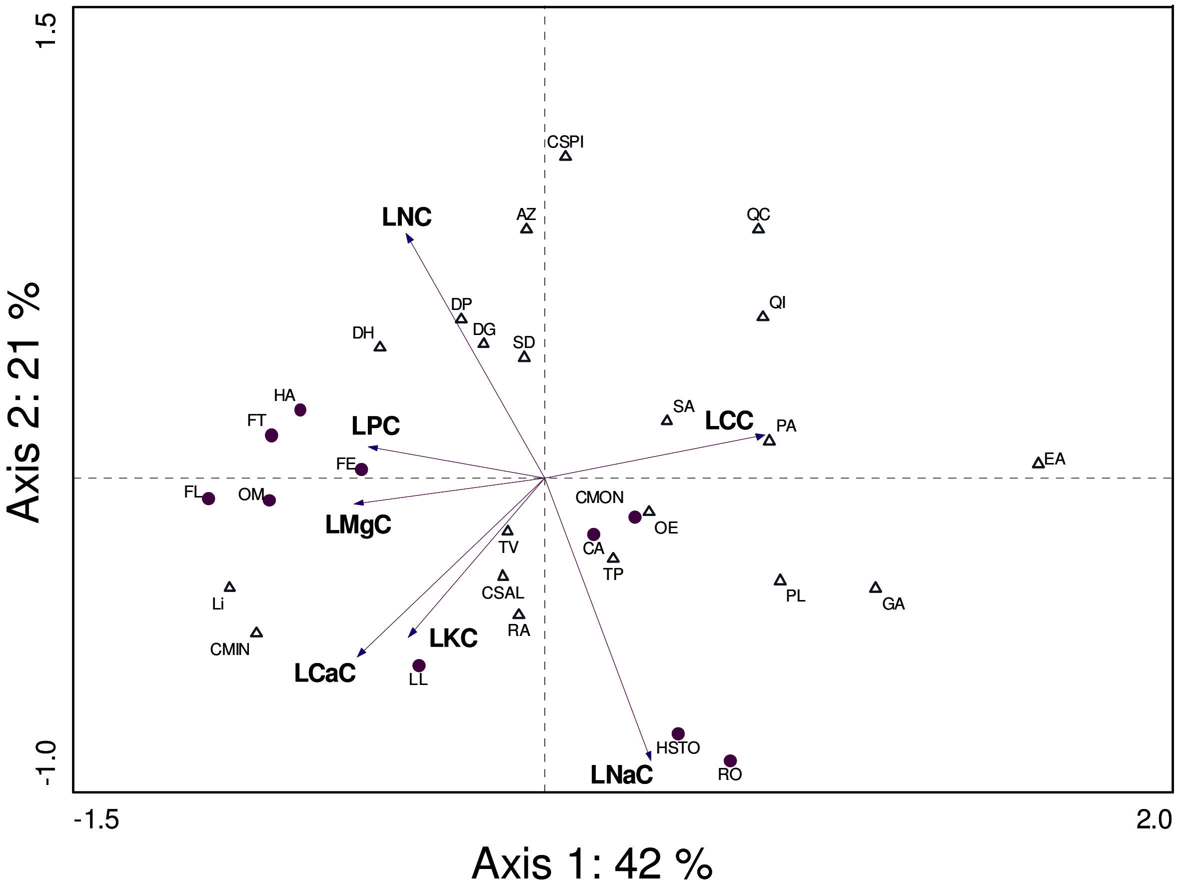

Figure 5. PCA for all the studied variables: LNC, LPC, LCC, LKC, LCaC, LMgC and LNaC. Axis 1 explains the 42% variation in the total data set while axis 2 explains the 21% variation in the ordination. The circle symbols are non-resprouters and the triangles symbolize resprouter species. See figure 1 for abbreviations.

DISCUSSION

This study suggests that resprouters and non-resprouters differ not only in the type of post-fire regeneration but also in some of their leaf nutrient concentrations. This fact supports the hypothesis of a differential role of regenerative types on the functional properties of the ecosystem. Although there were no differences in LNC between resprouters and non-resprouters, resprouters showed higher foliar N:P mass. The lack of differences on LNC is probably due to the low inter-specific variation of LNC previously described in plant Mediterranean ecosystems (Garnier *et al*., 2001). Other authors have found differences between LNC_a (area-based leaf nitrogen concentration) in these two groups from measurements obtained in summer (Paula & Pausas, 2006). It is known that leaf nitrogen concentration may vary from season to season (Garnier *et al*., 2001; Milla *et al*., 2006). The aim was to find differences between resprouters and non-resprouters, based on their intrinsic characteristics rather than on seasonality. Thus, LNC was sampled in February, when the studied species were expected to be in a similar metabolic state, since the growth season had not yet started (Floret *et al*., 1989; Milla, 2005; Milla *et al*., 2006). Moreover, nutrient concentration was measured in mass terms because the co-variation between leaf traits appears to be stronger on this basis than on an area basis (Wright *et al*., 2004). In fact, most studied species showed values of LNC that can be considered adequate for the requirements of plants (Larcher, 1995), although the soil C:N ratio suggests relatively low N availability in the soil (Klute, 1986; Larcher, 1995).

LPC showed a contrasting behaviour in the two regenerative groups: while it is clearly correlated to LNC in non-resprouters, the relationship between LPC and LNC is weaker in resprouters. The LPC of resprouters is clearly under the leaf P level required for a normal functioning (approx. 1.5 mg g^{-1}, according to Larcher 1995), while non-resprouter LPC is almost at the required level. Mediterranean soils have been described as P-limited (Henkin *et al*., 1998; Sardans *et al*., 2004), thus supporting the hypothesis that leaf nitrogen concentration can be determined by leaf phosphorous concentration. Since the foliar N:P mass ratio is a good indicator of the type of nutrient limitation (Koerselman & Meuleman, 1996; Aerts & Chapin, 2000), the value obtained in resprouters (20.0) indicates that plant growth would be limited by P (since this value is higher than 16), while the value observed in non-resprouters (14.4) suggest that growth is limited by both N and P (Aerts & Chapin, 2000). Thus, our results suggest that the main nutrient limitation on plant growth in this Mediterranean ecosystem type is due to P, being especially relevant for the resprouter regenerative group. Furthermore, (Wright *et al.*, 2004) explored the worldwide leaf economics spectrum, finding that species with quick returns on carbon and nutrients investments (and thus high nutrient concentrations, high rates of photosynthesis and respiration, short leaf lifetimes and low dry-mass investment per area) had a lower N:P ratio compared to species with slow returns on investments. The results of the present study situate non-resprouters as species with quick returns on investments of carbon and nutrients, while the opposite would apply to resprouters. This concurs with the descriptions of the life strategies of the two regenerative groups, and it may cause a less efficient use of some nutrients, resulting in a higher accumulation in the leaves.

Soils at the study site are characterized by relatively high quantities of P in the first 0-5 cm, and by low values at a depth of 5-20 cm deep. Dawson and Pate (1996) described different root morphologies for Australian woody species with different resistance to fire: the most sensitive species had a single main root and a number of shallow lateral roots, while fire-resistant species had multiple lateral and main roots arising from a lignotuber. Similar descriptions have been recorded for woody species from the Mediterranean basin: *Pistacea lentiscus* has deep-rooted seedlings, while *Cistus* seedlings has shallower root systems (Kummerow, 1981; Clemente *et al.*, 2005). Thus, it is feasible that resprouter and non-resprouter species also differ with respect to the depth and extension of their root systems. This factor could play a part in the ability to uptake nutrients such as P, which is normally more abundant on the surface of these soils (Porta *et al.*, 1999). Since non-reprouters evolved under Mediterranean soil conditions that are characterized by their paucity of P (Henkin *et al.*, 1998; Sardans *et al.*, 2004), it could also be possible that these group of short-lived species have achieved physiological adaptation endowing them with a higher P uptake from the first centimeters of soil, and ultimately higher P leaf accumulation. More physiological and biochemical studies need to be undertaken to confirm this hypothesis explaining lower limitation by P in non-seeder species.

As expected, resprouters have higher LCC than non-resprouters, probably because resprouters are species with longer life cycles, longer leaf life-span (Villar & Merino, 2001; Navas *et al.*, 2003) and higher leaf dry mass (Pausas *et al.*, 2004; Saura-Mas & Lloret, 2007). Most of the leaf dry mass, basically due to cell walls, is constituted by carbon. Shipley *et al.* (2006) studied the multivariate patterns of co-variation between four key variables in the leaf spectrum (leaf mass per area, nitrogen concentration per mass, leaf longevity and maximum photosynthetic rate) and proposed a causal explanation for the observed patterns based on a latent variable corresponding to the ratio of cytoplasmic to cell-wall volume. Since these models describe a positive relationship between cell wall volume and LCC, non-resprouters should have cells with thinner walls than resprouters. In addition, results support the model of Shipley *et al.* (2006) since LCC is negatively related with most of the other nutrient leaf concentrations which are expected to be more abundant in the cell cytoplasm fraction.

LKC may not reflect the high levels of K found in the soil because the uptake of this nutrient by plants may be diminished by the abundance of Ca in the soil (Klute, 1986). Both resprouters and non-resprouters show average values of LCaC, LKC, LMgC and LNaC, following the Ca > K > Mg > Na relationship that is characteristic of plants growing in dry, Ca-enriched soils; these values are all within the plant requirement ranges (Larcher, 1995). However, when comparing the two post-fire regenerative strategies, non-resprouters show higher values for most of the mineral nutrients in leaves except for N (Table 5) (P, Ca, K, Mg, Na, although only P and Ca have significant differences).

Table 5. Means for each one of the seven leaf nutrients contents for the two regenerative strategies. Standard error is indicated in brackets.

	Resprouters	**Non-resprouters**
LNC (mg g^{-1})	18,123 (0,388)	17,141 (0,524)
LPC (mg g^{-1})	0,945 (0,020)	1,242 (0,037)
LCC (mg g^{-1})	471,027 (1,582)	453,049 (2,487)
LNaC (mg g^{-1})	0,625 (0,042)	0,841 (0,070)
LKC (mg g^{-1})	7,599 (0,230)	8,435 (0,283)
LCaC (mg g^{-1})	13,937 (0,542)	19,071 (0,639)
LMgC (mg g^{-1})	1,518 (0,042)	1,802 (0,061)

Taxonomic affiliation had a relevant role to explain the differences between regenerative strategies in leaf nutrient concentrations, especially in LPC and LCC. These differences are rooted in family-level properties, especially for LCC. Resprouters and non-resprouters are not equally distributed among families (only the four families

Cistaceae, Compositae, Labiatae and Leguminosae are present in the non-resprouters group, while up to families with a single member are found among resprouters), which in turn have experienced different evolutionary histories: non-resprouters taxa evolving in the Mediterranean conditions emerging during the Quaternary, and respouters taxa surviving from the pre-Pleistocene non-Mediterranean conditions (Verdú, 2000; Verdú *et al.*, 2003; Pausas & Verdú, 2005).

This study suggests that ecosystems dominated by non-resprouter species may present different nutrient dynamics, with more P in the leaf portion and lower growth limitation by P than ecosystems dominated by resprouters. Therefore, changes in the proportion of these species resulting from shifts in fire regime (Pausas, 2001; Lloret *et al.*, 2003; Eugenio & Lloret, 2004) may cause important modifications in the P cycle as well as in the Ca and C fluxes. The study also supports the usefulness to investigate the covariation of functional groups defined by different criteria (role on resource fluxes, disturbance response) in order to model the dynamics of ecosystem functioning under scenarios of changing environmental conditions.

ACKNOWLEDGEMENTS

I would like to thank L. Galiano, Ll. Benejam and M. Mas for helping in the field and in the lab. Especial thanks go to J. Font for his knowledge of the Montgrí and its flora, and S. Palacio, G. Montserrat-Martí, J. Sardans, J. M. Alcañiz and D. Sol for their advice and suggestions. This study was funded by the Department of Universities, Research and Information Society of the Generalitat de Catalunya, the European social funds, and the Spanish MCYT projects REN 2003-07198 and CGL2006-01293/BOS. It also contributes to the European research group (GDRE) “Mediterranean and mountain ecosystems in a changing world” funded by the Generalitat de Catalunya and CNRS.

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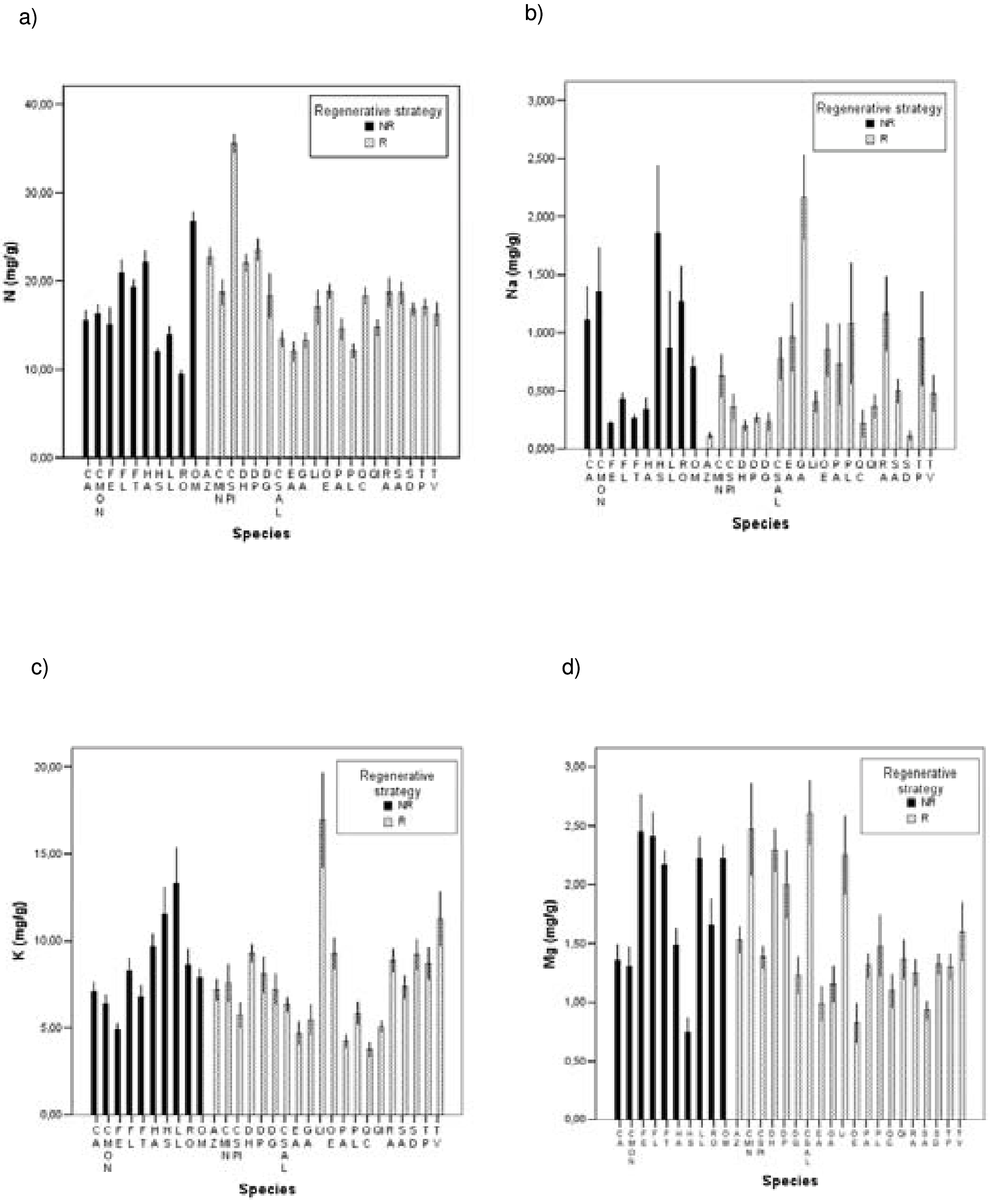
APPENDIX 1. LEAF NUTRIENT CONCENTRATIONS. Summary table with mean values for LNC, LCC, LPC, LKC, LMgC, LNaC, LCaC, C : N, C :P and C : N for all study species. For abreviations see Figure 1.

	Post-fire regenerative strategy												
Species	**Seeding**	**Resprouting**	**Life-form**	**LNC(mgg-1)**	**LCC(mgg-1)**	**LCaC(mgg-1)**	**LKC(mgg-1)**	**LMgC(mgg-1)**	**LNaC(mgg-1)**	**LPC(mgg-1)**	**C : N**	**C : P**	**N : P**
AZ	+	+	C	22,77	453,25	10,26	7,18	1,54	0,112	0,698	19,91	649,05	32,61
CA	+	-	NP	15,55	467,37	11,97	7,07	1,37	1,107	1,337	30,06	349,68	11,63
CMIN	-	+	C	18,70	420,16	40,61	7,55	2,49	0,633	0,822	22,47	511,20	22,75
CMON	+	-	NP	16,26	477,14	11,42	6,37	1,32	1,348	1,369	29,34	348,57	11,88
CSAL	+	+	NP	13,44	447,93	14,32	6,33	2,61	0,780	0,886	33,33	505,60	15,17
CSPI	+	+	NP	35,55	481,20	8,59	5,73	1,38	0,353	1,096	13,54	439,15	32,44
DG	-	+	NP	18,36	458,84	12,16	7,20	1,23	0,230	1,498	24,99	306,22	12,25
DH	+	+	C	22,06	461,07	13,03	9,28	2,28	0,194	1,054	20,90	437,62	20,94
DP	+	+	C	23,54	468,49	11,38	8,07	2,01	0,263	1,020	19,90	459,35	23,08
EA	-	+	MP	12,00	507,69	6,48	4,71	1,00	0,958	0,505	42,31	1005,34	23,76
FE	+	-	C	15,12	431,72	27,07	4,87	2,45	0,219	0,917	28,55	470,77	16,49
FL	+	-	C	20,98	431,49	24,69	8,29	2,40	0,429	1,589	20,57	271,47	13,20
FT	+	-	C	19,35	431,44	22,71	6,78	2,16	0,261	1,396	22,30	309,14	13,86
GA	+	+	NP	13,27	493,17	10,40	5,45	1,15	2,158	0,686	37,16	719,33	19,36
HA	+	-	C	22,11	434,70	14,63	9,64	1,50	0,341	1,669	19,66	260,46	13,25
HSTO	+	-	C	11,97	442,20	12,98	11,54	0,74	1,883	0,861	36,94	513,59	13,90
Li	-	+	PV	17,01	439,23	17,01	16,95	2,25	0,405	1,539	25,82	285,37	11,05
LL	+	-	C	13,88	477,97	17,60	13,29	2,23	0,863	1,473	34,44	324,60	9,43
OE	-	+	MP	18,80	483,01	14,91	9,28	0,82	0,848	1,052	25,69	459,17	17,87
OM	+	-	C	26,76	437,27	27,71	7,89	2,23	0,706	1,083	16,34	403,93	24,72
PA	-	+	NP	14,55	494,98	12,07	4,24	1,30	0,724	0,905	34,02	546,77	16,07
PL	-	+	MP	12,07	488,46	12,17	5,84	1,47	1,079	0,719	40,47	679,50	16,79
QC	-	+	NP	18,33	482,44	9,26	3,77	1,09	0,218	0,813	26,32	593,23	22,54
QI	-	+	MP	14,67	475,90	6,40	5,06	1,38	0,360	0,910	32,44	522,87	16,12
RA	-	+	P	18,69	445,36	21,60	8,83	1,27	1,162	0,758	23,83	587,85	24,67
RO	+	-	NP	9,43	499,19	19,96	8,59	1,66	1,268	0,700	52,94	713,05	13,47
SA	-	+	PV	18,62	485,09	12,93	7,34	0,93	0,499	0,984	26,05	493,10	18,93
SD	+	+	C	16,83	480,42	14,86	9,21	1,33	0,114	0,966	28,55	497,13	17,42
TP	+	+	C	17,01	484,80	16,14	8,67	1,30	0,949	0,960	28,50	504,85	17,71
TV	+	+	C	16,19	469,04	14,18	11,24	1,59	0,474	1,023	28,97	458,35	15,82

APPENDIX 2. LEAF NUTRIENT CONCENTRATIONS. N (mg/g), Na (mg/g), K (mg/g), Mg (mg/g) means for each of the 30 study species. Values are grouped in resprouters (R) and non-resprouters (NR). Vertical bars denote +/- 2 standard error. Each species is abbreviated with two letters (the first one indicates de genus and the second one indicates species). *Coronilla minima*, *Cistus monspeliensis* and *Calicotome spinosa* are abbreviated in a different way, CMIN, CMON and CSPI, respectively. Species are ordenated by family and alphabetically in each one of the two groups (resprouters and non-resprouters). For family of each species see Table 2.



IV. TESTING CAUSALITY ON LEAF TRADE-OFFS IN MEDITERRANEAN WOODY SPECIES: POST-FIRE REGENERATIVE STRATEGY LINKS WATER REGULATION AND LEAF DRY MATTER CONTENT

The main contents of this chapter have been submitted to Functional Ecology as:
Saura-Mas, S., Shipley, B., Lloret, F. Testing leaf trade-offs in Mediterranean woody species: Post-fire regenerative strategy links water regulation and leaf dry matter content.

ABSTRACT

- Recent work has identified global scale relationships between key leaf traits and it has been hypothesized that these are linked via an unmeasured attribute of leaves: the volume occupied by cytoplasm relative to the volume occupied by cell walls. Based on this and using structural equation modeling and exploratory path analysis, alternative models were developed to test how interspecific leaf traits are related to the seasonal variation of water content and to the type of post-fire regenerative strategy (PFRS) of the species.

- Analises start with two constant submodels that consider traits of species coexisting in a shrubland of the western Mediterranean Basin. First, I used a model where correlations between specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen (LNC), phosphorus (LPC) and carbon (LCC) concentrations are due solely to a common latent cause. Second, I allow relative seasonal variation of Relative Water Content (RWC_{rsv}) and Life Fine Fuel Moisture ($LFFM_{rsv}$) to freely covary.

- The best-fitting model shows that RWC and LFFM are not common effects of the latent variable. Rather, the correlation between LDMC and RWC_{rsv} is generated by a phylogenetic effect (PFRS): seeder species (those that recruit via seeds immediately after fire) have lower LDMC and higher RWC_{rsv} than non-seeders.

- I hypothesize that since seeder species evolved under the Mediterranean climate, they developed a particular strategy of drought tolerance (without causing an effect to the relation between the volume occupied by cytoplasm relative to the volume occupied by cell walls), which is the cause of the observed relation between LDMC and RWC_{rsv}.

Key words: Carbon, causal, LDMC, leaf trait, nitrogen, phosphorous, post-fire, regenerative, SLA, water content, woody species.

INTRODUCTION

The relationship among leaf traits has been intensely studied because of their ecological significance. Besides affecting species' performance, some leaf traits such as most of those studied in this paper (for example, leaf dry matter content, specific leaf area, leaf nitrogen concentration) are also indicators of ecosystem functioning (Lavorel *et al.*, 1999; Garnier *et al.*, 2001a). Thus, understanding how these traits are interrelated and how they vary is a major goal for plant ecology since this information allows us to understand plant functioning in a more integrative way than studying these traits separately (Wright *et al.*, 2004; Shipley *et al.*, 2006; Whitfield, 2006).

Reich *et al.* (1997) demonstrated globally valid relationships between such functional leaf traits that allow for the development of more quantitative and predictive models of vegetation productivity, distribution and dynamics. Wright *et al*. (2004) described similar relationships using a global plant trait network (Glopnet) including a larger number of species and describing a global spectrum of leaf economics according to chemical, structural and physiological properties. They concluded that this spectrum operated largely independently of growth form, plant functional type or biome.

Despite such large-scale results, it is important to determine to what extent this approach can be applied to smaller subsets of species facing similar environmental constraints. If the large-scale patterns reflect unavoidable morphological and physiological constraints in leaf construction then one would expect the same patterns to be found in more restricted environments. If the large-scale patterns reflect the response of natural selection to major large-scale environmental gradients of inherently plastic traits, then one might expect different patterns in more restricted environments that differ from the general selection pressures. In the present study several variables (specific leaf area, leaf dry matter content, leaf nitrogen, phosphorus and carbon concentration) are considered, but I concentrate on a group of 28 Mediterranean woody species that coexist in a community that is periodically affected by fire. Moreover, Mediterranean-type ecosystems are subjected to a strong seasonal climatic regime with hot summers, mild winters, and rain concentrated in the fall and springm, that also determines a seasonal fire regime. For this reason, the relative seasonal variation of relative water content and of live fine fuel moisture were also considered in the analyses.

Shipley *et al.* (2006), using structural equation modeling and exploratory path analysis, studied the multivariate patterns of covariation between four key variables in the leaf spectrum (leaf mass per area, nitrogen content per mass, leaf longevity and maximum photosynthetic rate) and proposed a causal explanation for these patterns based on two general causes. The first cause reflected Kikuzawa's (1995) hypothesis that links maximum net photosynthetic rate, leaf lifespan and leaf construction costs. Since there was strong statistical evidence that interspecific patterns of correlation among these four leaf traits were generated by one or more variables not considered in the model (i. e. latent variables), the second causal variable was a latent variable representing the ratio of cytoplasmic to cell wall volume. This ratio describes a necessary tradeoff between processes occurring in the cytoplasm, thus scaling with the volume occupied by cytoplasm, and leaf dry mass, thus scaling with the volume occupied by cell walls. I hypothesize that this ratio should explain the relationship between leaf water relative seasonal variation and leaf dry matter content, extending the original model.

In this paper the model of Shipley *et al.* (2006) is tested, involving specific leaf area, leaf dry matter content, leaf nitrogen, phosphorous and carbon concentrations, and then extend it to include relative seasonal variations of relative water content and of live fine fuel moisture, in the group of Mediterranean woody species. Since fire plays an important ecological role in Mediterranean ecosystems, the post-fire regenerative strategy was also considered as another variable since most Mediterranean woody species display post-fire regenerative mechanisms. Populations of some species (hereafter, seeders) are propagule-persisters species in which the population locally persists in propagule form (seed, fruit) after a fire. These are species that their populations regenerate by establishing seedlings just after fire since they have a persistent seed bank (seeds resist or are protected from fire), and the recruitment of new individuals is often enhanced by fire (Pausas *et al.*, 2004). Also, seedlings established shortly after fire usually present higher survival and growth rates than those establishing in periods between fires (Lloret, 1998). This category includes species that only regenerate after fire from seeds (obligate seeders) and species that both resprout and establish seedlings after fire (facultative seeders). Non-seeders (hereafter) are species in which the propagule (seed, fruit) does not persist after fire. Consequently, propagules may only occur by dispersal from outside the fire affected area. Often, in the Mediterranean basin, non-seeders are species that can regenerate after fire, by resprouting (Trabaud, 1987; Trabaud, 1991; Keeley, 1995) from underground or aerial parts of the plant. Of course, a significant variability can be found within these groups, according to the degree of vulnerability to fire intensity, and the type of structures promoting regrowth (such as lignotubers, crown roots, rhizomes or bulbs) (Lloret, 2004). Here, I hypothesize that differences of species in post-fire regenerative strategy will be related to leaf trade-offs and eventually may influence the functional properties of ecosystems subjected to fire regimes.

MATERIALS AND METHODS

Study species and study area

The study was carried out on a subset of 28 woody plant species (Table 1) growing in the study region and belonging to as many different families and regenerative strategies as possible in this type of community (16 seeders and 12 non-seeders) (Cucó, 1987; Papió, 1988; Lloret & Vilà, 1997; Verdú, 2000; Alberdi & Cavero, 2003; Lloret & Vilà, 2003; Paula & Pausas, 2006). In this study, two types of post-fire regenerative strategies (PFRS) were considered: seeders are species that germinate after fire (S+ R-, S+ R+, *sensu* Pausas & Verdú, 2005), and non-seeders do not germinate, but they resprout (S- R+). Species that neither germinate nor resprout were not considered since they were not present in the studied community.

Table 1. List of the study species including their Post-fire Regenerative Strategies (PFRS).

Study Species	**PFRS**
Argyrolobium zanonii (Turra) P. W. Ball	Seeder
Cistus albidus L.	Seeder
Cistus monspeliensis L.	Seeder
Cistus salviifolius L.	Seeder
Coronilla minima (L.)	Non-seeder
Daphne gnidium L.	Non-seeder
Dorycnium hirsutum (L.) ser. In DC.	Seeder
Dorycnium pentaphyllum Scop.	Seeder
Erica arborea L.	Non-seeder
Fumana ericoides (Caav.) Gandg.	Seeder
Fumana thymifolia (L.)	Seeder
Globularia alypum L.	Seeder
Helianthemum apenninum (L.)	Seeder
Lavandula latifolia Med.	Seeder
Lonicera implexa Aiton	Non-seeder
Olea europaea L.	Non-seeder
Osyris alba L.	Non-seeder
Phillyrea angustifolia L.	Non-seeder
Pinus halepensis Mill.	Seeder
Pistacia lentiscus L.	Non-seeder
Quercus coccifera L.	Non-seeder
Quercus ilex L.	Non-seeder
Rhamnus alaternus L.	Non-seeder
Rosmarinus officinalis L.	Seeder
Smilax aspera L.	Non-seeder
Staehelina dubia L.	Seeder
Teucrium polium L.	Seeder
Thymus vulgaris L.	Seeder

All individuals were sampled in the same study area, sited on the Massís del Montgrí, a Mediterranean protected coastal area located in the NE of Catalonia, (north-east Iberian Peninsula, 42.16ºN, 3.24ºW). Vegetation grows on limestone and is mainly dominated by open pine forests and by Mediterranean shrublands with a prevalence of *Quercus coccifera, Cistus albidus, Cistus monspeliensis*, and *Rosmarinus officinalis* (Polo & Masip, 1987). Sampling was conducted in mature shrubland vegetation (1-2 m high shrubs) that had been untouched by wildfire for over 10 years. The mean annual precipitation is 654.6 mm, with cool winters (mean minimum annual temperature: 4.1ºC) and warm summers (mean maximum annual temperature: 26.8ºC) (Ninyerola *et al.*, 2000; Ninyerola *et al.*, 2003).

Leaf traits measurements

Specific leaf area (SLA, m^2 kg^{-1}), leaf dry matter content (LDMC, mg g^{-1}), leaf nitrogen (LNC, mg g^{-1}), phosphorus (LPC, mg g^{-1}) and carbon (LCC, mg g^{-1}) concentrations were studied, as well as relative seasonal variations of relative leaf water content (RWC_{rsv}), and of live fine fuel moisture ($LFFM_{rsv}$), i.e. of branches less than 0.6 cm diameter. Measures of each variable were obtained from ten individuals of each species coexisting in the same area. However, measures of all variables could not be obtained from the same individuals because of the removal of leaves and shoots which could influence the estimations of other variables such as leaf nutrient concentrations. For this reason, I worked with means of the 10 individuals for each species and each variable.

SLA was obtained from projected leaf area of fully developed and water saturated leaves (to achieve water saturation they were stored 8h at 4ºC in dark conditions (Garnier *et al.*, 2001b). They were digitalized with a flatbed scanner and SLA was measured with image processing methods. After that, samples were oven-dried at 60ºC for at least 48h, and weighed to obtain the dry weight of the leaf.

LDMC is the proportion of the leaf matter, related to the mass of the leaf with the maximum water content (Garnier *et al.,* 2001b). LDMC was measured along the four seasons, and a mean of the four seasons was obtained for each species.

LNC, LPC and LCC are the proportions of nitrogen, phosphorus and carbon mass relative to the dry weight of the leaf. Measures were obtained from fully developed leaves of each species that were sampled during February, when the studied species are likely to remain at a very similar phenological state (Floret *et al.*, 1989; Milla *et al.*, 2006) LPC analyses were measured using ICP-OES (Optical Emission Spectroscopy with Inductively Coupled Plasma) in a PERKIN ELMER, Optima 4300 (Shelton, Maryland, USA) while LNC and LCC were measured with an elemental analyzer NA 2100 (Thermofisher Sicentific, Milano, Italia).

Relative Seasonal Variation of Relative Leaf Water Content (RWC_{rsv}) is defined as the proportional change in the relative water content (RWC) of leaves between the winter and summer: $RWC_{rsv} = ((RWC_{winter} - RWC_{summer}) / (RWC_{winter}))$, where RWC is the proportion of the leaf water content related to the maximum water content that can potentially be achieved by the leaf ($RWC = 100 \times ((Mf - Md) / (Mt - Md))$, where Mf is the fresh mass, Mt is the turgid mass after re-hydrating the leaves, and Md is the dry mass after drying the leaves in an oven, 70ºC at least 48h).

Relative Seasonal Variation of Life Fine Fuel Moisture ($LFFM_{rsv}$) is defined as: $LFFM_{rsv} = ((LFFM_{winter} - LFFM_{summer}) / (LFFM_{winter}))$, where LFFM is the water content of shoots (< 6 mm of diameter) under field conditions in relation to its dry mass ($LFFM = 100 \times ((Mf - Md) / Md))$.

Some data of relative seasonal variations of Relative Water Content (RWC_{rsv}), Live Fine Fuel Moisture ($LFFM_{rsv}$) and Leaf Dry Matter Content (LDMC) have been previously published in Saura-Mas and Lloret (2007).

Statistical analyses

To assure homogeneity of variance and linearity, LDMC was transformed to its log-odds ratio (log (LDMC - (1 / LDMC)), and LCC, LNC and LPC were transformed to their natural logarithms. The hypothesized causal relationships were tested using structural equations modeling (Shipley, 2000) using the EQS 6.1 statistics program (Multivariate Software Inc., www.mvsoft.com). Fit of the data to the models was judged by the overall null probability of the model, by the probabilities of each path coefficient being zero, and by the likelihood ratios of each model relative to be best-fitting one (Royall, 1997). All probability values of the obtained structural equations were obtained with MCX2, a program to obtain probability estimates for the Maximum Likelihood Chi-squared statistic based on small sample sizes (Shipley, 2000).

The first model involves only the five variables directly related to the leaf economics spectrum (SLA, LPC, LNC, LCC and LDMC) and it is tested simply to determine if the data agree with the previously proposed model of Shipley *et al*. (2006) (Figure 1). The second model assumes that the two measured variables related to seasonal variation in water content are simply additional manifestations of the same basic model (Figure 2). To develop the alternative models (models 3 to 8) I started with two constant submodels. First, I specified that the correlations between LCC, LNC, LPC, SLA and LDMC are due solely to a common latent cause, following Shipley *et al* (2006); I call this the "leaf economics" submodel. Second, we allow RWC_{rsv} and $LFFM_{rsv}$ to freely covary since there is no obvious reason to hypothesize that either seasonal changes in the water content of leaves or in fine woody tissues would cause each other; I call this the "seasonal water variation" submodel. Based on these two submodels, a series of alternate hypotheses concerning how the two submodels are linked with respect to the post-fire regenerative strategies (PFRS) were proposed (Figures 3-9).

Model 3 hypothesizes that the leaf economics and seasonal water variation submodels are independent of each other and unrelated to the post-fire regenerative strategy. Model 4 hypothesizes that species having a large potential proportion of their leaf fresh mass being water (i.e. a low LDMC) causes them to express a larger variation in seasonal water content, again with the post-fire regenerative strategy being independent of both submodels. Model 5 hypothesizes that LDMC and RWC are correlated due to a common selection with respect to post-fire regenerative strategies but that this common selection is not directed to the underlying morphological driver of the leaf economics spectrum itself. Model 6 is similar to model 5 except that, in addition to the common selection due to the post-fire regenerative strategies, I allow a second causal path linking the variation in water content directly to the potential for high leaf water content. Model 7, in contrast to model 5, assumes that the common selection due to the post-fire regenerative strategies acts directly on the underlying morphological driver of the leaf economics spectrum, thus implying only a spurious correlation between LDMC and RWC. Model 8 is similar to model 7 except that selection for the post-fire regenerative strategies acts both on the underlying morphological driver and on LDMC. Finally, model 9 posits that each of LDMC, RWC and the post-fire regenerative strategy are common causes of some unmeasured cause (L_2).

RESULTS

Model 1 was not rejected (Table 2), meaning that it is consistent with the original model of Shipley *et al.* (2006); the overall fit was good and each path coefficient was significantly different from zero. When RWC and LFFM were added as additional indicators of the same underlying latent variable (model 2), the path coefficients linking the latent variable to each of these two variables were weak and clearly non-significant, meaning that RWC and LFFM are not simply additional variables responding to the same underlying structure. Therefore, model 2 was rejected. Models 3, 4 and 7 were unambiguously rejected at the 5% significance level (Table 2). Thus, the two submodels are not independent (model 3), any dependence between the two submodels must involve the post-fire regenerative strategy (model 4) and the effect of the post-fire regenerative strategy does not act directly on the underlying driver of the leaf economics spectrum (model 7).

Table 2. Summary of the fit statistics of the nine models (see Figures 1 to 9). Likelihood ratio was calculated as the p-value of each model divided by the p-value of the best fitting model (model 5).

Model	X^2	df	p	Likelihood ratio relative to **model 5**
1	2.902	5	0.742 +/- 0.019	2.040
2	20.807	14	0.147 +/- 0.016	0.403
3	46.332	22	0.007 +/- 0.004	0.018
4	40.889	21	0.017 +/- 0.006	0.047
5	23.647	20	0.364 +/- 0.021	1
6	21.816	19	0.407 +/- 0.021	1.120
7	35.585	20	0.045 +/- 0.009	0.124
8	23.645	19	0.322 +/- 0.020	0.884
9	23.512	19	0.322 +/- 0.020	0.884

Models 5, 6, 8 and 9 were not rejected based on the overall model fit (Table 2). However, the LDMC→RWC path in model 6 that differentiates it from model 5 is not significantly different from zero. Similarly, the PFRS→L path in model 8 that differentiates it from model 5 is not significantly different from zero. Thus, model 5 is the most parsimonious model relative to 6 and 8. Finally, model 9, while providing an almost equivalent level of fit relative to model 5 and with all path coefficients being significantly different from zero, has no significant residual variance associated with PFRS (residual variance = 0.033, s. e. = 0.071, z - value = 0.468, p = 0.6736), implying that the second latent variable (L_2) is essentially the same as PFRS, thus leading again back to model 5.

Figures 1 to 9 present the models along with their path coefficients. Standard errors are in parenthesis; * indicates that it is a signifcant path coefficient. Values of r^2 are also in the model. L_1 and L_2 are the latent variables. L_1 is an unmeasured variable representing the ratio of cytoplasmatic to cell wall volume. L_2 is the PFRS (post-fire regenerative strategy).

Figure 1.

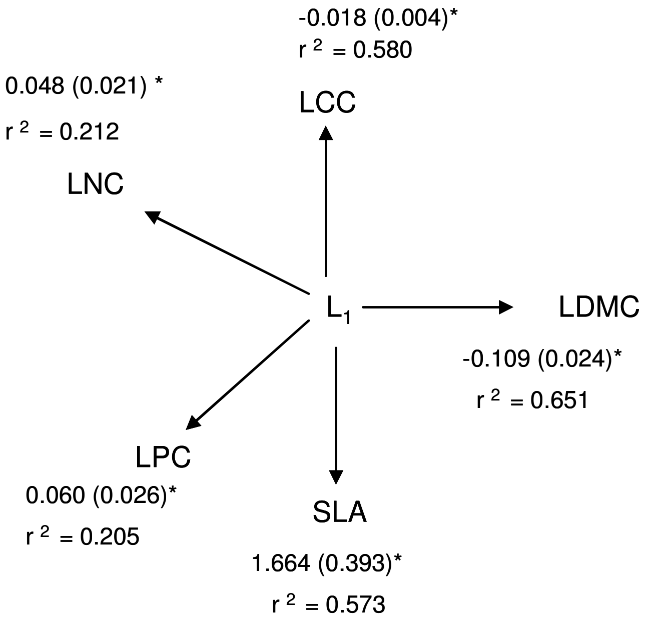


Figure 2.

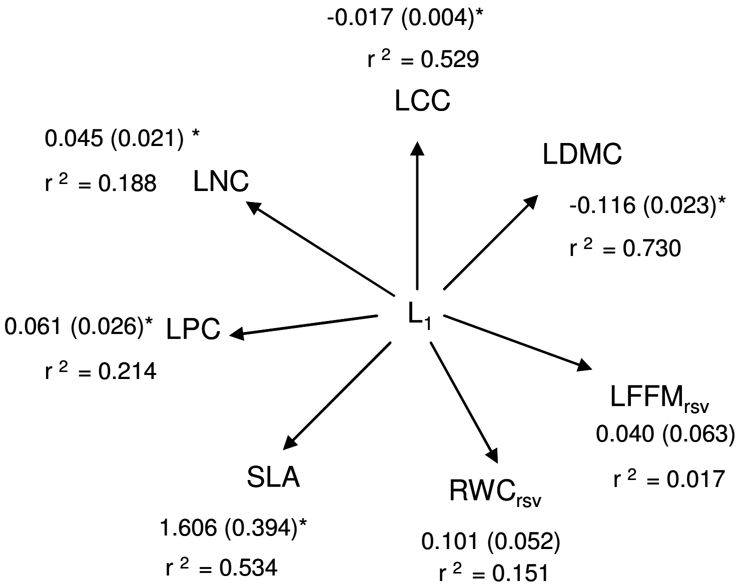


Figure 3.

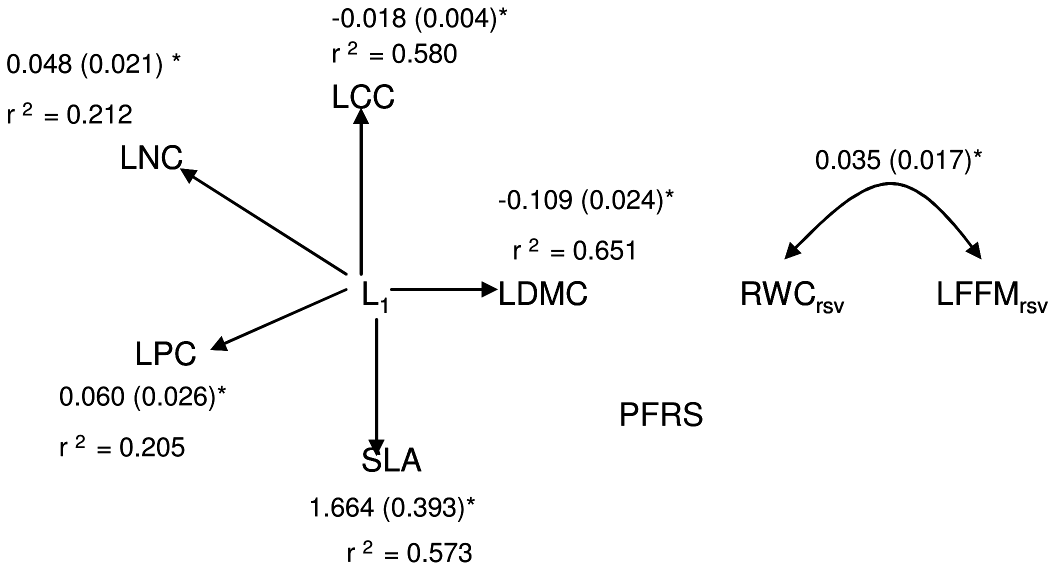


Figure 4.

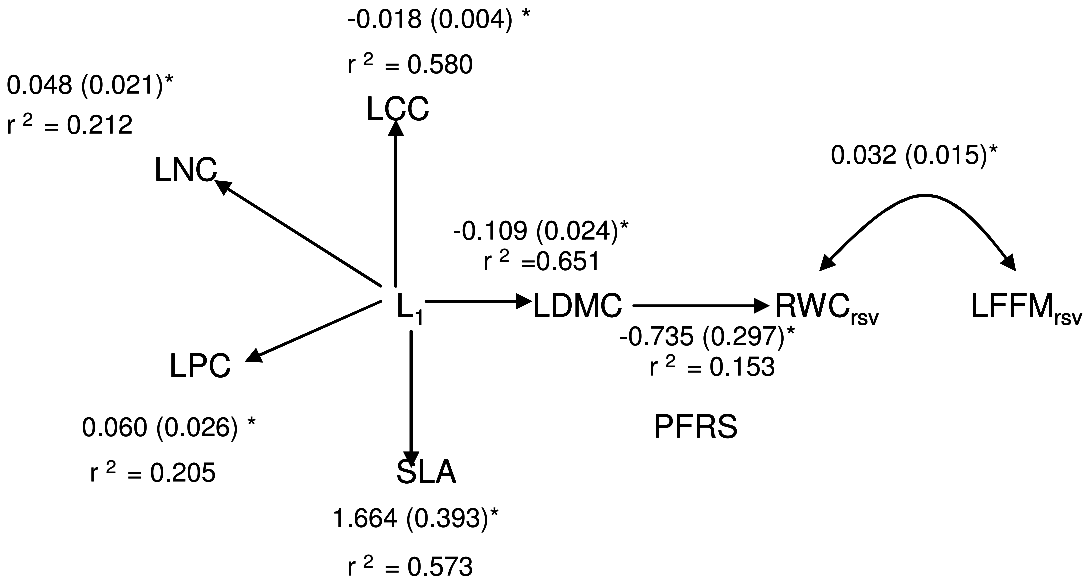


Figure 5.

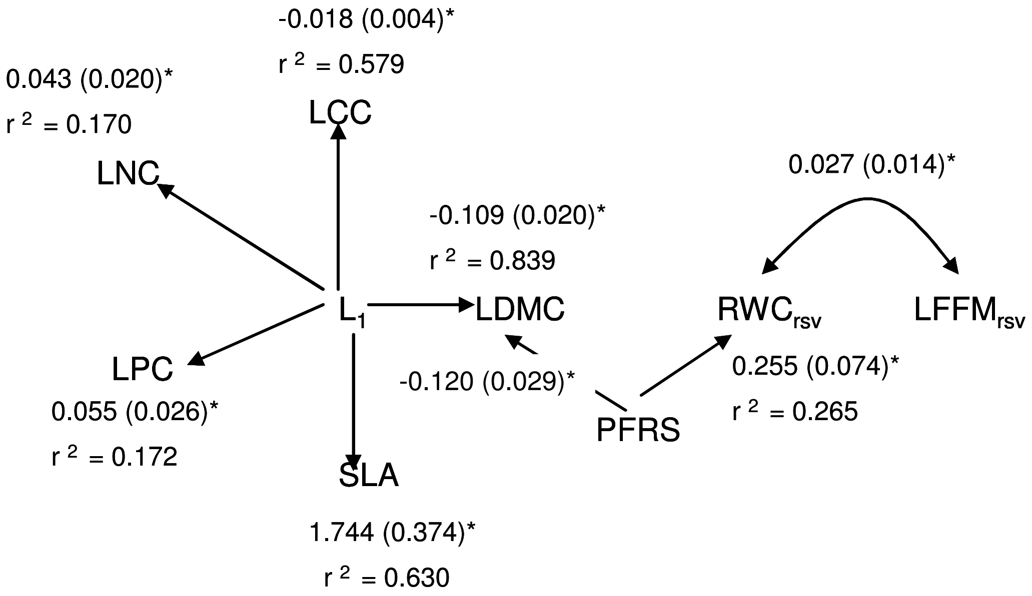


Figure 6.

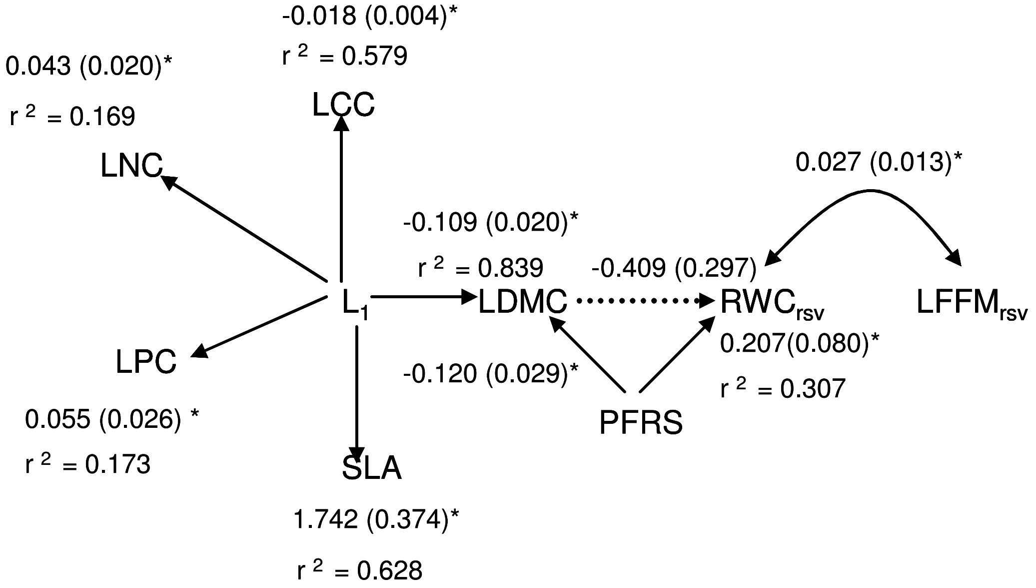


Figure 7.

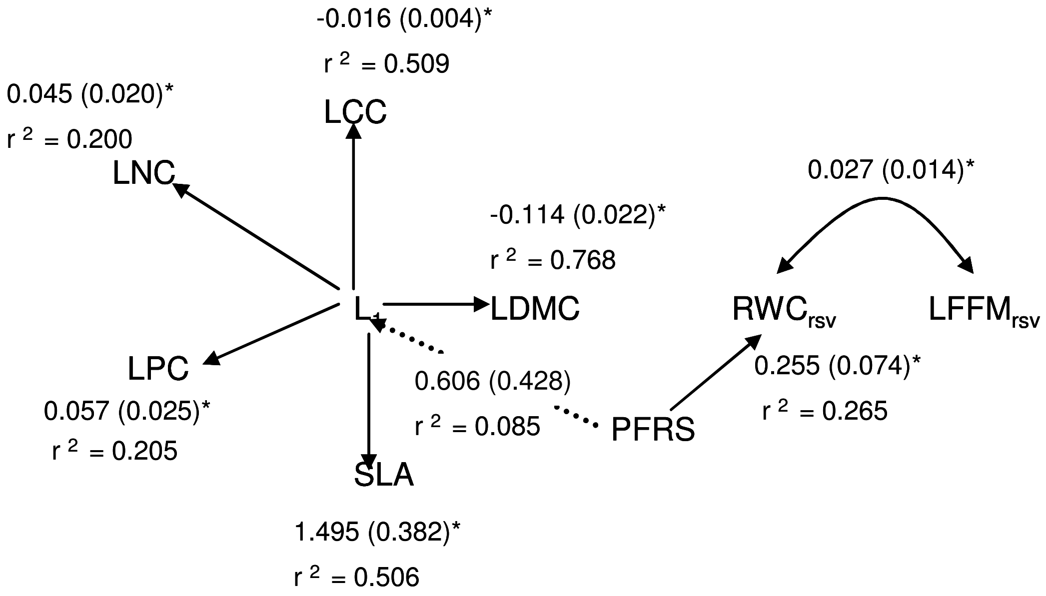


Figure 8.

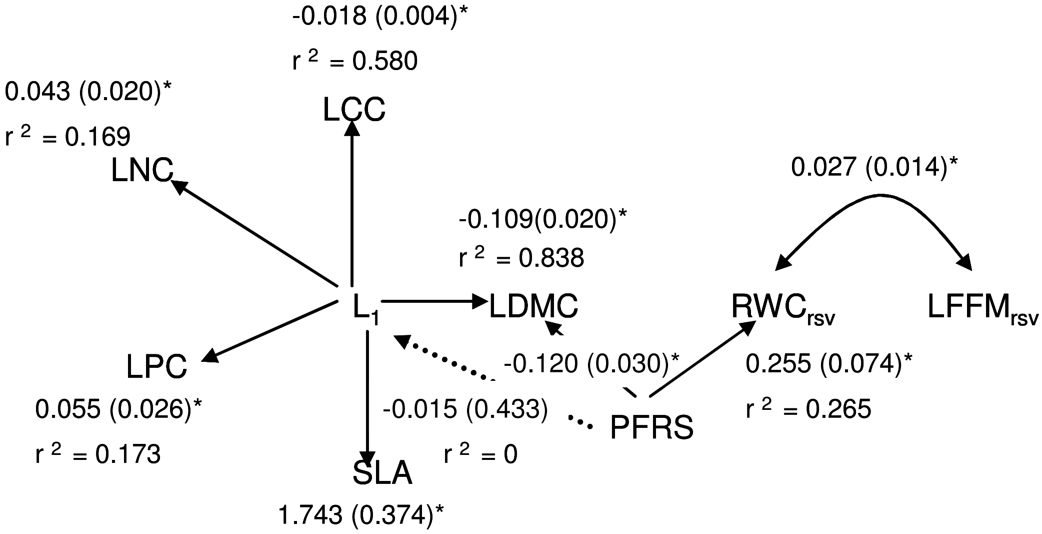
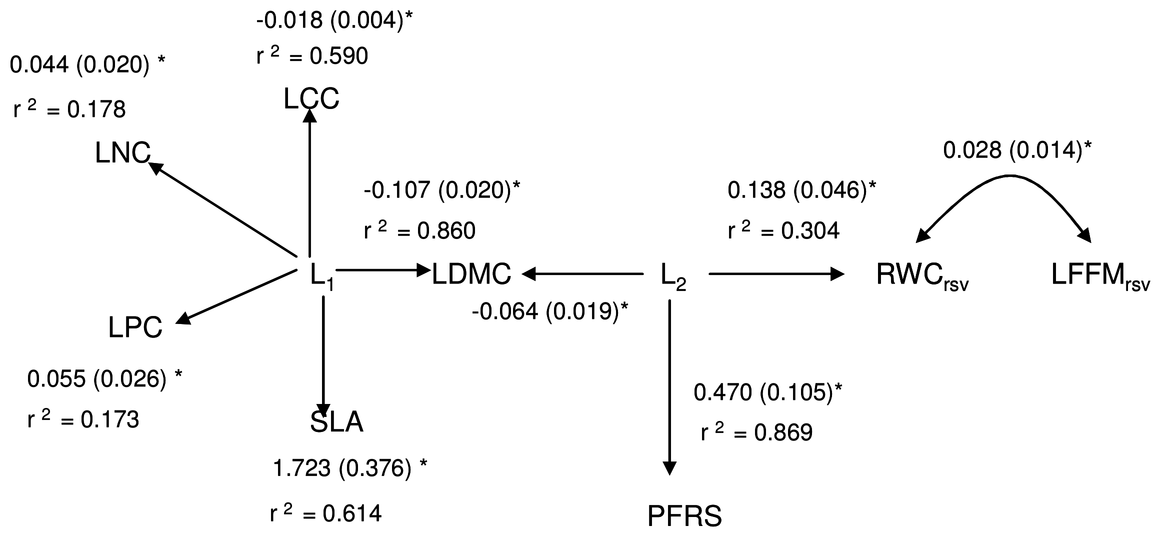


Figure 9.


-0.018 (0.004)*
r 2 = 0.590
LCC
0.044 (0.020) *
r 2 = 0.178
LNC
0.028 (0.014)*
-0.107 (0.020)*
r 2 = 0.860
0.138 (0.046)*
r 2 = 0.304
L1
LDMC
L2
RWCrsv
LFFMrsv
-0.064 (0.019)*
LPC
0.055 (0.026) *
r 2 = 0.173
SLA
1.723 (0.376) *
r 2 = 0.614
0.470 (0.105)*
r 2 = 0.869
PFRS

DISCUSSION

Results provide support for the model of Shipley *et al* (2006) to explain the fundamental leaf trade-offs generating the leaf economics spectrum. As expected, LNC, LCC, LPC, SLA, LDMC are all caused by the same latent variable (L_1). Following Shipley *et al* (2006), this latent variable is interpreted as the ratio between the volume of the leaf occupied by water (V_c) to the volume of the leaf occupied by the cell wall (V_w), although this physical interpretation has not yet been experimentally verified. More important to the present paper is to understand how variables related to the seasonal variation in water content of leaves and fine branches relates to the leaf economics spectrum. Is this seasonal variation simply another manifestation of the leaf economics spectrum, is it independent of the leaf economics spectrum, or is the relationship between the two more indirect? Variables related to the seasonal relative variation of water are very important to the functioning of Mediterranean plants, since water deficit is an important stress (Larcher, 1995; Terradas, 2001) in these ecosystems which is also related to perturbations such as wildfires.

The analyses suggest that the seasonal relative variation in tissue water is not simply a further manifestation of the leaf economics spectrum. Following the causal explanation based on the current interpretation of the latent variable (i.e. the ratio of cell cytoplasmic volume to cell wall volume), it was expected that higher values of this latent variable would cause lower LDMC, so that higher values of LDMC would have higher values of RWC_{rsv}. In other words, plants with thicker cell walls would have higher water relative seasonal variation since these types of cells can better resist dehydration of the cell. But, perhaps surprisingly, none of these variables related to water content was directly caused by the latent variable (L_1). However, model 3 shows that water relative seasonal variation is explained by the post-fire regenerative strategy which, at the same time, also causes an effect to LDMC. Seeder species have lower LDMC and higher RWC_{rsv} than non-seeders. The most parsimonious fitting causal model (model 5) states that selection for the post-fire regenerative strategy doesn't affect the underlying driver variable (L_1) of the leaf economics spectrum, which it is interpreted as the relation between cell and cell wall volume. As a result, covariation between LNC, LCC, LPC and SLA is due only to L_1 independently of the post-regenerative strategy of the species, while variation in LDMC would be due both to these volume cell relations and to some other cause associated with being a seeder vs. a non-seeder.

Recent studies have pointed out that most seeder species of the study region have evolved under the Mediterranean climate established in the Quaternary, while many non-seeder species have evolved from the Pre-Mediterranean climate, in the Tertiary (Herrera, 1992; Verdú, 2000; Pausas & Verdú, 2005). The seeders' tolerance to higher RWC_{rsv} and lower LDMC contents may be the result of an adaptation of seeders to the Mediterranean climate which is characterized by seasonal drought periods. According to the best fitting model (Figure 5), I suggest that the intrinsic factor that would allow seeders to succeed in this Mediterranean climate would be related to their leaf dynamics and their life cycle. Leaves of most of the studied seeders are short-lived and they are renewed at the end of the summer (Floret *et al.*, 1989), probably because of the thin cell walls of the cells that achieve big water deficits in summer (Saura-Mas & Lloret, 2007). There are no species with short-lived, thin leaves and low mass-based net photosynthesis since it would be a poor strategy; a low instantaneous productivity plus a short leaf duration would result in a low total productivity over the leaf life-span, making it unlikely for a leaf to maintain the costs of the leaves' economics (Reich *et al.*, 1997). Since seeders have short-lived thin leaves, it is expected that seeders will have a high mass-based net photosynthesis. Moreover, seeders often show a short life cycle with high recruitment after disturbances such as fire (Lloret & Vilà, 1997; Lloret *et al.*, 2003; Pausas *et al.*, 2004). As a result, this high mass-based net photosynthesis plus the short leaf life-span and life cycle could be some of the intrinsic factors of being seeder that explain the low values of LDMC and the high RWC_{rsv} for seeder species.

In conclusion, this study suggests that the leaves of Mediterranean woody species follow the general leaf economics spectrum (Wright et al. 2004) but that interspecific seasonal variation in one of the leaf economics variables, LDMC, is also due to some other selective force associated with post-fire regenerative strategies. Since seeders species evolved under the Mediterranean climate, they developed a particular strategy of drought tolerance (without causing an effect to Vc/Vw) which would be the cause of the observed relationship between LDMC and RWC_{rsv} in Mediterranean woody species.

ACKNOWLEDGEMENTS

Thanks to everyone who helped in the field work. This study was funded by the Department of Universities, Research and Information Society of the Generalitat de Catalunya, the European social funds, and the Spanish MCYT projects REN 2003-07198, and CGL2006-01293.

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V. FOLIAR STABLE CARBON AND NITROGEN ISOTOPES

The main contents of this chapter have been submitted to Plant Biology as:
Saura-Mas, S., Lloret, F. Foliar stable carbon and nitrogen isotopes among woody Mediterranean species with different life-form and post-fire regeneration.

ABSTRACT

- Not a lot of studies have been conducted to analyze wildfire effects in the functioning of ecosystems. In the Mediterranean basin, most of the woody species of shrubland ecosystems can regenerate after fire (resprouting or seeding).
  Here I hypothesize that post-fire regenerative syndromes may potentially covariate with traits directly related to functional properties involved with resource use. Concretely, I hypothesize that seeders may have lower water use efficiency (WUE) and that they may take nutrients, such as nitrogen, from more superficial parts of the soil because of the physiological and morphological characteristics of this group of species.

- Leaf $\delta^{13}C$ and $\delta^{15}N$ from 29 woody species with different post-fire regenerative strategies are compared. I also considered taxonomic affiliations in the statistical analyses and life-form as an additional explicative variable of the differences between post-fire regenerative groups since they may also be strongly related to water and nutrient use.

- Data support the hypothesis that seeder species have lower water use efficiency than non-seeders and consequently more consumption of water per produced biomass. However, this distinction must be analyzed together with the role of life-form, since results suggest that shorter life-forms have lower WUE. Furthermore, this study supports the hypothesis that resprouters are species with deeper root systems as described before for some resprouter species in Mediterranean ecosystems.

- Finally, this study suggest that seeders are species that live under soil drought conditions with a lower water use efficiency and lower stomatal control than non-seeders. These physiological properties are mainly explained by the fact that seeders have a life history with smaller size and shorter life and leaf life-span. It is also suggested that differences in life history between post-fire regenerative groups may be because seeders are species which have evolved under Mediterranean climate during the Quaternary while non-seeders did it during the Tertiary.

Key words: efficiency, leaf, plant functional trait, regeneration, resprouter, seeder, water use, wildfire, WUE.

INTRODUCTION

Post-fire regenerative syndromes may potentially covariate with traits directly related to functional properties, that is, those involved with resource use (Ackerly, 2004). For example, recent studies have showed that species that germinate after fire have a coherent pattern of seasonal water use (Saura-Mas & Lloret, 2007).

Water use efficiency is a major determinant of plant functioning Mediterranean plant communities, since Mediterranean-type ecosystems are subjected to a strong seasonal climatic regime with mild winters and hot and dry summers. Leaf carbon isotope ratio ($\delta^{13}C$) has been proposed to reflect plant metabolism and environment since during photosynthesis plants discriminate against the heavier isotope of carbon (^{13}C) (Farquhar *et al*., 1989). Then, depending on stomatal conductance and rate of CO_2 assimilation, the discrimination against ^{13}C varies. In C_3 species, $\delta^{13}C$ is positively related with long-term water use efficiency (WUE, the ratio of the biomass produced to the water consumed to produce it) and it has been extensively used as an indicator of WUE (Farquhar *et al*., 1989; Impa *et al*., 2005; Monclus *et al*., 2006).

Studies of plant species leaf $\delta^{15}N$ have also reported that stable isotopes of nitrogen can be a powerful tool for evaluating N cycling because of their ability to integrate over time and space (Nadelhoffer & Fry, 1994; Llorens *et al*., 2003; Pardo *et al*., 2006). $\delta^{15}N$ can be used as an integrator of terrestrial N cycling and it can detect if a range of plants has access to the same N source (Robinson, 2001). Moreover, some authors have suggested that examining leaf $\delta^{15}N$ values may also improve understanding of how plant ecosystems respond to the cascading effects of N deposition, as evidenced by the strong relationship between foliar $\delta^{15}N$ and nitrification (Pardo *et al*., 2006).

Here, I hypothesize that different groups of post-fire regenerative strategies may have differences in water use efficiency and in the nitrogen source they use. Consequently, functioning of the ecosystem will vary depending on the abundance of the post-fire regenerative strategies. The hypothesis is based on the differences on evolutionary history and life-history type of these species. Seeders tend to show a “r”-like life strategy with relatively short life span, great recruitment after disturbance and shallow roots while resprouters present a “K”-like life strategy with long life, low recruitment after disturbances, and deeper roots (Lloret & Vilà, 1997; Lloret, 1998; Pausas, 2001; Pausas *et al*., 2004). Thus, I hypothesize that seeders are species with lower WUE and they take nutrients from the more superficial parts of the soil because they have a less conservative life-strategy. This idea is consistent with morphological and water stress data for stems and leaves (Ackerley, 2004; Jacobsen *et al.*, 2007; Pratt *et al.*, 2007). Thus, high mass-based net photosynthesis and quick returns of investments plus the short leaf life-span and life cycle, and resistance to cavitation could be some of the intrinsic factors of being seeder that would explain the low water use efficiency of this species. To test the hypothesis, $\delta^{13}C$ and $\delta^{15}N$ from species coexisting in the same site (this is, under similar temperature, soil and water conditions) are considered. Since other studies have shown that the resprouting syndrome is narrowly related to nutrient use (Canadell & Lopez-Soria, 1998; Cruz & Moreno, 2001; Cruz *et al.*, 2003; Paula & Pausas, 2006), comparisons between resprouters (R: S- R+, S+ R+) and non-resprouters (NR: S- R-) were preferred when analyzing ^{15}N:^{14}N ratios ($\delta^{15}N$), instead of seeders and non-seeders.

Since measures obtained in phylogenetically related species are likely to be autocorrelated (Blackburn & Duncan, 2001; Garland *et al.*, 2005; Sol *et al.*, 2007) taxonomic affiliations were also considered in the statistical analyses. Life-form was also considered as an additional explicative variable of the variance between post-fire regenerative groups since it may also be strongly related to water and nutrient use. Furthermore, this study expands knowledge of the performance of stable isotopes of carbon and nitrogen in Mediterranean plants ecosystems, and consequently it can be very useful to other ecology subjects, such as trophic ecology (Kelly, 2000; Adams & Grierson, 2001).

MATERIALS AND METHODS

Study area and species

The study area was located on the Montgrí Massís, a protected coastal area located in the NE of Catalonia, (north-east Iberian Peninsula, 42.16ºN, 3.24ºW). Vegetation is mainly dominated by open pine forests and also by shrublands, dominated by *Quercus coccifera*, *Cistus albidus*, *Cistus monspeliensis*, and *Rosmarinus officinalis* (Polo & Masip, 1987). Sampling was conducted in mature shrubland (1-2 m high) that had been untouched by wildfire for over 10 years. The annual precipitation is 654.6 mm, with cool winters (mean minimum annual temperature: 10.7ºC) and warm summers (mean maximum annual temperature: 18.9ºC) (Ninyerola *et al.*, 2000; Ninyerola *et al.*, 2003).

The study was carried out on a subset of 29 woody plant species growing in the study area, representative of the studied community and belonging to as many different families, life form types and regenerative strategies as possible in this type of community (Table 1). They were classified into the three regenerative groups (S+ R-, S+ R+, S- R+) (*sensu* Pausas & Verdú, 2005) depending on their post-fire regenerative strategies (Cucó, 1987; Papió, 1988; Lloret & Vilà, 1997; Verdú, 2000; Alberdi & Cavero, 2003; Lloret *et al.*, 2003), and after direct field observations in a close area that burned in September 2004.

Table 1. Study species (and abbreviation), family, post-fire regenerative strategies and life-form (according to Raunkiaer classification). Chamaephyte = C, Nano-phanerophyte = NP, Macro-phanerophyte = MP, Phanerophyte-Vine = PV.

		Regenerative strategy		
Study Species	**Family**	**Seeding**	**Resprouting**	**Life form**
Argyrolobium zanonii (Turra) P. W. Ball	Leguminosae	+	+	C
Cistus albidus L.	Cistaceae	+	-	NP
Cistus monspeliensis L.	Cistaceae	+	-	NP
Cistus salviifolius L.	Cistaceae	+	-	NP
Coronilla minima L.	Leguminosae	-	+	C
Daphne gnidium L.	Thymelaeaceae	-	+	NP
Dorycnium hirsutum (L.) ser. In DC.	Leguminosae	+	+	NP
Dorycnium pentaphyllum Scop.	Leguminosae	+	+	NP
Erica arborea L.	Ericaceae	-	+	MP
Fumana ericoides (Caav.) Gandg.	Cistaceae	+	-	C
Fumana laevipes (L.) Spach.	Cistaceae	+	-	C
Fumana thymifolia (L.) Spach.	Cistaceae	+	-	C
Globularia alypum L.	Globulariaceae	+	+	NP
Helianthemum appeninum (L.) Miller	Cistaceae	+	-	C
Helichrysum stoechas (L.) Moench.	Compositae	+	-	NP
Lavandula latifolia Med.	Labiatae	+	+	C
Lonicera implexa Aiton	Caprifoliaceae	-	+	PV
Olea europaea L.	Oleaceae	-	+	MP
Ononis minutissima L.	Leguminosae	+	-	C
Phillyrea angustifolia L.	Oleaceae	-	+	MP
Pistacia lentiscus L.	Anacardiaceae	-	+	MP
Quercus coccifera L.	Fagaceae	-	+	NP
Quercus ilex L.	Fagaceae	-	+	MP
Rhamnus alaternus L.	Rhamnaceae	-	+	MP
Rosmarinus officinalis L.	Labiatae	+	-	NP
Smilax aspera L.	Liliaceae	-	+	PV
Staehelina dubia L.	Compositae	+	+	C
Teucrium polium L.	Labiatae	+	+	C
Thymus vulgaris L.	Labiatae	+	+	C

Sampling and measurements

Sampling was carried out at the end of the summer (August 2006) to ensure that collected leaves had experienced summer drought. Replicate samples were collected from ten different plants for each species. Thus, 10 isotopic analyses (for both $\delta^{13}C$ and $\delta^{15}N$) were done for each species. Leaf nitrogen concentration (LNC, here after) was also measured as the quantity of nitrogen (mg) per leaf mass (g). Individuals of the same species were collected on the same site and under similar conditions (i. e. outside forest canopy). Leaf samples were collected from well–grown plants and they were harvested from branches less than one year-old located in the canopy exposed to direct sunlight. In the laboratory, leaves were oven-dried for 48 h at 60ºC and ground. All analyses were carried out with an elemental analyzer EA1108 (Carlo Erba, Milano, Italy) attached to a Delta C isotope mass spectrometer and using a CONFLO III interface (Thermo Finnigan MAT, Bremen, Germany).

The carbon isotopic composition of a sample ($\delta^{13}C$) was calculated as the ratio (%o):
$\delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 1000$
where R_{sample} and $R_{standard}$ are the ^{13}C:^{12}C ratios in plant tissue and the standard, respectively. The universally accepted Pee Dee Belemnite (PDB) standard for carbon was used.

The nitrogen isotopic composition of a sample ($\delta^{15}N$) was calculated as the ratio (%o):
$\delta^{15}N = [(R_{sample}/R_{atm}) - 1] \times 1000$
where R_{sample} and R_{atm} are the ratios in plant tissue and the standard, respectively. Foliar $\delta^{15}N$ values were reported respect to the ratio of ^{15}N:^{14}N in atmospheric N_2 (Vienna - AIR).

Statistical analyses

The differences in leaf $\delta^{13}C$ and $\delta^{15}N$ between the species belonging to different regenerative strategies were tested by using general linear mixed models (GLMM), where the dependent variables were leaf $\delta^{13}C$ and leaf $\delta^{15}N$, and the fixed-effect was regenerative strategy (seeders (S) and non-seeders (NS) for $\delta^{13}C$, and resprouters (R) and non-resprouters (NR) for $\delta^{15}N$). In these analyses, the replicates were the ten sampled individuals of each species, and species was considered a random factor in all the analyses. To be able to better explain the $\delta^{13}C$ differences between seeders and non-seeders, the same statistical analyses was applied to LNC.

GLMM was used to test whether there was any autocorrelation on account of the higher taxonomical level "family" for the two variables by considering a hierarchical nested design of species among families. Since this autocorrelation existed only for leaf $\delta^{15}N$, I created an additional GLMM that considered the post-fire regenerative strategy as the fixed effect, and species as the random factor nested within family. Order was not considered, as there was nearly the same number of orders as families. This approach ensured that the significance tests for the fixed-effect predictors were not biased by taxonomical affiliations. I also constructed a GLMM that considered the post-fire regenerative strategy as the fixed effect, species as the random factor and life-form (C = chamaephyte: with persistent buds situated 0.2 - 0.5 m height, NP = nano-phanerophyte: with persistent buds situated 0.5 - 2 m height, MP = macro-phanerophyte: with persistent buds situated 0.5 - 5 m height and PV = phanerophyte-vine: with persistent buds situated more than 0.5 m height and creepper) as a second fixed effect. A Chi-squared test was performed to study if life form and lineage age were equally distributed among the different post-fire regenerative groups. Finally, since life-form is mainly defined by plant height, to better understand the relation between life-form and leaf $\delta^{13}C$, a linear regression between these two variables was constructed. Height was transformed to its logarithm to better approximate normality ($\log_{10}$(height)).

Analyses were performed using Statistica 6.0 (Statsoft), Sigmaplot 8.0 (SPSS) and SPSS 13.0 (SPSS).

RESULTS

Seeders had lower (more negative) values of $\delta^{13}C$ than non-seeders (F = 4.33 p = 0.047), while resprouters presented higher $\delta^{15}N$ values (less negative) than non-resprouters (F = 6.94, p = 0.014) (Figure 1 and 2).

When analysing $\delta^{13}C$ values, and considering species nested within family as a random factor, no autocorrelation associated with taxonomical affiliation was observed (F = 1.23, p = 0.343).

When considering the effect of life-form, this trait showed significant effect on $\delta^{13}C$, and the difference between seeders and non-seeders became weaker (Table 2). Post-hoc analyses indicated that each life-form show different values of $\delta^{13}C$, except for phanerophytes-vines which had the same value as nano-phanerophytes and macro-phanerophytes (Table 2). Lower values of $\delta^{13}C$ were found in camephytes, followed by nano-phanerophytes and macro-phanerophytes. Phanerophyte-vines showed similar values to nano-phanerophytes and macro-phanerophytes.

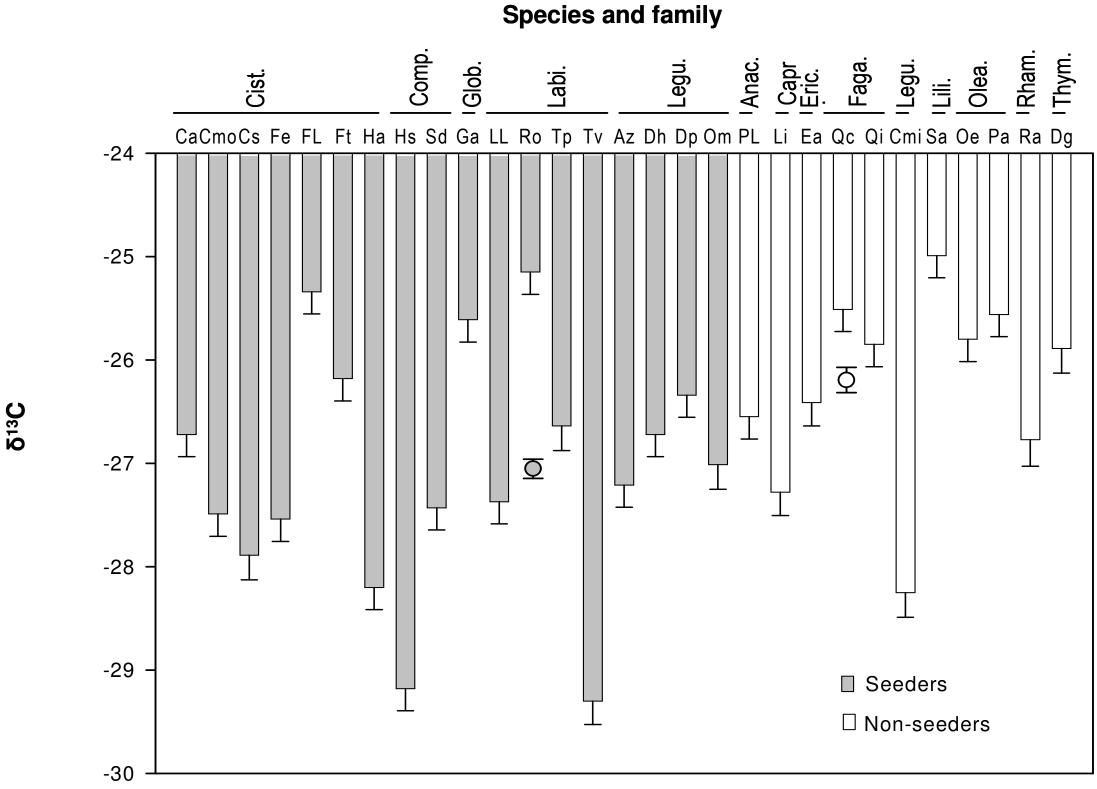

Figure 1. $\delta^{13}C$ ($^{o}/_{oo}$) means for each of the 29 studied species. Values are grouped in seeders (S, vertical grey bars) and non-seeders (NS, vertical open bars). Standard deviation is denoted by bars. See Table 1 for species abbreviations. The circle symbol indicates the mean of each one of the regenerative strategies. Species belonging to the same family are grouped. Anac. = Anacardiaceae; Capr. = Caprifoliaceae; Cist. Cistaceae; Comp. = Compositae; Eric. = Ericaceae; Faga. = Fagaceae; Glob. = Globulariaceae; Labi = Labiatae; Legu. = Leguminosae; Lili = Liliaceae; Olea = Oleaceae; Rham = Rhamnaceae; Thym = Thymelaeaceae.

Table 2. Summary of results of generalized linear mixed model (GLMM) accounting for variation in $\delta^{13}C$ and $\delta^{15}N$ respect to the two fixed factors: regenerative strategy and life form (see Table 1). Regenerative strategies were: seeders (S+ R- and S+ R+) and non-seeders (S- R+) in $\delta^{13}C$ analyses and resprouters (S- R+ and S+ R+) and non-resprouters (S+ R+) in $\delta^{15}N$.

	$\delta^{13}C$		$\delta^{15}N$	
	F	**P-value**	**F**	**P-value**
Regenerative strategy	0,289	0,596	12,851	0,002
Life form	3,117	0,046	1,475	0,247
Regenerative strategy x Life form	1,764	0,197	1,237	0,278
Species	21,551	< 0,001	22,919	< 0,001

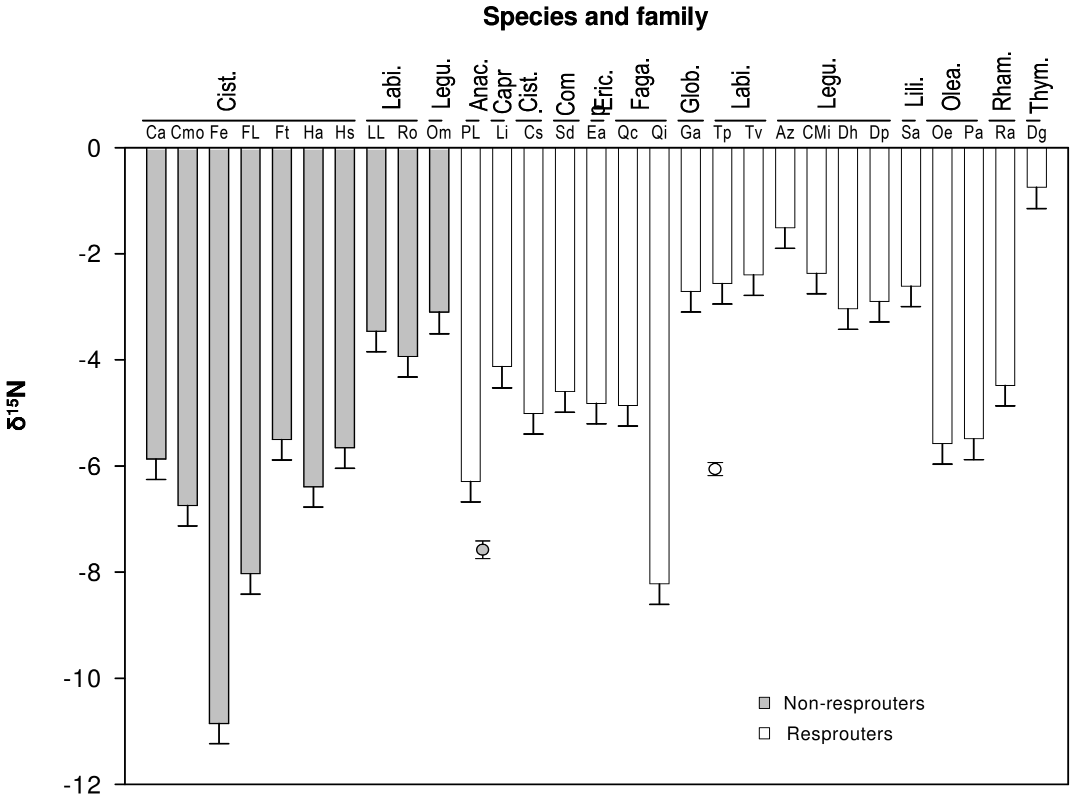

Figure 2. $\delta^{15}N$ ($^{o}/_{oo}$) means for each of the 29 studied species. Values are grouped in resprouters (R, vertical open bars) and non-resprouters (NR, vertical grey bars). Standard deviation is denoted by bars. See Table 1 for species abbreviations. The circle symbol indicates the mean of each one of the regenerative strategies. Species belonging to the same family are grouped. Anac. = Anacardiaceae; Capr. = Caprifoliaceae; Cist. Cistaceae; Comp. = Compositae; Eric. = Ericaceae; Faga. = Fagaceae; Glob. = Globulariaceae; Labi = Labiatae; Legu. = Leguminosae; Lili = Liliaceae; Olea = Oleaceae; Rham = Rhamnaceae; Thym = Thymelaeaceae.

Plant height is positively correlated to $\delta^{13}C$, and seeders are the species with lower height and lower $\delta^{13}C$ (Figure 3). This result is in agreement with the chi-squared comparisons which indicate that seeders are mainly chamephytes and nano-phanerophytes. When looking to the obtained results, *Coronilla minima* behaved as non-seeder with worth mentioning low $\delta^{13}C$. This species has been considered as non-seeder in some studies (Alberdi & Cavero, 2003) and has also been observed to produce seedlings after fire (Cucó, 1987), but I failed to find them in recently burned areas close to the sampling locality.

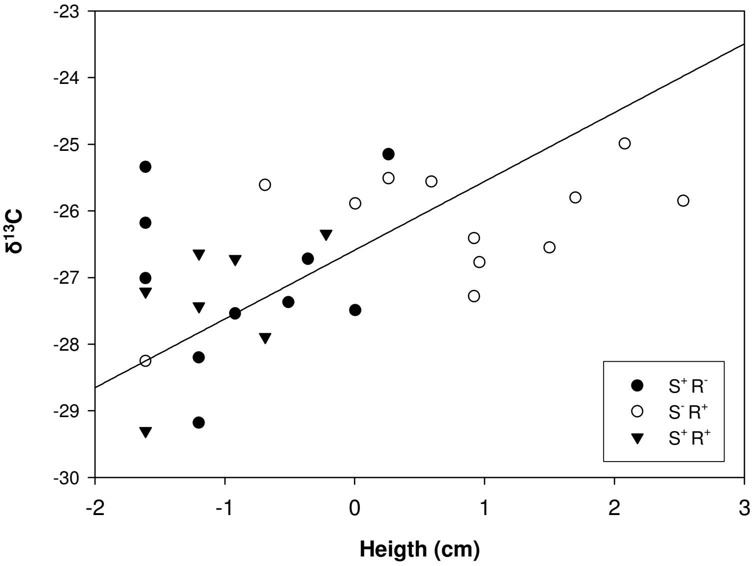

Figure 3. Linear regression for leaf $\delta^{13}C$ ($^{o}/_{oo}$) and plant height ($R^2 = 0.25$; $p = 0.005$).
Plant height is expressed in logarithmical scale. Each point represents a species.
Different post-fire regenerative strategies are showed with different symbols.

Seeders were mostly attributed to an origin in the Quaternary while non-seeders are species with an origin in the Tertiary (Figure 4).

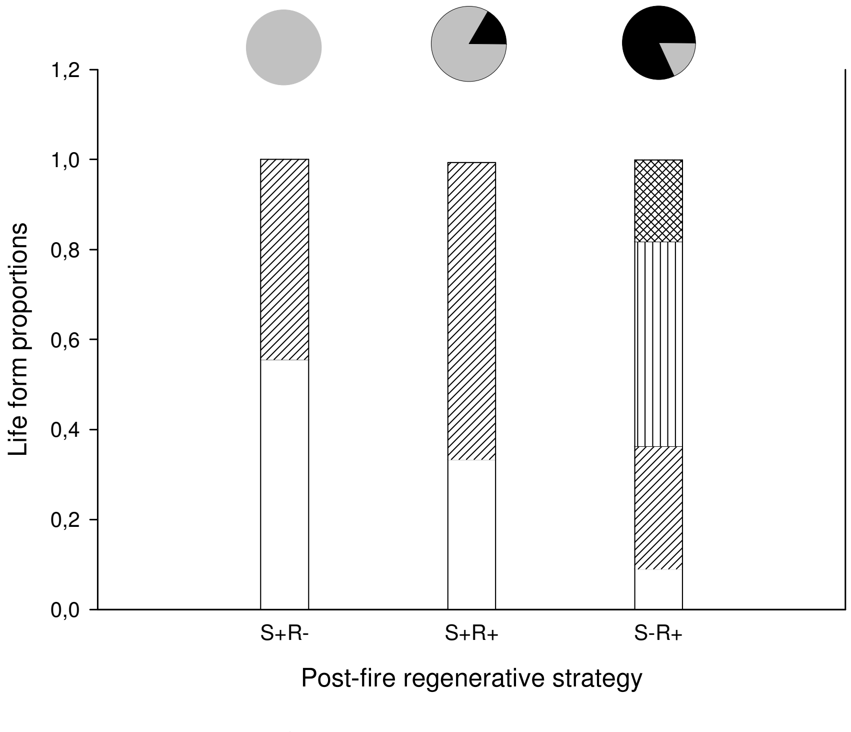

Figure 4. Life-form (right column) $\chi^2 = 14.47$, $p = 0.025$) and lineage age (left column) ($\chi^2 = 15.56$, $p < 0.001$) proportions for each post-fire regenerative strategy. Proportions of Tertiary (black) and Quaternary (grey) species are shown in pie charts. Proportion of species with different life-forms are shown in bars.

▭ = chamaephyte ▨ = nano-phanerophyte ▥ = macro-phanerophyte
▩ = phanerophyte-vine

$\delta^{15}N$ content presented autocorrelation associated with taxonomical affiliation when considering species nested within family as a random factor (F = 4.068, p = 0.005). Significant differences in $\delta^{15}N$ between resprouters and non-resprouters became marginally significant when considering taxonomic affiliations (F = 3.450, p = 0.091). Resprouters presented significally higher $\delta^{15}N$ than non-resprouters when considering life-form types in the statistical model, but there were no differences between life-forms, so life-form seems not to play an important role determining $\delta^{15}N$ (Table 2).

There were not significant differences in LNC between seeders and non-seeders and neither between resprouters and non-resprouters.

DISCUSSION

The hypothesis that seeder species have lower water use efficiency than non-seeders and consequently more consumption of water, per produced biomass, is confirmed in this study. However, this distinction must be analyzed together with the role of life-form. There were not differences in LNC among seeders and non-seeders supporting that differences in water use efficiency among the different regenerative groups are mostly due to variations in stomatal conductance, and not to differences in photosynthetic assimilation (Farquhar *et al*., 1989; Reich *et al*., 1997; Wright *et al*., 2004).

Life-form presents a strong effect on the $\delta^{13}C$ differences among seeders and non-seeders. In the studied community, most seeders are chamaephytes or nano-phanerophytes that tend to be of smaller size and shorter life-span that most non-seeders (macro-phanerophytes, nano-phanerophytes and vines). Thus, the results show that shorter woody species tend to present lower water use efficiency. Smaller species, such as nano-phanerophytes and chamephytes, are more present in arid environments and show anatomical differences such as narrower and shorter xylem conducts (Villar 2000) which could suggest higher resistance to embolism (Villar, 2000; Martinez-Vilalta *et al*., 2002). Recent studies comparing worldwide species suggest that taller trees have greater stomatal closure (Bond, 2000; Ryan *et al*., 2006), that is higher water use efficiency. Results comparing species from Mediterranean basin shrublands are consistent with this idea since taller species have also higher WUE. As a result, this study gives evidence that differences in $\delta^{13}C$ of seeders and non-seeders, from the Western Mediterranean Basin, are likely to be mostly due to their differences in plant height and life-form type.

Wright *et al.* (2004) studied worldwide leaf economics spectrum and they suggested a gradient of species defined by quick returns of carbon and nutrients investments. In one side of the gradient there are species with high nutrient concentrations, high mass-based net photosynthesis and respiration, and short leaf life-span and low dry-mass investment per area. On the other side of the axis there are species with slow return of investments, that is, species with long leaf life-span, high leaf construction costs, low nutrient concentrations, and high mass-based net photosynthesis and respiration. This pattern fits the distinction between regenerative traits, since most of the studied seeder species have short leaf life-span (Villar & Merino, 2001; Navas *et al.*, 2003). Our results also suggest that those species with an strategy of quick returns of investments of carbon and nutrients would also show a low water use efficiency. Ackerly (2004) also suggested that seeders are species with tolerance to water deficit and tolerance to turgor loss, while resprouters are species with avoidance of water deficit. Properties of resistance to cavitation are strongly related to water use efficiency too, and Pratt *et al.* (2007) have suggested that seeders from chaparral ecosystems have greater resistance to cavitation of stems and roots than resprouters, concluding that seeders have more resistance to water stress. There are more evidences in agreement with the results, such as the greater ability that seeders of the Western Mediterranean Basin have to modify water leaf content along seasons, with special depletion in summer (Saura-Mas & Lloret, 2007), and that some seeder species abroad have been described to have shallower and abundant roots in the first centimeters of soil, compared to non-seeders (Kummerow, 1981; Dawson & Pate, 1996; Clemente *et al.*, 2005).

Analyses at the species level can present autocorrelation due to taxonomical affiliations, but results show that the differences on carbon isotopic discrimination are not due to taxonomical bias.

More over, this study demonstrate that, in the Mediterranean basin, most seeders are species which have evolved under Mediterranean climate during the Quaternary while non-seeders have their origin in the Tertiary (Herrera, 1992; Verdú, 2000; Paula & Pausas, 2006). Consequently, seeders have a life history, with shorter life-forms and shorter life and leaf span properties which allows them to live under soil drought conditions with a lower water use efficiency and lower stomatal control. In agreement with that, Lloret *et al.* (2005) suggested that, in the Mediterranean basin, seeders are more abundant in more typical Mediterranean and arid environments.

Higher $\delta^{15}N$ in resprouters than in non-resprouters may indicate differences in root patterns and in the depth of N uptake source (Pardo *et al.*, 2006). Soil $\delta^{15}N$ generally increases with depth (Nadelhoffer & Fry, 1994; Pardo *et al.*, 2002), thus, this study supports the hypothesis that resprouters are species with deeper root systems as described for some resprouter species in Mediterranean ecosystems (Kummerow, 1981; Dawson & Pate, 1996; Ackerly, 2004). Moreover, some studies reveal that species starting the growth season early might show lower foliar $\delta^{15}N$ since they would take up more N before nitrification has enriched the dissolved inorganic N pools (Pardo *et al.*, 2006). Thus, more studies on the phenology of the studied species should be done to assess the seasonal patterns of N uptake in resprouters and non-resprouters. Significant differences in $\delta^{15}N$ between resprouters and non-resprouters became marginally significant when keeping constant the effect of taxonomic affiliation. Thus, it can not be concluded at which extent the patterns of $\delta^{15}N$ leaf content is determined by phylogenetical constraints or regenerative strategies, although in this case life-form type seems to be less relevant than for $\delta^{13}C$.

In conclusion, height has an important role in determining water use efficiency, and this study suggest that differences between seeders and non-seeders WUE are mainly due to the fact that seeders are smaller than non-seeders. Moreover, the fact that seeders were originated in the Quaternary and non-seeders in the Tertiary may also have been important in determining life-forms and WUE properties of plants, since the different post-fire regenerative groups evolved under different climatic conditions. Alternatively, non-seeders species which evolved in the Tertiary may have higher water use efficiency due to their drought avoidance strategy with greater stomatal control (Choi *et al.*, 2005), lower consumption of water and deeper roots.

ACKNOWLEDGMENTS

I would like to thank A. Vila and J. Garcia for helping in the field and in the laboratory. Especial thanks go to J. Font for his knowledge of the Montgrí and its flora, and J. Martínez-Vilalta, J. Peñuelas, S. Palacio, and D. Sol for their support and suggestions. This study was funded by the Department of Universities, Research and Information Society of the Generalitat de Catalunya, the European social funds, and the Spanish MCYT projects REN 2003-07198 and CGL2006-01293/BOS. It also contributes to the European research group (GDRE) “Mediterranean and mountain ecosystems in a changing world" funded by the Generalitat de Catalunya and CNRS. This study comply with the current laws of the country in which they were performed.

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VI. FUEL LOADING AND FLAMMABILITY

The main contents of this chapter are in preparation to be submitted as:

Saura-Mas, S., Paula, S., Pausas, J., G., Lloret, F. Fuel loading and flammability in species with different post-fire regeneration from Mediterranean shrublands

ABSTRACT

- Morphological and physiological properties might make many Mediterranean woody species fire-prone. Thus, the flammability and combustibility of Mediterranean basin communities will be determined by the species and its properties. Furthermore, differences in flammability of species with different post-fire regenerative strategies can be determinant for plant community dynamics when considering fire-prone ecosystems.

- In the Mediterranean basin, post-fire regeneration properties of seeders, were mainly originated during the Quaternary, and they may be due to their adaptation to fire and Mediterranean climate (especially summer drought). Since their germination is enhanced by these two events, they could have developed more flammable properties than non-seeders, species often characterized by resprouting after fire.

- Flammability and fuel loading characteristics of the main woody species, with different post-fire regeneration (seeders and non-seeders), were measured in two shrublands in the Eastern Iberian Peninsula.

- The results suggest that ecosystems dominated by seeder species are more flammable and thus more susceptible of fire-risk than ecosystems dominated by non-seeder species since seeders inflame at lower temperatures and have higher proportions of dead and fine fuel. Therefore, the proportion of these types of species resulting from previous fire or management history is likely to determine the characteristics of future fire events.

Keywords:
Combustibility, fire, flammability, fuel, moisture, seeder, woody

INTRODUCTION

Wildfires are an important disturbance in the Mediterranean basin ecosystems which can determine species composition and ecosystem functioning (Whelan, 1995; Lloret & Vilà, 2003; Eugenio & Lloret, 2004; Rodrigo *et al.*, 2004; Bond *et al.*, 2005). In turn, it has been reported that morphological and physiological properties (low moisture content, abundant resins, oils, and volatile products, persistence of dead parts in the canopy, etc…) make many Mediterranean woody species fire-prone (Papió & Trabaud, 1991; Bond & Midgley, 1995; Schwilk & Ackerly, 2001; De Luis *et al.*, 2004; Alessio, 2006; Scarff & Westoby, 2006).

Post-fire regeneration is determined by different mechanisms exhibited by the species and there is evidence that the proportion of regenerative types in plant communities may be sensitive to fire regime (Bellingham & Sparrow, 2000; Franklin *et al.*, 2001; Pausas *et al.*, 2004; Lloret *et al.*, 2005a; Pausas & Lloret, 2007). Thus, differences in flammability of species with different post-fire regenerative strategies can be determinant for the dynamics of fire-prone communities, even as establishing positive feedbacks as reported for fire and grasses (Vilà & Lloret, 2000; Vilà *et al.*, 2001; Grigulis *et al.*, 2005). It seems appropriate to consider species in two large groups, according to their regenerative strategy after fire: seeders and non-seeders. Seeders are propagule-persisters species in which the population locally persists in propagule form (seed, fruit) after a fire. These are.species that their populations regenerate by establishing seedlings just after fire since they have a persistent seed bank (seeds resist or are protected from fire), and the recruitment of new individuals is often enhanced by fire (Pausas *et al.*, 2004). Also, seedlings established shortly after fire usually present higher survival and growth rates than those establishing in periods between fires (Lloret, 1998). This category includes species that only regenerate after fire from seeds (obligate seeders) and species that both resprout and establish seedlings after fire (facultative seeders). Non-seeders are species in which the propagule (seed, fruit) does not persist after fire. Consequently, propagules may only occur by dispersal from outside the fire affected area. Often, non-seeders are species that can regenerate after fire by resprouting from underground or aerial parts of the plant. Commonly, seeders are species with a relatively short life cycle and a high recruitment after a fire while non-seeders are often species with longer life cycle and lower recruitment after fire (Pate *et al.*, 1990; Verdaguer & Ojeda, 2002; Knox & Clarke, 2005; Schwilk & Ackerley, 2005). In the Mediterranean basin, many non-seeders are typically found in late successional communities, and many seeders, in addition to fast establishment after fire, may recruit after disturbances such as clearing.

Two different types of factors that determine the behaviour of wildfires can be considered. Meteorological factors such as wind, humidity and temperature change quickly during the fire event. Other factors are more constant such as the ones associated to topography and fuel (Papió, 1994). Particularly, structural and chemical plant traits are inherent factors of the vegetation cover that will determine the combustibility and flammability of the community. This study will focus on two fuel characteristics: fuel loading and flammability, which are factors with an important role in fire risk (Van Wilgen *et al.*, 1990; Posshingham *et al.*, 1995; Bond & Van Wilgen, 1996).

Many elements affect species flammability: received amount of heat, vegetation structure, chemical composition and water content (Philpot, 1970; Trabaud, 1989; Cornelissen *et al.*, 2003). Particularly, tissues moisture and morphology (surface to volume ratio) are essential since they determine, respectively, the amount of energy needed to start the fire reaction and the contact between the reagents (fuel and the atmospheric oxygen) (Papió, 1994; Massari & Leopaldi, 1995; Dimitrakopoulos & Panov, 2001; Ralph, 2001).

Following the terminology of (Troumbis & Trabaud, 1989), the thermal degradation of plant fuels can be simplified by considering two phases. The first endothermic process is the ‘pyrolysis’, which breaks down the plant matter into low molecular mass gases (volatiles), tars, carbonaceous char, and mineral ash. After pyrolysis, ‘combustion’ occurs as an exothermic process, constituting the typical burning. ‘Ignition’ is the transition between pyrolysis and combustion. ‘Flammability’ is the property of a plant to get in flame since the instant in which it is in contact with a source of heat. Often, the term combustibility is confused with flammability, but, according to (Trabaud, 1976), flammability in fact includes three components: ignitability, combustibility and sustainability. The ignitibility determines how easily the fuel ignites. Combustibility refers as how plants burnt after they have been ignited. Sustainability counts the stability of the burning rate, that is, how well the fuel continues to burn. This latter factor was not investigated in this study.

Since fire and fire risk is related to species characteristics (Ward, 2001), here I study the flammability properties of the leaves of Mediterranean species. Usually, time to flaming is the most used variable in flammability studies (Trabaud, 1976; Massari & Leopaldi, 1995). However, other variables, mainly describing the ignitability and combustibility factors of flammability, are considered. To describe these factors, the following phases were studied:

-*Appearance of smoke*, which is related to the moment that pyrolysis starts (smoke phase or phase I hereafter),
-*Combustion start*, recognized because red spots appear, ignition takes place and combustion starts (smoldering phase or phase II hereafter),
-*Appearance of flame*, when there is flame emission (flaming phase or phase III hereafter).

Fuel load and fuel characteristics such as the proportion of live and dead material or the amount of fine and coarse material are determinants of combustibility, and thus, of wildfire intensity and spread. Dead branch retention can increase fire temperatures and heat release (Schwilk, 2003) and specifically, dead fine fuel fractions are an indicator of the fire-risk (Bond & Van Wilgen, 1996; De Luis *et al.*, 2004). In fact, many fire-risk prevention and extinction programs as well as general forest fire prevention planning are based on information of fuel loading properties (Valette *et al.*, 1994; Pons & Vayreda, 1996; Viegas *et al.*, 2001) .

The main objective of this study is to explore the flammability behavior and the fuel loading of species showing different post-fire regenerative strategy. Some variables influencing flammability, such as leaf morphology (surface to volume ratio), and leaf moisture were also considered. I accounted for the weight of taxonomical linkage among species on flammability and fuel characteristics. Species information about flammability and fuel characteristics might be of great importance for the management of fire prevention and extinction. The last years, fires have increased their frequency in the western Mediterranean Basin (Moreno & Oechel, 1995; Piñol *et al.*, 1998; Pausas, 2004). The increasing fire frequency can determine vegetation dynamics (Zedler *et al.*, 1983; Lloret *et al.*, 2003; Bond *et al.*, 2005), which would be given by the post-fire characteristics of species (Pausas, 1999). I hypothesize that seeder species with morphological traits that enhance lower water contents in summer, thus a drought tolerance strategy (Saura-Mas and Lloret 2007) will have more flammable properties and higher proportions of dead fine fuel than non-seeders. The vegetation of two distant areas in the eastern Iberian Peninsula sharing structural and composition features, but with somewhat different climate, were considered. This approach reinforces the consistence of common patterns and accounts for variability that might result from phenotypic plasticity of flammability traits.

MATERIALS AND METHODS

Study areas and species

This study was conducted with species living in two sites located in the east coastal mountains of the Iberian Peninsula. One site was located in the Massís del Montgrí, in the north-east Iberian Peninsula (42º16’ N, 3º24’ W), and the second study site was located in the Serra de la Murta (39º4’ N, 0º12’ W), in the east Iberian Peninsula, 420 km south from the Montgrí site. In both areas, vegetation was dominated by open pine woodlands and coastal shrublands. The sampling was conducted in calcareous shrubland (1-2 m high) growing on limestone, that had been unaffected by wildfire for over 10 years. The monthly mean summer precipitation is 37.6 mm in Montgrí and 16.43 mm in Murta, with cool winters and warm summers (Table 1). Mean annual temperature is 14.8 ºC and 17.4 ºC, respectively, indicating higher water evapotranspiration and water demand in the southern locality (Murta).

Table 1. Climatic characterization of the study sites in Murta and Montgrí. Data were provided from Pérez 1994, Ninyerola *et al* 2000 and Ninyerola *et al* 2003. Precipitation (P), Mean temperature (T), Mean maximum temperature (T_M) and mean minimum temperature (T_m), for each month and annual mean.

	P (mm)		**T (ºC)**		**T_M (ºC)**		**T_m (ºC)**	
	Montgrí	**Murta**	**Montgrí**	**Murta**	**Montgrí**	**Murta**	**Montgrí**	**Murta**
January	55,1	58,5	8,3	10,7	12,5	15,9	4,1	5,4
February	39,0	41,6	8,9	11,4	13,0	17,0	4,8	5,8
March	54,3	55,0	10,6	13,0	14,7	19,1	6,6	6,8
April	58,3	48,8	12,5	15,1	16,6	21,4	8,4	8,9
May	58,8	42,6	15,8	18,6	19,9	25,0	11,8	12,1
June	44,9	24,4	19,4	22,2	23,5	28,5	15,4	16,0
July	25,3	10,0	22,5	25,5	26,8	32,0	18,3	19,0
August	42,7	14,9	22,4	25,7	26,5	31,6	18,3	19,7
September	54,4	55,9	20,0	23,0	23,9	29,1	16,0	17,0
October	112,9	114,1	15,9	18,3	19,9	23,9	12,1	12,7
November	66,4	91,7	11,9	13,8	15,7	19,2	8,0	8,4
December	42,5	75,6	9,5	11,0	13,6	16,1	5,4	5,8
Annual	654,6	633,1	14,8	17,4	18,9	23,2	10,8	11,5

The study was carried out on 29 woody plant species dominant in these shrublands and belonging to a wide range of families, life form types and regenerative strategies (Table 2). Species were classified into two regenerative groups depending on their post-fire regenerative strategies: seeders (R-S+ and R+S+ (*sensu* Pausas *et al.*, 2004 and Pausas & Verdú, 2005) and non-seeders (R+S-). Published information was considered (Cucó, 1987; Papió, 1988; Lloret & Vilà, 1997; Verdú, 2000; Alberdi & Cavero, 2003; Lloret & Vilà, 2003), and direct field observations from a recently burned area in Montgrí. Species that show both strategies, seeding and resprouting, were included in the group of seeders since in these species, the recruitment of new individuals is enhanced by fire. Moreover, previous studies have showed that they have a more similar water use strategy to seeders than to the species that can only resprout after fire (Saura-Mas & Lloret, 2007).

Fuel loading

Sampling was carried out in summer (July to August) 2006, in five non-senescent fully developed and healthy adult individuals per species in each one of the study areas. The same 15 species were sampled in both study sites. In addition, I also sampled some species that were only present in one of the study sites but that were representative of the respective community (Table 2). These additional species were not considered for the comparison between localities. Individuals from the same species were collected in the same area and under similar conditions (i. e. outside the forest canopy). Each individual was cut from the base of the stem at ground surface, then dead and live fuel fractions were separated in the field and weighted (fresh weight, fw).. Shoots of both dead and live material, including branches and logs, were separated in the laboratory according to two diameter classes (Ø < 6 mm and Ø > 6 mm). Leaves of live material were considered as a separate fraction. Finally the classified material was oven-dried (3 days at 60ºC) to obtain the dry weight.

Table 2. Study species, families and post-fire regenerative strategies (seeder = S, non-seeder = NS). F and C columns indicate if the species was used in the experiment to determine flammability (F) and fuel loading (FL). Numbers indicate the localities where the species were sampled (1 = Montgri, 2 = Murta).

Study Species	Family	F	FL	Regenerative strategy
Calicotome spinosa (L.) LK	Fabaceae	1,2		S
Cistus albidus L.	Cistaceae	1,2	1,2	S
Cistus crispus L.	Cistaceae		1,2	S
Cistus monspeliensis L.	Cistaceae	1,2	1,2	S
Cistus salviifolius L.	Cistaceae	2	1,2	S
Coronilla minima L.	Fabaceae	1,2	1,2	NS
Daphne gnidium L.	Thymelaeaceae	1,2	1,2	NS
Dorycnium hirsutum (L.) ser. In DC.	Fabaceae	1		S
Dorycnium pentaphyllum Scop.	Fabaceae	1		S
Fumana ericoides (Caav.) Gandg.	Cistaceae	1,2		S
Fumana laevipes (L.) Spach.	Cistaceae	1		S
Fumana thymifolia L.	Cistaceae	1,2		S
Globularia alypum L.	Globulariaceae	1,2	1,2	S
Helichrysum stoechas (L.) Moench.	Asteraceae	1	1,2	S
Lavandula latifolia Med.	Lamiaceae		1,2	S
Lonicera implexa Aiton	Caprifoliaceae		1	NS
Olea europaea L.	Oleaceae		1	NS
Osyris alba L.	Santalaceae	1,2		NS
Phillyrea angustifolia L.	Oleaceae	1,2	1,2	NS
Pistacia lentiscus L.	Anacardiaceae	1,2	1,2	NS
Quercus coccifera L.	Fagaceae	1	1,2	NS
Quercus ilex L.	Fagaceae		1	NS
Rhamnus alaternus L.	Rhamnaceae	1,2	1,2	NS
Rhamnus lycioides L.	Rhamnaceae	2		NS
Rosmarinus officinalis L.	Lamiaceae	1,2	1,2	S
Smilax aspera L.	Liliaceae		1	NS
Staehelina dubia L.	Asteraceae		1	S
Teucrium polium L.	Lamiaceae	1,2	1,2	S
Thymus vulgaris L.	Lamiaceae	1,2		S

Flammability

Leaves samples were collected during August 2006, the month of the year with the highest fire risk in the studied areas. The samples were homogenized by only considering leaves samples and avoiding mixtures with shoots that show very different structural properties. Individuals from the same species were collected on the same area and under similar conditions (i. e. outside the forest canopy). Leaf samples were harvested from well–grown plants growing in the canopy and exposed to direct sunlight. They were fully-expanded leaves, free of herbivore or pathogen damage. The number of leaves sampled from each individual varied according to the size and weight of the leaves of each species.

Once they were collected, the material of each plant was closed in a hermetic plastic bag and stored under ice-box conditions to avoid water loss during transport between the field and the laboratory (Viegas *et al.*, 2001). The leaf moisture (LM) was estimated at the time that flammability was measured in the laboratory with part of the material not used in the flammability test. Fresh (M_f) and dried (M_d, oven-dried for 48 h at 70ºC) material were weighed with a precision of 0.01 g.

Leaf moisture (LM) (%) was determined as

$$LM = 100 \times [(M_f - M_d) / M_d]$$

Before oven drying, thickness of ten leaves for each plant was measured to estimate the surface : volume ratio (S : V) as

$$S : V = S / (S * T) = 1 / T$$

where S is surface, V is volume and T is thickness of the leaf. The thickness of each leaf was measured with a slide range (in the central part of the leaf but avoiding the raquis).

15 species that were present in both study sites were sampled. In Montgrí five additional species were also sampled (Table 2).

In some cases the species considered in fuel load measures could not be used in the flammability test because their very small leaf size; in turn, some species that were not considered in the fuel load estimations were included in flammability tests (Table 2). Five to ten replicate samples from different individuals of each species were collected in each site (total of 225 plants).

Ten grams of fresh leaves from each plant were tested with a quartz epiradiator (Trabaud, 1976; Massari & Leopaldi, 1995) (Photograph 1). The leaves were placed on a wire mesh at a distance of 4 cm from the epiradiator source. The instrument was coupled to a digital thermometer equipped with a probe in contact with the sampled leaves. A digital timer was used to record the time at which the three phases appeared: Smoke phase (first smoke appearance indicating beginning of pyrolisis, phase I), smoldering (presence of embers, combustion starts, phase II) and flaming (burning with flame, phase III). The time to start was set when the temperature reached 60ºC, to ensure that all species received the same quantity of heat. The epiradiator releases heat and it induces the first phase; afterwards the temperature progressively increases until flames appeared. All experiments were conducted in a closed environment avoiding any wind influence. The test ended when the whole sample was burned and the maximum temperature was reached, so that temperature started to decrease.
Surface to volume ratio (S : V) and leaf moisture were also included in the analysis leaf morphology and tissues moisture (Papió, 1994; Massari & Leopaldi, 1995; Ralph, 2001; Alessio, 2006).

Photograph 1. Picture of the method used to measure flammability. Leaves sample in the smoldering phase under a a quartz epiradiator.

Statistical analyses

The variables derived from the fuel fractioning were: live fine fuel, dead fine fuel, live coarse fuel, dead coarse fuel, total live fuel, total dead fuel and leaves. All these variables where considered relative to the total dry biomass of the individual; thus a ratio was obtained for each variable. Moreover, total dry biomass, total plant moisture and dead fuel : live fuel ratio where also considered. A two-factor ANOVA was conducted for each one of the mentioned variables with two fixed factors: regenerative strategy (seeder, non-seeder) and site (Montgrí, Murta). The dependent variables were the mean of the five individuals for each species. To better approximate normality all variables were log-transformed.

Six variables were considered to study flammability: Temperature and Time to reach each of the three phases, smoking, smoldering, and flaming. The differences in flammability between the species belonging to the two regenerative strategies were tested by using GLM (General Linear Models) to include two covariates (leaf moisture LM and leaf surface–to-volume ratio S : V). Two main fixed-effects were considered: regenerative strategy (seeders and non-seeders) and site (Montgrí, Murta).

Differences between regenerative groups on the temperatures at which the flammability phases arise were also analyzed by a Repeated-Measures ANOVA where regenerative strategy and site were the between-subject factors and the within-subject factor was flammability phase (with three levels: smoke, smoldering, flaming). In these analyses, the data used were the mean values of each species obtained from the sampled individuals. In these analyses, S : V and LM were also included as covariates since they explained part of the studied variables.

Differences between regenerative groups and sites for the variables S : V and LM were also analysed with a 2-factor ANOVA for each variable. To better approximate normality, LM was transformed to its Log (x+1) and S : V to its Log (x). The relationships between leaf moisture and time to smoke and flaming, and between S : V and time to smoke and smoldering, were fitted by a linear regression only for Montgrí data, since it was the site with more species.

In all these analyses I worked with the species means. Species that did not flame were not considered in the analyses of variables including the flaming phase.

The relationship between temperature and time was explored by linear regression with the species data from Montgrí only because this site includes more species (Table 2).

Differences between regenerative strategies on the slope of the fitted functions were analysed by one-factor ANOVA.

One difficulty in species level analyses is the need to deal with the autocorrelation that may exist in parameter measured to species sharing a common ancestor (Blackburn & Duncan, 2001; Garland *et al.*, 2005; Sol *et al.*, 2007). A GLMM (General Linear Mixed Model) was used to test whether there was any autocorrelation on account of the higher taxonomical level "family" for all the fuel and combustion variables by considering a hierarchical nested design of species (as a random factor) among families.

Finally, a Principal Components Analysis (PCA) was performed with the four most significant and representative variables that showed significant differences between regenerative strategies, one related to fuel loading (dead fine fuel ratio) and one related to flammability (temperature to achieve flaming phase). Leaf moisture and S : V ratio were also considered since results show that they can have effects on the flammability and fuel loading variables. PCA was done only with Montgrí data to avoid pseudo-replication by sites.

RESULTS

Fuel loading

Although seeder species are smaller ($F_{1,30}$ = 16.37, $p < 0.001$, Figure 1a) they produce a type of fuel loading that make them more prone to burn. The dead to live fuel ratio ($F_{1,30}$ = 4.04, $p = 0.055$, Figure 1b), the live fine fuel proportion ($F_{1,30}$ = 6.83, $p = 0.015$, Figure 2a) and the dead fine fuel proportion ($F_{1,30}$ = 5.99, $p = 0.021$, Figure 2b) are higher in seeders than in non-seeders. On the contrary, seeder species show lower live coarse fuel proportion than non-seeders ($F_{1,30}$ = 14.25, $p = 0.001$, Figure 2c, Figure 3, Table 3), but similar values in the dead coarse fuel proportions ($F_{1,30}$ = 0.05, $p = 0.810$).

Accordingly, plant fuel moisture was lower in seeder than in non-seeder species ($F_{1,30}$ = 22.08, $p < 0.001$). The total plant moisture is the only variable related to fuel loading that showed significant differences both between regenerative strategies and between sites ($F_{1,30}$ = 13.60, $p = 0.001$) (Figure 4). There were any significant interactions between regenerative strategy and site in any of the analyzed variables.

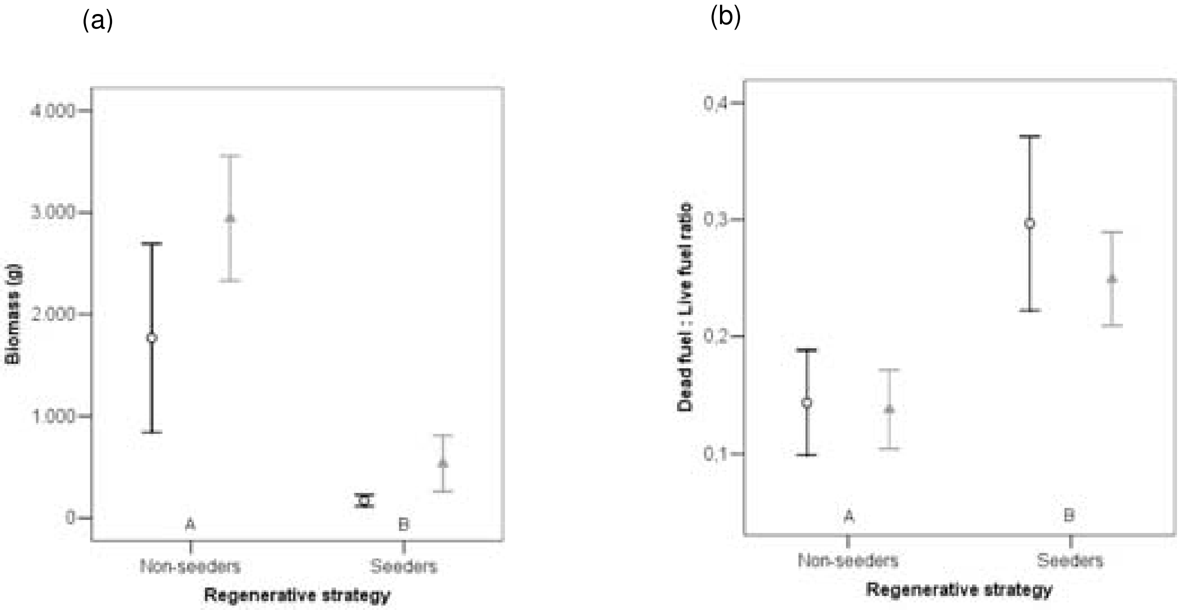
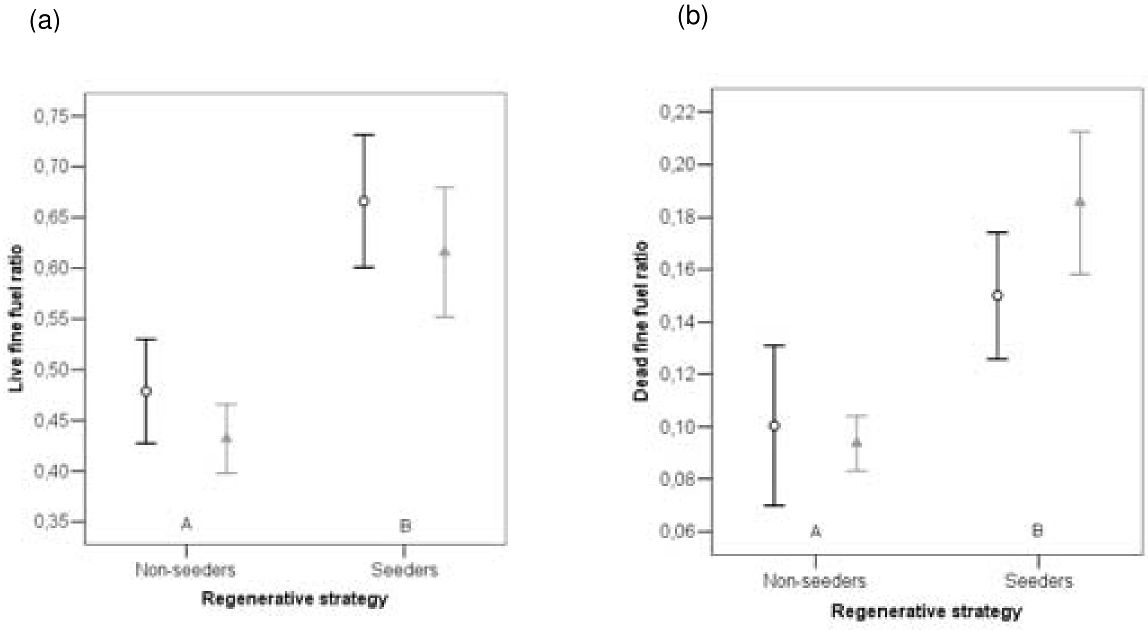


Figure 1. Means and standard errors of total plant biomass (a) and dead fuel : live fuel ratio (b), for the regenerative strategies (seeders and non-seeders) and for the two study sites (Murta and Montgri). Montgrí values are represented with circles (o) and Murta with triangles (▲). Significant differences ($p < 0.05$) are indicated with different letters. Upper case letters (A, B) indicate differences between regenerative strategies. Lower case letters (a, b) indicate differences among collection times for a given regenerative strategy. Differences between sites were not significant.



(c)

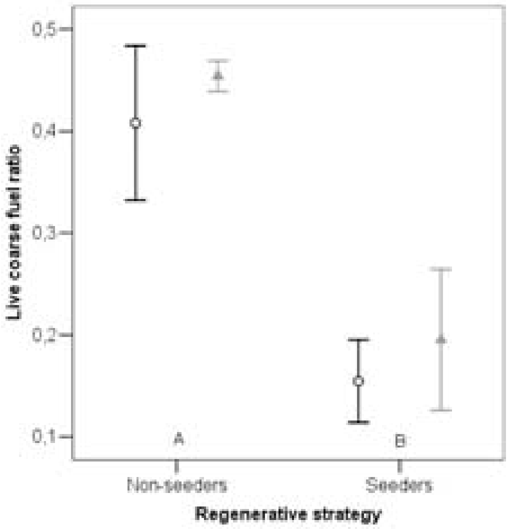


Figure 2. Means and standard error of different plant fractions related to fuel loading: live fine fuel ratio (a), dead fine fuel ratio (b), live coarse fuel ratio (c). Means and standard errors are represented for each regenerative strategy (seeders and non-seeders) and for the two study sites (Murta and Montgri). Montgrí values are representated with circles (o) and Murta with triangles (▲). Significant differences ($p < 0.05$) are indicated with different letters. Upper case letters (A, B) indicate differences between regenerative strategies. Differences between sites were not significant.

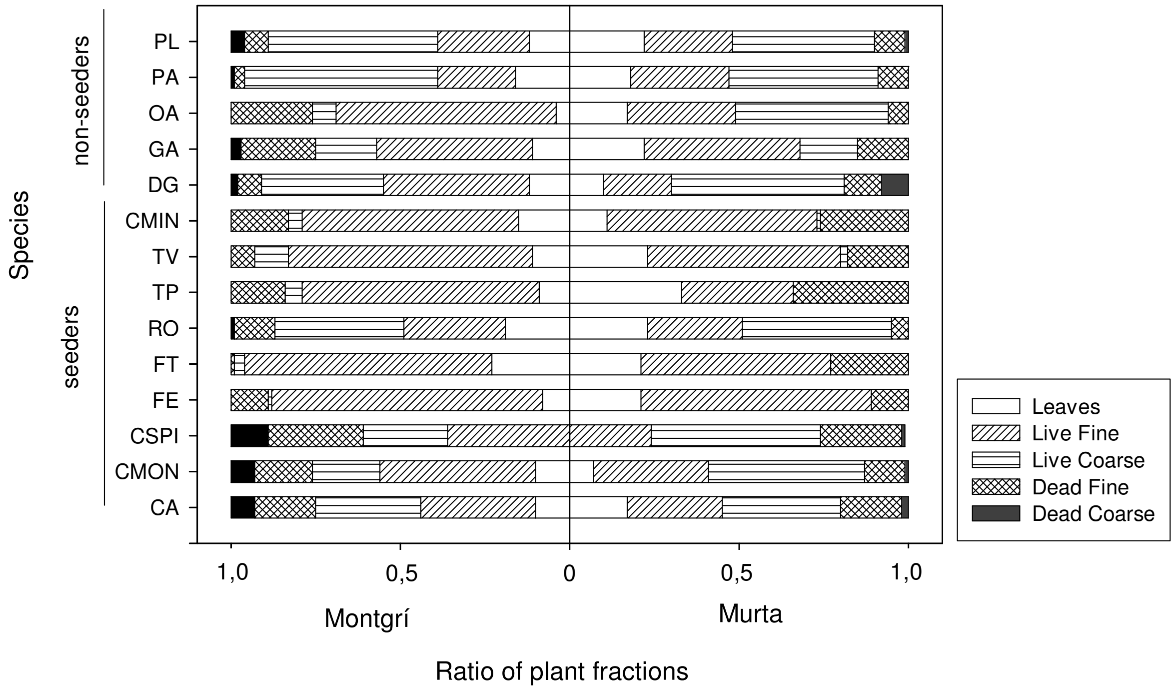


Figure 3. Proportion of each fraction (leaves, dead, live, fine and coarse material) respect to the total dry weight for each species in the two study sites (Montgrí and Murta). Species are first sorted according to the two regenerative and secondly following alphabetical order. Horizontally, values for each species in each site (Murta and Montgri) are represented. Especies code is: PL = *Pistacia lentiscus*, PA = *Phyllirea angustifolia*, OA = *Osyris alba*, GA = *Globularia alypum*, DG = *Daphne Gnidium*, CMIN = *Coronilla minima*, TV = *Thymus vulgaris*, TP = *Teucrium poleum*, RO = *Rosmarinus officinallis*, FT = *Fumana thymifolia*, FE = *Fumana ericoides*, CSPI = *Calicotome spinosa*, CMON = *Cistus monspeliensis*, CA = *Cistus albidus.*

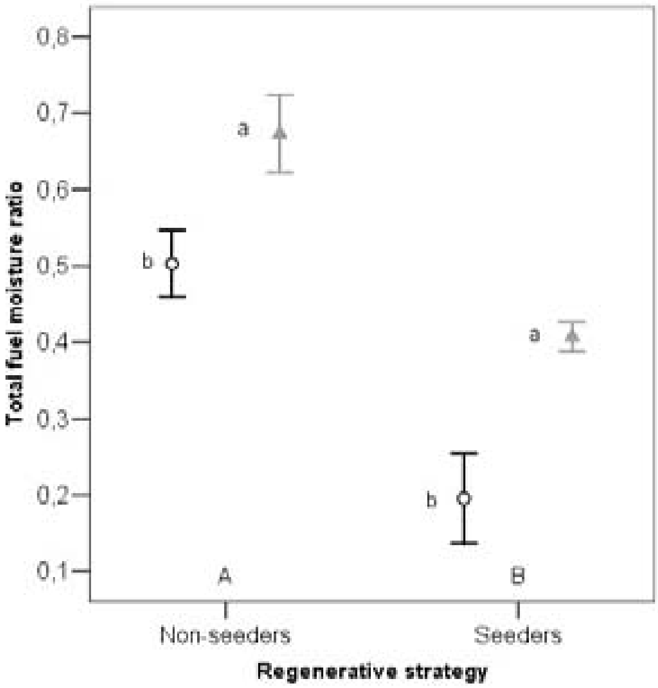


Figure 4. Means and standard error of total fuel moisture ratio. Means and standard errors are represented for each regenerative strategies (seeders and non-seeders) and for the two study sites (Murta and Montgri). Montgrí values are represented with circles (o) and Murta with triangles (▲). Significant differences ($p < 0.05$) are indicated with different letters. Upper case letters (A, B) indicate differences between regenerative strategies. Lower case letters (a, b) indicate differences among sites.

Table 3. Ratio of total weight (mean and standard error in brackets) for fuel fractioned in fine, coarse, dead and live fuel (all classes combined for all studied species). Leaves are included in the live fine fuel fraction.

		Fine < 6mm				**Coarse > 6 mm**				**Total**			
		Live		**Dead**		**Live**		**Dead**		**Live**		**Dead**	
		Montgri	**Murta**	**Montgri**	**Murta**	**Montgri**	**Murta**	**Montgri**	**Murta**	**Montgri**	**Murta**	**Montgri**	**Murta**
Seeder	*Calicotome spinosa*	0,36 (0,05)		0,29 (0,04)		0,11 (0,08)		0,39 (0,07)		0,61 (0,07)		0,39 (0,07)	
	Cistus albidus	0,44 (0,07)	0,46 (0,05)	0,18 (0,06)	0,18 (0,02)	0,31 (0,05)	0,35(0,04)	0,07 (0,04)	0,02 (0,02)	0,75 (0,10)	0,80 (0,02)	0,25 (0,10)	0,20 (0,02)
	Cistus monspeliensis	0,56 (0,11)	0,41 (0,04)	0,17 (0,06)	0,12 (0,02)	0,20 (0,05)	0,46 (0,03)	0,07 (0,07)	0,01 (0,01)	0,76 (0,12)	0,87 (0,03)	0,24 (0,12)	0,13 (0,03)
	Cistus salviifolius		0,24 (0,01)		0,24 (0,02)		0,51 (0,01)	0,11 (0,08)	0,01 (0,003)		0,75 (0,02)		0,25 (0,02)
	Dorycnium hirsutum	0,88 (0,03)		0,12 (0,03)		0,00		0,00		0,88 (0,03)		0,12 (0,03)	
	Dorycnium pentaphyllum	0,74 (0,03)		0,25 (0,04)		0,01 (0,01)		0,00		0,75 (0,04)		0,25 (0,04)	
	Fumana ericoides	0,88 (0,04)	0,89 (0,02)	0,11 (0,03)	0,11 (0,02)	0,01 (0,01)	0,00	0,00	0,00	0,89 (0,03)	0,89 (0,02)	0,11 (0,03)	0,11 (0,02)
	Fumana laevipes	0,97 (0,01)		0,03 (0,01)		0,00		0,00		0,97 (0,01)		0,03 (0,01)	
	Fumana thymifolia	0,95 (0,03)	0,77 (0,02)	0,01 (0,01)	0,23 (0,02)	0,03 (0,03)	0,00	0,00	0,00	0,99 (0,01)	0,77 (0,02)	0,01 (0,01)	0,23 (0,02)
	Globularia alypum	0,57 (0,09)	0,69 (0,02)	0,22 (0,05)	0,15 (0,01)	0,18 (0,03)	0,17 (0,03)	0,03 (0,02)	0,00	0,75 (0,07)	0,85 (0,01)	0,25 (0,07)	0,15 (0,01)
	Helichrysum stoechas	0,72 (0,06)		0,19 (0,04)		0,08 (0,03)		0,01 (0,01)		0,81 (0,05)		0,19 (0,05)	
	Rosmarinus officinalis	0,48 (0,06)	0,52 (0,03)	0,12 (0,03)	0,05 (0,01)	0,38 (0,03)	0,44 (0,03)	0,01 (0,01)	0,00	0,86 (0,03)	0,95 (0,01)	0,14 (0,03)	0,05 (0,01)
	Teucrium polium	0,80 (0,05)	0,66 (0,05)	0,16 (0,04)	0,34 (0,05)	0,05 (0,02)	0,00	0,00	0,00	0,84 (0,04)	0,66 (0,05)	0,16 (0,04)	0,34 (0,05)
	Thymus vulgaris	0,83 (0,03)	0,80 (0,04)	0,07 (0,04)	0,18 (0,03)	0,10 (0,02)	0,02 (0,02)	0,00	0,00	0,93 (0,04)	0,82 (0,03)	0,07 (0,04)	0,18 (0,03)
Non-seeder	*Coronilla minima*	0,79 (0,04)	0,73 (0,03)	0,17 (0,03)	0,26 (0,02)	0,04 (0,02)	0,01 (0,01)	0,00	0,00	0,83 (0,03)	0,74 (0,02)	0,17 (0,03)	0,26 (0,02)
	Daphne gnidium	0,55 (0,09)	0,30 (0,07)	0,07 (0,03)	0,10 (0,02)	0,36 (0,06)	0,51 (0,04)	0,02 (0,01)	0,08 (0,04)	0,91 (0,04)	0,81 (0,06)	0,09 (0,04)	0,19 (0,06)
	Osyris alba	0,68 (0,06)	0,49 (0,01)	0,24 (0,05)	0,06 (0,01)	0,07 (0,05)	0,45 (0,01)	0,00	0,00	0,76 (0,05)	0,94 (0,01)	0,24 (0,05)	0,06 (0,01)
	Phillyrea angustifolia	0,39 (0,03)	0,47 (0,03)	0,03 (0,01)	0,09 (0,01)	0,57 (0,02)	0,44 (0,02)	0,01 (0,003)	0,003(0,002)	0,96 (0,01)	0,90 (0,01)	0,04 (0,01)	0,10 (0,01)
	Pistacia lentiscus	0,39 (0,06)	0,47 (0,01)	0,07 (0,01)	0,09 (0,004)	0,50 (0,05)	0,42 (0,02)	0,04 (0,02)	0,01 (0,003)	0,89 (0,03)	0,89 (0,01)	0,11 (0,03)	0,11 (0,01)
	Quercus coccifera	0,50 (0,01)		0,11 (0,01)		0,39 (0,01)		0,00		0,89 (0,01)		0,11 (0,01)	
	Rhamnus alaternus	0,36 (0,05)	0,43 (0,03)	0,07 (0,02)	0,12 (0,01)	0,55 (0,04)	0,45 (0,02)	0,01 (0,01)	0,005 (0,003	0,91 (0,03)	0,87 (0,02)	0,09 (0,03)	0,13 (0,02)
	Rhamnus lycioides		0,35 (0,03)		0,18 (0,02)		0,40 (0,02)		0,06 (0,01)		0,76 (0,03)		0,24 (0,03)

Flammability

Regenerative groups significantly differ on the temperature to reach the smoldering and flaming phases while time to reach smoke phase was marginally significant (Table 4). Seeders show lower smoldering and flaming temperatures and higher time to smoke than non-seeders (Figure 5). Repeated-measures analysis of differences in temperatures among time gives support to the obtained results since the main difference between seeders and non-seeders is that seeders inflame (get flaming phase) at lower temperatures and they have lower increments of temperature among time (Table 5, Figure 6). No differences where found among study sites for any flammability variable (Table 4 and Table 5).

Table 4. Summary of results for GLM accounting for the variation in temperature and time needed to reach the phases of smoke, smoldering and flaming. Two fixed-effects: regenerative strategy (seeder and non-seeder) and site (Montgrí and Murta); and two covariates: leaf moisture (LM) and surface to volume ratio of the leaf (S :V) were considered in this statistical analysis.

	Temperature						**Time**					
	Smoke		**Smoldering**		**Flaming**		**Smoke**		**Smoldering**		**Flaming**	
	F	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
LM	5,210	0,032	1,576	0,221	5,436	0,029	14,428	0,001	0,382	0,542	7,427	0,013
S:V	7,071	0,014	1,485	0,235	0,239	0,630	13,773	0,001	3,994	0,057	0,427	0,521
Regenerative strategy	1,421	0,245	9,686	0,005	5,114	0,034	3,961	0,058	2,241	0,147	0,628	0,438
Site	4,200	0,052	1,222	0,280	0,673	0,421	1,148	0,295	0,078	0,783	1,102	0,307
Reg. strategy x Site	0,767	0,390	0,316	0,579	0,971	0,335	0,038	0,847	0,005	0,946	0,323	0,576

Table 5. Summary of results of the Repeated-Measures ANOVA considering Temperature as the dependent variable and flammability phase (FP) (smoke, smoldering and flaming) as the within-subject factor. Two between-subject factors (regenerative strategy and site) and two covariates (LM and S : V) were considered in the model.

	Without S:V and LM		**With S:V and LM**	
	F	**p**	**F**	**p**
Regenerative strategy	4,898	0,037	6,903	0,015
Site	0,367	0,550	0,045	0,833
Reg. Strategy x Site	0,312	0,582	0,890	0,356
FP	93,854	0,000	5,035	0,011
FP x Reg. Strategy	2,880	0,066	4,303	0,020
FP x Site	0,099	0,906	1,346	0,271
FP x Reg. Strategy x Site	0,057	0,945	0,895	0,416

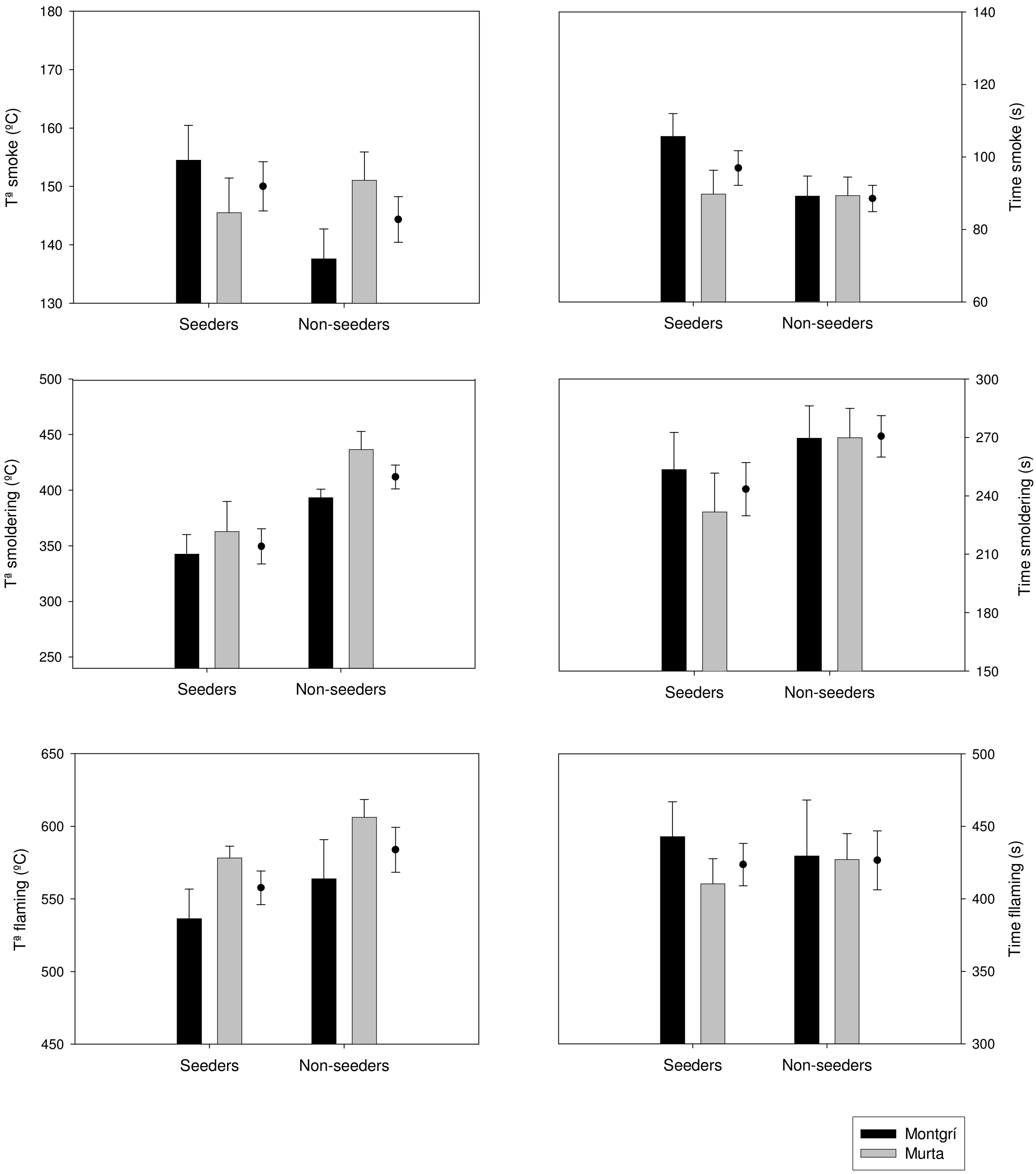


Figure 5. Mean and standard errors of temperature and time needed to achieve the flammability phases: smoke, smoldering and flaming. Values are drawn for each regenerative strategy (seeders and non-seeders) and site (Montgrí and Murta). Mean and standard error of each regenerative strategy is drawn with a black circle after pooling the data of both sites for each species. For statistical analysis see Table 4.

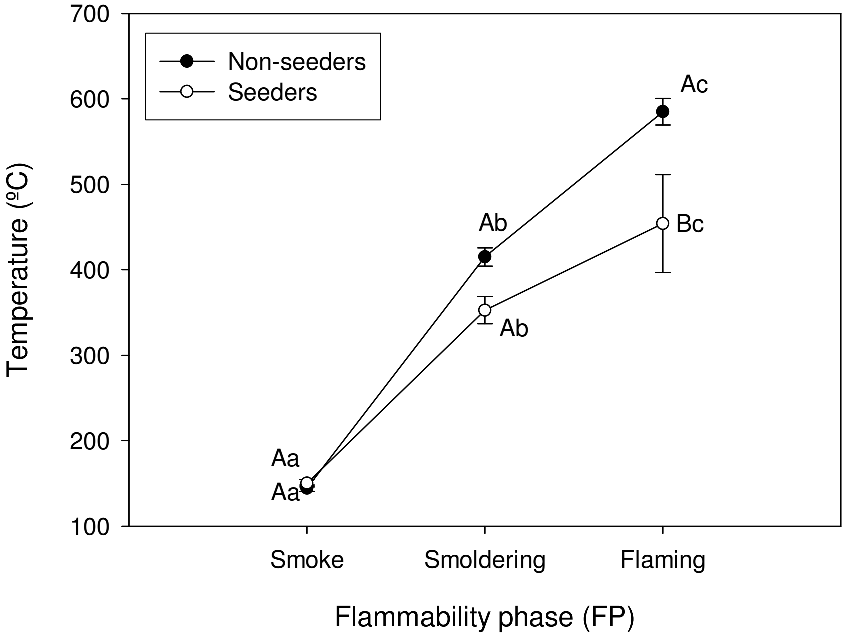


Figure 6. Mean and standard error of temperature needed to achieve each flammability phase for the two regenerative strategies. Low letters indicate the results from the post-hoc Fisher LSD analyses. Letters indicate differences among flammability phases for each regenerative strategy and capital letters indicate differences between regenerative strategies for each time (Post-hoc Fisher LSD, repeated-measures ANOVA including leaf moisture and leaf surface:volum as covariates.

Plants did not present significant differences between leaf moisture among regenerative strategies, but it was significantly higher in Montgrí than Murta (mean +/- s. e.: Montgrí = 1.18 +/- 0.1; Murta = 0.80 +/- 0.09 , Table 6). S : V was not significant different between regenerative strategies and neither interactions between site and regenerative strategies were found (Table 6).

Table 6. Summary of results for the 2-factor ANOVA with LM and S :V as dependent variables, and two fixed effects (regenerative strategy: seeder and non-seeder; and site: Murta and Montgrí).

	LM		**S:V**	
	F	**p**	**F**	**p**
Regenerative strategy	0,132	0,720	0,036	0,850
Site	6,246	0,019	2,335	0,139
Reg. Strategy x Site	2,042	0,165	1,607	0,216

Leaf moisture plays a significant role determining temperature and time to smoke and flaming but there was no effect to reach the phase of smoldering (Table 4, Fig 7a, 7b). S : V, significantly reduced the time and the temperature to reach smoke (Table 4, Fig. 7c, 7d).

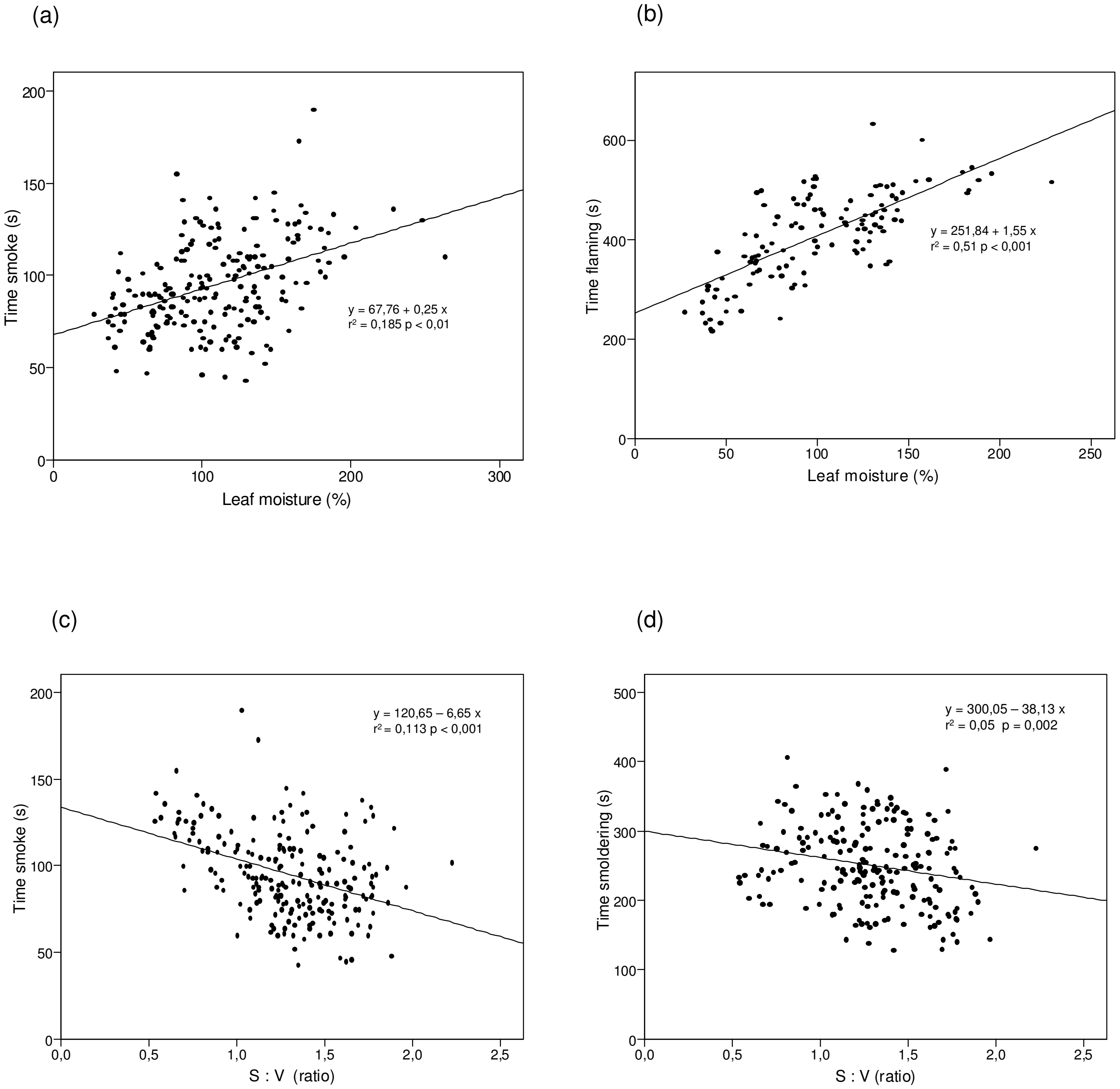


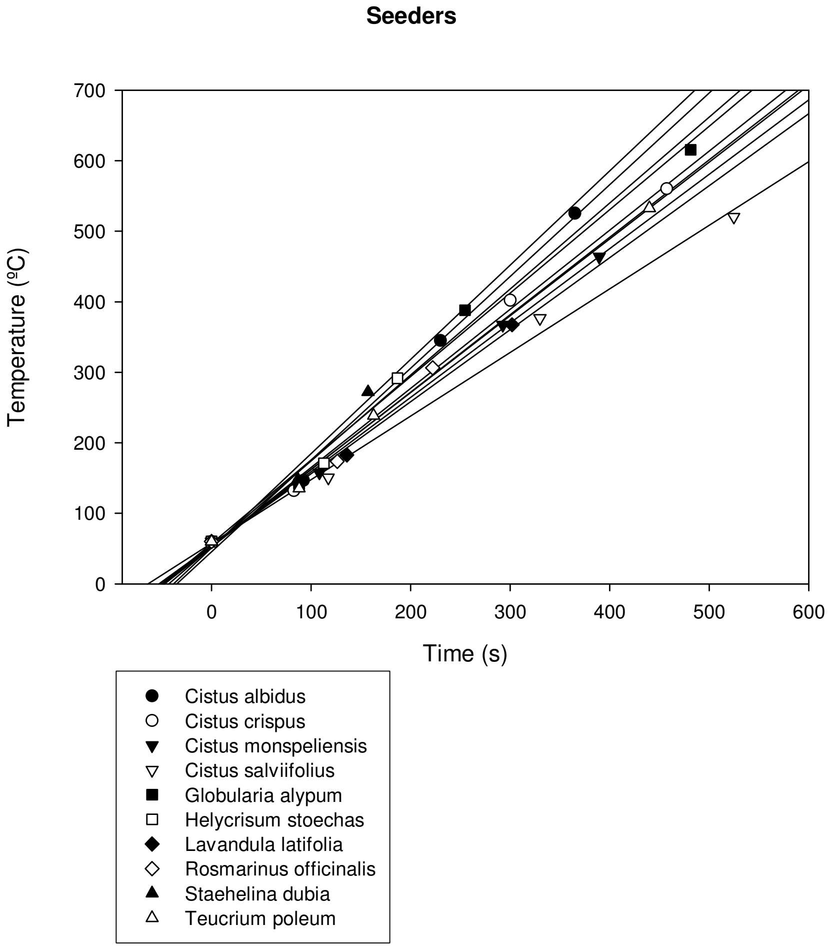
Figure 7. Relationship between time to achieve smoke phase (a) and flaming phase (b) and leaf moisture; and between time to achieve smoke phase (c) and smoldering phase (d) and S : V ratio, following a linear regression for species from Montgrí site. S : V ratio was transformed to its Ln (x) to better approximate normality.

There were not significant differences, among the two regenerative groups, in the slopes of regressions between temperature and time to attain the different flammability stages shown (Table 7 and Figure 8a and 8b). Temperature and time relationship is a fixed relation, and it was expected that species differ in time to get different phases but not in the relation between temperature and time. Regressions were defined by three points, so that statistical power may be low.

No significant effect of the taxonomical affiliations were found in any of the studied variables, suggesting that taxonomical effects did not explain the variability found between regenerative strategies.

Table 7. Summary of the linear regressions between time and temperature for all the study species

Study Species	Regenerative strategy	R^2	b	p
Cistus albidus	S	0,982	1,160	0,009
Cistus crispus	S	0,980	1,055	0,091
Cistus monspeliensis	S	0,988	1,054	0,069
Cistus salviifolius	S	0,983	0,877	0,083
Coronilla minima	NS	0,987	0,870	0,074
Daphne gnidium	NS	0,970	1,123	0,111
Globularia alypum	S	0,969	1,183	0,113
Helichrysum stoechas	S	0,985	1,107	0,079
Lavandula latifolia	S	0,996	0,966	0,039
Lonicera implexa	NS	0,958	1,219	0,131
Olea europaea	NS	0,891	1,165	0,215
Phillyrea angustifolia	NS	0,924	1,236	0,178
Pistacia lentiscus	NS	0,971	1,085	0,110
Quercus coccifera	NS	0,898	1,166	0,207
Quercus ilex	NS	0,939	1,066	0,159
Rhamnus alaternus	NS	0,942	1,221	0,155
Rosmarinus officinalis	S	0,988	1,004	0,070
Smilax aspera	NS	0,942	1,011	0,155
Staehelina dubia	S	0,977	1,179	0,097
Teucrium polium	S	0,989	1,023	0,005



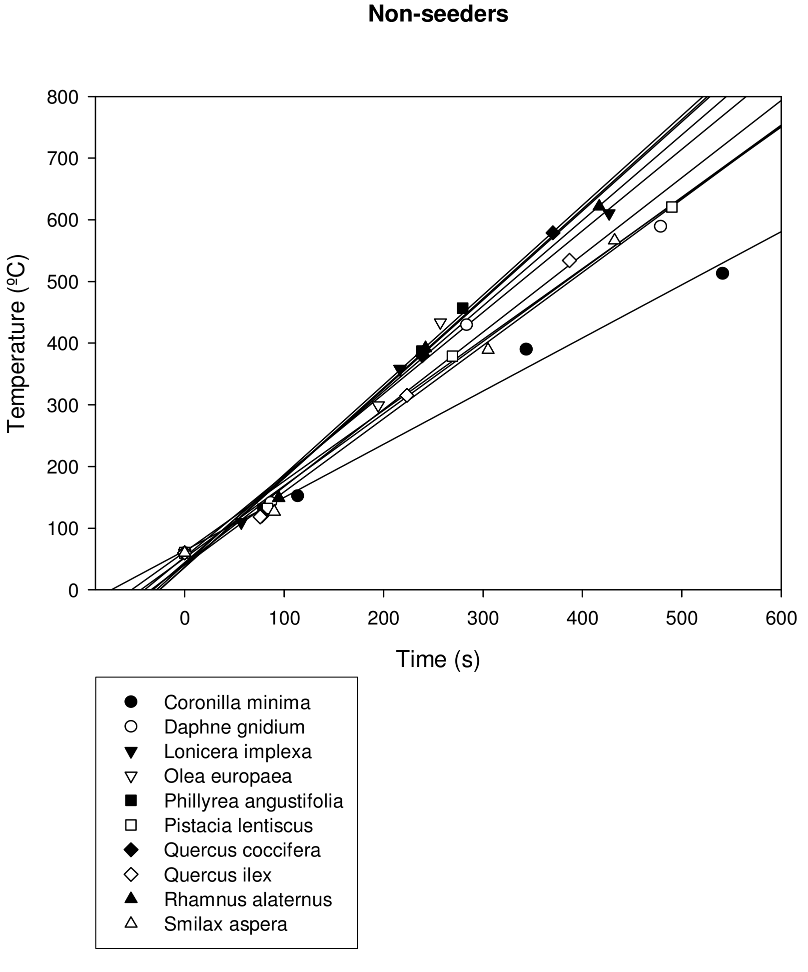


Figure 8. Linear regression between the three studied temperatures and times (smoke, smoldering and flaming) for each one of the studied species in Montgrí study site. Each point is the mean of all replicates per species. Some species present four points (Phase O, phase I, phase II and phase III) but some species present only three because they did not present presence of flame so that phase III of flaming was not contempled. Figure 8a is the representation of the group of seeders and 8b the group of non-seeders.

PCA clearly illustrated the most significant variables and their differences between species and regenerative strategies (Figure 9). Seeders are species with lower temperature to achieve flaming phase, and higher dead fine fuel proportion. *Phillyrea angustifolia* is the only species that appears separated from both groups probably because it showed very low moisture and high S :V.

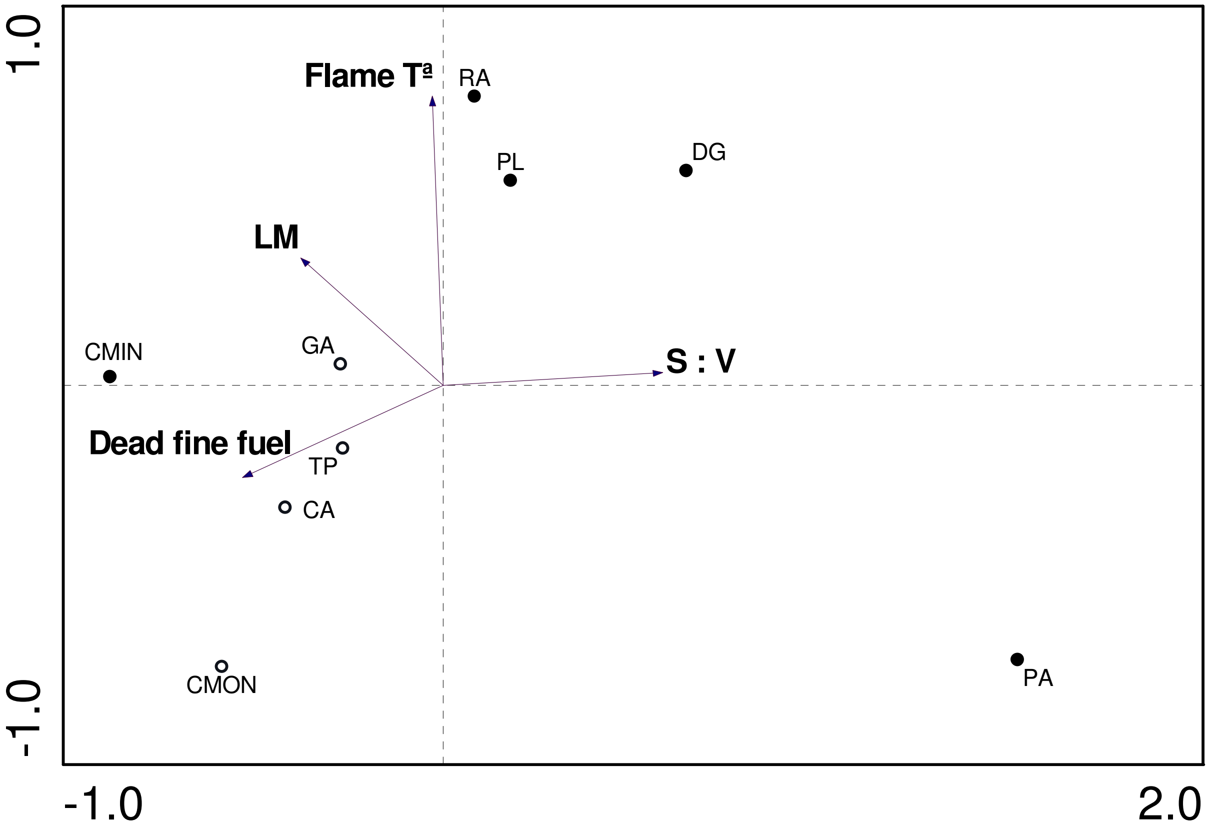


Figure 9. Principal Components Analysis for the studied variables: S : V ratio, leaf moisture, time to achieve flaming phase and dead fine fuel moisture in Montgrí site. Axis 1 explains 46.2% of variation in the total data set while axis 2 explains 26.7 %.
White circle symbols represent seeders and black circles simbolize non-seeders.

DISCUSSION

The measure of fuel loading by size classes is a useful approach for estimating the fuel available to feed a fire. Ignition becomes easier with thinner material due to the higher contact of fuel with atmospheric oxygen. In contrast, the ignition of large materials is energetically more expensive than the ignition of fine materials (Papió & Trabaud, 1991; Viegas *et al.*, 2001). Seeders show a higher proportion of fine dead material and less moisture content than non-seeders. Therefore, species with thinner and dryer material, such as seeders, favor fire spread and they are a better source of heat increasing fire hazard. Seeders are also species of rapid combustion, as suggested by lower smoldering and flaming temperatures of leaves, while non-seeders have more coarse fuel, promoting longer but slower fires (Andrews & Bevins, 2003). The absence of differences between the two localities confirms that this pattern is mostly due to intrinsic properties of species and not to phenotypic plasticity linked to local conditions. The only variable with differences between sites is plant and leaf fuel moisture and it is probably due to climatologic differences at the time that sampling was conducted.

This study indicates that seeders of the studied community show lower biomass than non-seeder. This trait agrees with the life-strategy of the studied seeders, characterized by a short-life span, a high reproduction effort, and relatively high seedling establishment, while non-seeders would show the opposite syndrome (high biomass, low investment in reproduction, but high survival after fire thanks to the resprouting capacity) (Lloret, 1998; 2004).

Low water content of leaves was determinant to achieve pyrolisis and to produce flame more easily and high S : V contributed to achieve pyrolisis and ignition. Leaves with higher S : V reach the temperature and time needed to achieve the flammability phases more easily since they have higher surface for heat accumulation, and to get in contact with oxygen. This pattern seems to indicate that the ignition (smoldering phase) depend more on intrinsic plant properties such as the leaf morphology while leaf water content, a variable that depends more on the environmental conditions, is more determinant to produce flame.

Other components of flammability, such as chemical composition (i.e. percent mineral contents) , and volatile compounds were not recorded in this study, but some information on mineral nutrients (Saura-Mas & Lloret, chapter 3) suggests that the studied seeders present more content of some minerals such as Calcium and Phosphorous. This may contribute to explain the higher seeders flammability (lower temperatures to achieve flammability phases), compared to non-seeders (Philpot, 1970).

Among regeneration traits, resprouting can hardly be seen as a ‘fire adaptation’, because it is a widespread trait in angiosperms, present in old lineages (Lloret *et al.*, 1999). In the Mediterranean basin, most of the resprouting species appeared during the Tertiary, before the Mediterranean climate appeared (Herrera, 1992; Verdú *et al.*, 2003; Pausas & Verdú, 2005). Seeder lineages diversified during the Quaternary, and their ability to abundantly germinate after disturbances may be due to fire and Mediterranean climate with summer drought. Both types of environmental variability likely became more prevalent during this period (Jalut *et al.*, 2000; Scott, 2000; Scott, 2002). In recent years, there has been an intense debate about the evolution of flammability. Some authors maintain the hypothesis that plants in fire-prone ecosystems have evolved flammability, based on the idea of existence of plants “born to burn” so that the plants with higher flammability properties, are plants with higher fitness in fire-prone habitats (Mutch, 1970; Zedler, 1995; Bond & Keeley, 2005; Bond *et al.*, 2005). This study supports the hypothesis that seeders exhibit more flammable characteristics than non-seeder. However, some authors point that fire may not be the only throttle for diversification in fire-prone Mediterranean ecosystems (Verdú *et al.*, 2007). Certain chemical and physical properties of the plant that might be related to flammability could also be the results of physiological and morphological responses to other environmental constraints typically found in Mediterranean ecosystems, with seasonal high temperatures, low water storage and great radiation (Arnan *et al.*, 2007; Lloret *et al.*, 2007). In fact in many communities of the western Mediterranean basin seedling recruitment of these species is not exclusively fire-dependent, (Lloret, 1998; Lloret *et al.*, 2005b) (Lloret, *personal observation*). Thus, flammable properties of seeders could allow them to survive and enhance population establishment after fires and other disturbances but also after climatic events such as drought periods.

This study suggests that seeders need less energy to inflame, enhancing fire-risk. Although the heat released by the combustion of seeders was not measured, other studies (Heim, 1974; Elvira, 1989) and the lower fuel load documented in this study suggest that these species may have lower specific heat power promoting low to moderate temperatures. This moderate fire intensity would enhance seed germination, but without achieving the high temperatures that deplete seed viability (Fenner, 1992; Salvador & Lloret, 1995; De Luis *et al.*, 2005). As a result, this strategy could promote a positive feed-back to maintain seeders populations as it has been suggested in Mediterranean grassland ecosystems dominated by *Ampelodesmos mauritanica*

(Grigulis *et al.*, 2005). More detailed studies of specific heat power of the different plants are required to better approach this hypothesis of fire promoting characteristics depending on the post-fire regenerative strategy.

In conclusion, seeders are more flammable than non-seeders with lower temperature to inflammability and rapid combustion, which is related to the high percentage of fine and dead fuel. As a result, ecosystems dominated by seeder species will be more susceptible to fire-risk than ecosystems dominated by non-seeder species. Also, seeder species show lower fuel load that is likely to result in less intense fires, easier to be fought. On the opposite, non-seeders need higher temperatures to start combustion, and the high amounts of fuel load may become in wildfires more difficult to extinct. Therefore, the proportion of these types of species resulting from previous fire or management history is likely to determine the characteristics of future fire events.

ACKNOWLEDGEMENTS

I would like to thank M. Jané, E. Martí, A. Vila, J.Garcia, B. Moreira, and C. Beseler for helping in the field and in the lab. Especial thanks go to J. Font for his knowledge of the Montgrí and its flora, and J. Piñol, J. Pausas, S. Paula and G. Alessio for their advice and suggestions. This study was funded by the Department of Universities, Research and Information Society of the Generalitat de Catalunya, the European social funds, and the Spanish MCYT projects REN 2003-07198 and CGL2006-01293/BOS. It also contributes to the European research group (GDRE) “Mediterranean and mountain ecosystems in a changing world” funded by the Generalitat de Catalunya and CNRS.

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VII. LEAF LITTER DECOMPOSITION: RESPONSES TO CLIMATE CHANGE

The main contents of this chapter are in preparation to be submitted as:
Saura-Mas, S., Lloret, F. Estiarte, M., Peñuelas, J. Leaf litter decomposition: climate change effects and differences between post-fire regenerative groups.

ABSTRACT

- Decomposition is determinant for ecosystems production because litter dynamics (litter fall and litter decomposition) constitute a key process for the functioning of ecosystems, regulating the recycling of carbon and nutrients in the ecosystem.

- Here, I study litter decomposition properties of a set of 19 Mediterranean basin woody species with different post-fire regenerative strategies (resprouters and non-resprouters) and under experimental climate manipulation (simulating warming and drought) during a 2-year period.

- Litter invests to the soil (g/year) are lower under drought conditions, being also influenced by the taxonomical affiliation of the species. Two years after the start of the experiment, the mass loss of the resprouters litter was lower than in the other groups, being the taxonomical affiliation of the species determinant for this pattern.

- Non-resprouters show higher nutrients concentration per mass of leaf litter after 2 years of experiment than resprouters, possibly because seeders have lost more mass while nutrients remain more concentrated in the remaining leaf litter. The N:P ratio was lower in non-resprouters than in resprouters .

- The expected future increment of drought in Mediterranean ecosystems altering soil humidity and biota conditions may also change functional properties of ecosystems. This study suggests that nutrients return from leaf litter to the soil will be slower. Furthermore, changes in the fire regimes conducting to modifications in the abundance of post-fire regenerative groups are likely to affect functional properties of the ecosystem. Thus, if new fire regimes enhance non-resprouters' abundance, higher return of invests to the soil and lower litter N:P is expected to occur than in communities dominated by resprouter species.

Key words:
Climate, decomposition rate, drought, k, leaf litter, Mediterranean type-ecosystems, post-fire, regeneration, warming.

INTRODUCTION

Future climatic predictions anticipate further warming and aridification over the coming decades in the Mediterranean regions (Peñuelas *et al.*, 2004b; IPCC, 2007). Mediterranean shrublands occupy extensive areas of the Mediterranean region (Moreno & Oechel, 1995; Riera *et al.*, 2007) and the availability of water is a key factor determining vegetation composition and patterns of plant distribution in these ecosystems. In fact, a trend to progressive aridification has taken place over the last few decades in Catalonia (North-east of the Iberian peninsula) as a result of increased evapotranspiration (caused by 1ºC average warming) without any parallel increase in rainfall (Piñol *et al.*, 1998; Peñuelas *et al.*, 2002; Peñuelas & Boada, 2003).

Litter dynamics (litter fall and litter decomposition) constitute a key process in the ecosystems functioning, and it determines the recycling of carbon and nutrients in the ecosystem. Litter fall represents an output of nutrients from the aerial parts of the plants, and also an input of nutrients to the soil. Subsequent decomposition is the route by which part of the carbon fixed by plants and nutrients are partially incorporated in to decomposers biomass, incorporated to the soil as inorganic nutrients or returned to atmosphere as CO_2. Thus, this process releases carbon to the atmosphere and nutrients in forms that can be used for plant and microbial production (Chapin III *et al.*, 2002; Gartner & Cardon, 2004). This conversion of dead organic matter (leaf litter) is done through the action of leaching (that removes soluble materials from decomposing organic matter), fragmentation (by soil animals that breaks large pieces of organic matter into smaller ones and mixes the decomposing organic matter into the soil) and chemical alteration (that is primarily done by the activity of bacteria and fungi). Thus, decomposition rate is regulated by a set of factors that affect soil biota activity: physical environment (mainly the climate), litter composition and substrate nutrients.

Decomposition is determinant for ecosystems production and there is a significant positive lineal relationship between decomposition rate and relative growth rate for different types of communities, including shrublands (Cebrián & Duarte, 1994; Cebrián & Duarte, 1995). Moreover, the balance between net primary production and decomposition strongly influences carbon and nutrients cycling at ecosystem scale (Chapin III *et al.*, 2002). Consequently, decomposition is a key factor to better understand effects of climate change, particularly those involving growth as well as carbon and nutrients cycles.

Drought and warming produce aridity and it can also increase the threat of wildfires in the Mediterranean basin. The frequency of wildfires has increased over the last few decades as a result of climate change and changes in land use and human socioeconomic activities (Piñol *et al.*, 1998; Pausas, 2004). Wildfires are an important disturbance in the evolution and dynamics of most Mediterranean-type ecosystems (Hanes, 1971; Whelan, 1995; Lloret *et al.*, 2002) and most Mediterranean woody species show mechanisms to regenerate after fire.

In the Mediterranean basin, the group of resprouters (S- R+, S+ R+ *sensu* Pausas *et al.*, 2004; Pausas & Verdú, 2005) is mostly constituted by long-lived species, typically found in late successional shrublands, that often show a high percentage of individuals that survive and resprout after fire, while they do not show significant recruitment of new individuals shortly after wildfire. In contrast, non-resprouters (S+ R-) show a shorter life cycle and a higher recruitment after disturbances such as fire or drought (Pate *et al.*, 1990; Verdaguer & Ojeda, 2002; Knox & Clarke, 2005; Schwilk & Ackerley, 2005). Thus, long-lived resprouters are expected to show a higher resource allocation to underground organs in order to sustain plant re-growth (Knox & Clarke, 2005), while short-lived non-resprouters would have shorter leaf life span, and higher photosynthetic rates (Bell, 2001; Ackerly, 2004), similarly to early successional species of mesic forests (Bazzaz, 1979). These traits are expected to be reflected on the leaf litter decomposition of these groups of species. These differences could be reinforced due to differences in leaves properties such as lower leaf dry matter content and higher seasonal re-hydration capacity in seeders versus resprouters (Saura-Mas & Lloret, 2007b).

To study the possible consequences of climate change in leaf litter decomposition of Mediterranean basin shrublands, I used a combination of manipulation experiment altering both temperature and rainfall to quantify the effect of warming and prolonged summer drought (the two main effects of climate change). Our second objective was to determine differences on the decomposition of plant litter between different post-fire regenerative groups. I hypothesized that resprouter species would have a lower leaf litter decomposition because they have higher leaf dry matter content (Saura-Mas & Lloret, 2007b). Interaction between post-fire regenerative strategy and climate warming to leaf litter decomposition was also considered. This study also tests the hypothesis that potential decomposition rate of leaf litter can be predicted from whole plant features that reflect the functioning of the plants in their natural environments. Thus, life-form traits were also considered because other related unpublished study and personal observations suggest that this trait affect functional properties of the species living in the studied community. The taxonomical affiliation of species were also considered since differences among functional properties of post-fire regenerative groups could be linked to their evolutionary history (Verdú, 2000; Pausas & Verdú, 2005; Saura-Mas & Lloret, 2007a; Verdú *et al.*, 2007).

MATERIALS AND METHODS

Species sampling

The study was carried out on a subset of 19 woody plant species growing in coastal shrublands over limestones. They were representative of the community and belonged to as many different families, life form types and post-fire regenerative groups as possible (Table 1). Depending on their post-fire regenerative strategy (Cucó, 1987; Papió, 1988; Lloret & Vilà, 1997; Verdú, 2000; Alberdi & Cavero, 2003; Lloret *et al.*, 2003), and after direct field observations in a close area burned in September 2004, species were classified into two post-fire regenerative groups: resprouters (R: S- R+, S+ R+) and non-resprouters (S+ R-). Freshly senescent leaves were collected from the plants of the different species through March 2003 to March 2004. The time of the year of collection depended on their phenology (Floret *et al.*, 1989).

Leaf litter was collected in the Montgrí Massís (except for *Arbutus unedo* and *Globularia alypum*, which were collected in Garraf), a protected coastal area located in the NE of Catalonia, (north-east Iberian Peninsula, 42.16ºN, 3.24ºW).

Vegetation is mainly constituted by open pine forests and shrublands, dominated by *Quercus coccifera*, *Cistus albidus*, *Cistus monspeliensis*, and *Rosmarinus officinalis* (Polo & Masip, 1987) The annual precipitation is 655 mm, with cool winters and warm summers (mean annual temperature: 14.8ºC) (Ninyerola *et al.*, 2000; Ninyerola *et al.*, 2003). Sampling was conducted in mature shrubland (1-2 m high) that had been untouched by wildfire for over 10 years.

The Montgrí community has been sampled for the characterization of different leaf attributes (Saura-Mas & Lloret, 2007b) of the main species, while Garraf was the nearest site with the same type of ecosystem (coastal shrubland on limestone) with an established experimental setting of climate manipulation (Peñuelas *et al.*, 2004a). Thus, the experiment was located in Garraf, a protected coastal area located in the NE of Catalonia, (north-east Iberian Peninsula, 41.19ºN, 1.49ºW). The vegetation is similar to the Montgrí shrubland, and it is mainly dominated by *Quercus coccifera*, *Globularia alypum, Erica multiflora* and *Rosmarinus officinalis*. The annual precipitation is 455 mm, with cool winters and warm summers (mean annual temperature: 15.1ºC). The study area soil type is described as a petrocalcic calcixerept soil (pH = 8.2) with low organic matter quantities in the upper soil horizons (7.8 %).

Experimental design

Climate treatments

Nine experimental plots (5 m x 4 m) (Photograph 1) were established in relatively homogeneous areas within Garraf study area. Three treatments were allocated: control (C), warming (W), and prolonged drought during the growing season (D). Around each plot, a light scaffolding structure was built of galvanized steel tubes covered by thin plastic sleeves to prevent contaminants from leaching into the plot. In the warming plots, this frame supports a retractable, reflective curtain made of strips of infrared-reflective material bound into a high-density polyethylene mesh. A small motor activated by a light sensor extends this curtain over the vegetation at night thus preventing heat loss. In this warming treatment, a tipping bucket rain sensor retracts the curtain at night to enable rain to enter the plot. To prevent damage to the cover, a wind sensor activates the retraction of the curtain at night if wind speeds exceed 10 m/s. Over the drought plots, a retractable curtain made of transparent polyethylene plastic prevents rainfall during the main growing seasons, between March and June in spring, and between September and December in autumn. Rain sensors activate the motor to extend this cover over the plots when rain is detected and to retract the cover when the rain stops. When the curtain is extended, wind sensors again retract the curtain to prevent damage during periods of high wind. This climate change experiment is functioning since 1999.

The effect of the warming treatments on mean air temperature (measured at 20 cm above the soil) was 0.59ºC in 2004, 0.68ºC in 2005 and 0.68ºC in 2006 (treatments in 2006 are considered from January to September, when the experiment was set out). The effect of the warming treatments on mean soil temperature (measured at 5 cm depth from the surface of the soil) was 0.66ºC in 2004, 0.78ºC in 2005 and 0.60ºC in 2006. The growing season drought treatment reduced precipitation by 48.87 % (2004, 155 days of treatment), 47.21 % (2005, 154 days of treatment), and 4.21 % (2006, 33 days of treatment) (Figure 1).

All measurements of climate variables and experimental design were made in an inner 4.5 m x 3.5 m plot avoiding an outer 0.5 m buffer to avoid edge effects.

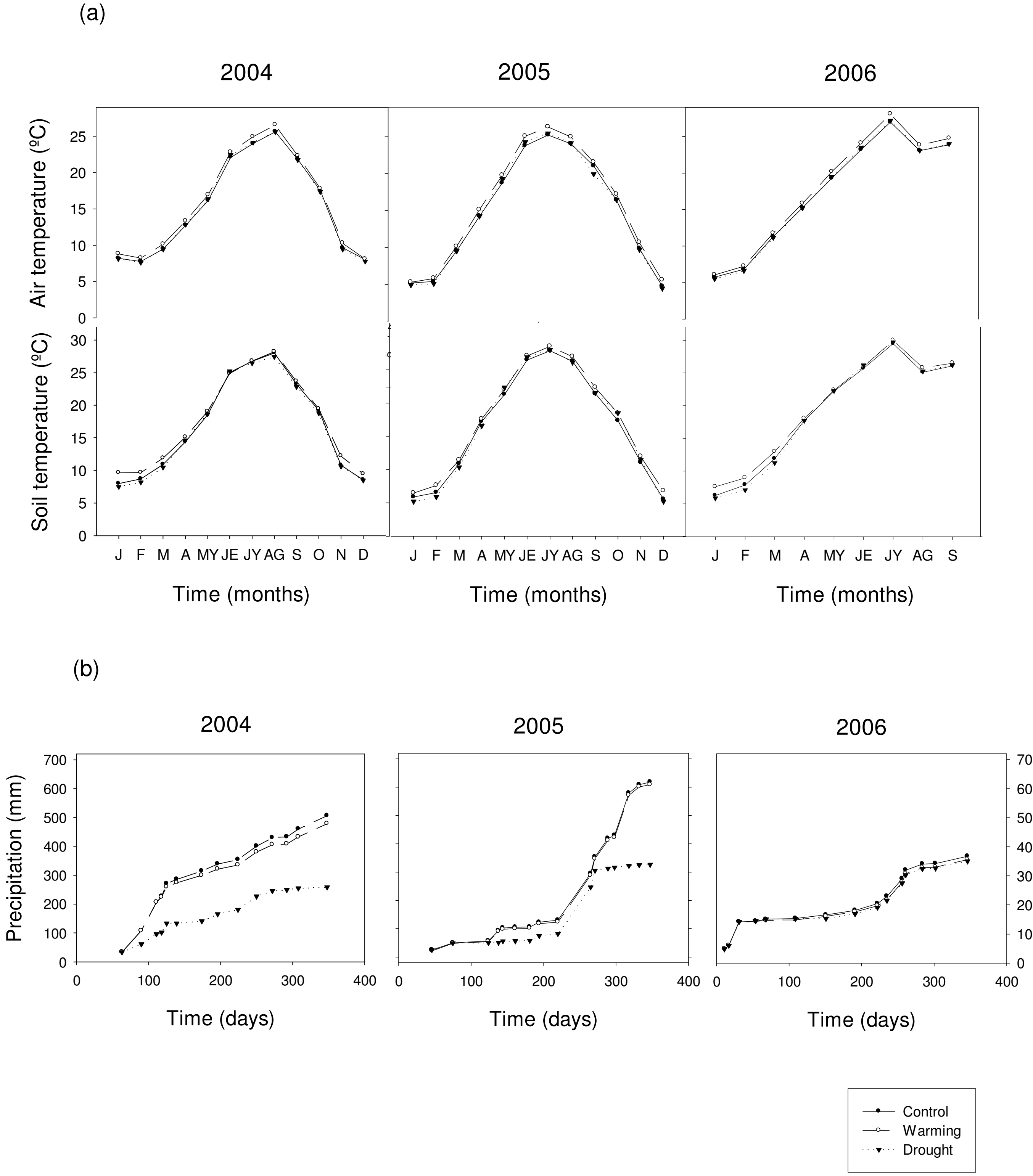


Figure 1. Temperatures and precipitation reached in each treatment in the years of the experiment. (a) Mean monthly soil temperature (5 cm depth) and air temperature (15 cm above ground). (b) Accumulated precipitation among the year.

Photograph 1. One of the nine climatic experimental plots.

Photograph 2. A litter bag used during the experiment.

Field decomposition

Decomposition experiments were carried out using the mesh bag technique placed over the soil surface (Gallardo & Merino, 1993; Murphy *et al.*, 1998; Kazakou *et al.*, 2006). Decomposition bags were 10 cm x 9 cm and made of 0.5 mm nylon mesh. Mesh size was small enough to prevent major losses of the smallest leaves, and yet large enough to permit microbial and fungi activity and free entrance of small soil animals (Killham, 1994; Lavelle, 1996).

Between 1 and 2 g of air-dried leaf litter of the 19 woody species (Table 1) was added to each handmade nylon mesh bag and the resulting mass was recorded (Photograph 2). The bags were sealed with stainless steel staples and labeled with aluminum tags.

Table 1. Study species, family, post-fire regenerative strategies and life-form (according to Raunkiaer classification). Chamaephyte = C, Nano-phanerophyte = NP, Macro-phanerophyte = MP, Phanerophyte-Vine = PV. [1] indicates that the study species was only considered in the non-treated experiment.

			Regenerative strategy		
Study Species	**Family**	**Species abbreviation**	**Seeding**	**Resprouting**	**Life form**
Arbutus unedo L.	Ericaceae	Au	-	+	MP
Cistus albidus L.	Cistaceae	Ca	+	-	NP
Cistus monspeliensis L.	Cistaceae	Cmo	+	-	NP
Cistus salviifolius L.	Cistaceae	Cs	+	-	NP
Daphne gnidium L.[1]	Thymelaeaceae	Dg	-	+	NP
Dorycnium hirsutum (L.) ser. In DC.	Leguminosae	Dh	+	+	NP
Dorycnium pentaphyllum Scop.	Leguminosae	Dp	+	+	NP
Fumana thymifolia L.[1]	Cistaceae	Ft	+	-	C
Globularia alypum L.	Globulariaceae	Ga	+	+	NP
Juniperus oxycedrus L.	Cupressaceae	Jo	-	+	MP
Lavandula latifolia Med.	Labiatae	LL	+	+	C
Phillyrea angustifolia L.	Oleaceae	Pa	-	+	NP
Pistacia lentiscus L.	Anacardiaceae	PL	-	+	MP
Quercus coccifera L.	Fagaceae	Qc	-	+	NP
Quercus ilex L.	Fagaceae	Qi	-	+	MP
Rhamnus alaternus L.	Rhamnaceae	Ra	-	+	MP
Rosmarinus officinalis L.	Labiatae	Ro	+	-	NP
Smilax aspera L.	Liliaceae	Sa	-	+	PV
Staehelina dubia L.	Compositae	Sd	+	+	C

Two decomposition experiments were performed, one within plots with climatic treatment (climatic experiment hereafter) and another outside the treated plots (non-treated experiment hereafter).This second experiment was performed to obtain additional information of the decomposition of each species along time. Experiments were set up on 6th September 2004 and finished after two years, on 6th September 2006.

For the climatic experiment, two bags for each species (except for *Daphne gnidium* and *Fumana thymifolia* because of the lack of enough leaf litter) were placed, in randomly selected sites, in each one of the nine experimental plots. One bag per species and plot were collected after 0.17 and 2 years of incubation (3 replicates per species, treatment and time).

For the non-treated experiment, 16 litter bags per especies were randomly placed outside the treatment plots and four replicates per species were collected after 0.17, 0.5, 1.17, 2 years of incubation. *Fumana thymifolia* had only three replicates, because it was not possible to obtain enough material, due to the small plant and leaf size.

Thus, a total of 608 litter bags were placed in the study area

Laboratory analysis

Samples were oven-dried at 60ºC for 24 hours immediately upon return from the field. After removal of litter from the bags, remaining litter was weighed to the nearest 0.0001 g and % of remaining mass was calculated as: remaining mass (t=2) / initial mass (t=0)).

Each individual sample was ground and analyzed for nitrogen (N), phosphorous (P), calcium (Ca), potassium (K), sodium (Na) and magnesium (Mg). Nutrient concentrations are expressed as mg of nutrient per g of leaf biomass, and nutrient contents per mg. P, K, Ca, Mg and Na analyses were undertaken using ICP-OES (Optical Emission Spectroscopy with Inductively Coupled Plasma) in a PERKIN ELMER, Optima 4300 (Shelton, Maryland, USA), while N was measured with an elemental analyzer NA 2100 (Thermofisher Sicentific, Milan, Italy).

Data analysis

Decomposition process

To analyze differences in mass loss we considered two variables: % of remaining mass, and decomposition rate (k). Decomposition rate, considered as the annual decomposition constant *k*, was calculated according to (Olson, 1963):

$$\ln(x_0/x_t) = kt$$

where x_0 is the initial litter mass, x_t is the mass remaining at time *t*, and *t* is the time in years. *k* values were estimated for every species and treatments in the climatic experiment (considering the two sampling times) as well as for each species in the non-treated experiment (considering the four sampling times). R^2 values express the variance explained by the exponential model.

Differences in *k,* were analyzed using a general linear mixed model (GLMM) with climatic treatment (C: control, W: warming, D: drought) and post-fire regenerative strategy (resprouters versus non-resprouters) as fixed factors, and species as a random factor.

Since in the non-treated experiment, there were more replicates for each time, I also analyzed effects of post-fire regenerative strategy on *k*-values obtained from these samples (with 4 collection times) by a GLMM with one fixed factor (regenerative strategy) and species as the random factor..

Alternatively, differences in % of remaining mass were analyzed by a repeated measures ANOVA in the two experiments. Differences among time (within-subject factor), climate treatments (considered only in the climatic experiment) and post-fire regenerative strategies (between-subject factors) were the factors. To better approximate normality, the % of remaining mass was transformed into its log-odd (i.e. log [(x / (1 – x)]).

Life-form types were considered as following: C = chamaephyte: with persistent buds situated 0.2 - 0.5 m height, NP = nano-phanerophyte: with persistent buds situated 0.5 - 2 m height, MP = macro-phanerophyte: with persistent buds situated 0.5 - 5 m height and PV = phanerophyte-vine: with persistent buds situated more than 0.5 m height and creeper. An additional GLMM was constructed for the two studied variables (decomposition rate (k) and % of remaining mass (at t = 0.17 years, and t = 2 years)).

Post-fire regenerative strategy, life-form and climatic treatment were considered the fixed effects, and species was the random factor nested within Family. Taxonomic Order was not considered, as there was nearly the same number of orders as families. This approach ensured that the significance tests for the fixed-effect predictors were not biased by autocorrelations in taxonomical affiliations.

For these statistical analyses, the mean values of each species obtained from the 3 sampled litter bags for each treatment and collection time were used as replicates.

Litter composition

First of all, differences among post-fire regenerative strategies of initial nutrient content (that is *litter quality*) were analyzed by a one-way ANOVA for each nutrient.

The influence of nutrient concentration on the rate of decomposition was analyzed by backward stepwise multiple linear regression. I used *k* for each species (from non-treated experiment) as the dependent variable and initial N, P, Ca, Na, K, Mg leaf litter concentration and N:P ratio as the independent variables. All variables were transformed to their ln(x).

Since litter composition is defined by several nutrients, a Principal Components Analysis (PCA) was performed to analyze overall litter composition changes during the decomposition process. The PCA resulted in a set of ordinations of species according to six variables describing the litter nutrient concentration (N, P, Ca, Na, K, Mg) for each climatic treatment and collection time. Differences in PCA coordinates over the first axis were considered as dependent variables in a repeated-measures ANOVA analyzing the differences among time (within-subject factor with two levels: 0.17 and 2 years), climate treatments (C, W, D) and post-fire regenerative strategy (resprouters and non-resprouters) (between-subject factors).

I also used GLMM to test separately whether there was any autocorrelation on account of the higher taxonomical level “Family” for the two PCA variables along time (PCA coordinates on the first axis at 0.17 years, and 2 years), and for each of the nutrient,by considering a hierarchical nested design of species (random factor) among families. Order was not considered, as there was nearly the same number of orders as families. This approach ensured that the significance tests for the fixed-effect predictors were not biased by taxonomical affiliations. This GLMM also considered life-form as a fixed effect.. N, P, Ca, Na, K, Mg concentrations and N:P ratio were log transformed to better approximate normality.

Finally, differences between post-fire regenerative groups for each nutrient concentration in non-treated experiment were also analyzed. For each nutrient, we used a repeated-measures ANOVA where time was the within subject factor (at 0.17, 0.5, 1.17 and 2 years) and post-fire regenerative strategy was the between-subject factor.

Analyses were performed using Statistica 6.0 (Statsoft), Sigmaplot 8.0 (SPSS) and SPSS 13.0 (SPSS).

RESULTS

Decomposition process

Drought was the climatic treatment that most affected litter decomposition by decreasing mass loss. Post-fire regenerative strategy showed an interaction with time since resprouters exhibited lower loss of mass several months after litter decay than non-resprouters.

Leaf litter decomposition followed an exponential decay pattern for all species, except for *Globularia alypum* and *Rhamnus alaternus* (Table 2), so that these two species were not considered in the statistical analyses of k-values. *K*-values and % of remaining mass for all species and treatments are summarized in Table 3.

Table 2. Decomposition rates for leaf litter for all the studied species. Data were obtained from litter bags of the non-treated experiment during the 2-year period. *K* is calculated from $\ln(x_0/x_t) = kt$ (Olson 1963).

	k	**R^2**
Cistus albidus	0,3099	0,9097
Cistus monspeliensis	0,3252	0,8209
Fumana thymifolia	0,4776	0,9408
Rosmarinus officinalis	0,3133	0,6730
Cistus salviifolius	0,3006	0,7926
Dorycnium hirsutum	0,3991	0,6249
Dorycnium pentaphyllum	0,3274	0,5477
Globularia alypum	0,6092	0,0001
Staehelina dubia	0,2164	0,7377
Arbutus unedo	0,1838	0,6512
Daphne gnidium	0,3853	0,6654
Juniperus oxycedrus	0,1339	0,7645
Phillyrea angustifolia	0,2983	0,6856
Pistacia lentiscus	0,1861	0,4208
Quercus coccifera	0,3849	0,8979
Quercus ilex	0,3795	0,9111
Rhamnus alaternus	0,5646	0,0001
Smilax aspera	0,2474	0,6303

Table 3. Percentage of remaining mass (at the two collection times: 0.17 and 2 years) and decomposition rates of leaf litter for all the studied species and for each climatic treatment during the 2-year litter bag study. *K* is calculated from ln(x0/xt) = *k*t (Olson 1963).

	Control				**Warming**				**Drought**			
	k	**R^2**	**%Remaining weight (2 months)**	**%Remaining weight (24 months)**	**k**	**R^2**	**%Remaining weight (2 months)**	**%Remaining weight (24 months)**	**k**	**R^2**	**%Remaining weight (2 months)**	**%Remaining weight (24 months)**
Cistus albidus	0,2819	0,9375	91,8351	57,3984	0,2634	0,8598	91,4276	59,6306	0,1948	0,9658	95,8120	67,8467
Cistus monspeliensis	0,2785	0,8948	89,1510	58,1530	0,2539	0,8320	89,2107	61,0646	0,2171	0,9836	94,4494	65,0267
Lavandula latifolia	0,2097	0,9333	91,9429	59,0948	0,1824	0,9857	90,3450	63,3025	0,1646	0,9024	95,5836	64,9924
Rosmarinus officinalis	0,2609	0,8162	85,1431	53,3119	0,2114	0,7017	82,5320	57,3803	0,2065	0,9835	88,1025	55,1251
Cistus salviifolius	0,2672	0,8586	85,2735	58,9989	0,2346	0,8716	83,9525	64,4842	0,2162	0,9322	90,0099	62,9302
Dorycnium hirsutum	0,3284	0,7608	66,9707	43,4206	0,2940	0,4782	71,7780	46,5700	0,3071	0,8897	90,3958	46,3141
Dorycnium pentaphyllum	0,2761	0,6369	95,2562	65,8970	0,2318	0,2008	95,6842	69,5794	0,2379	0,7793	98,1334	71,8511
Globularia alypum	0,4806	0,0001	88,4384	60,3274	0,4263	0,0001	88,9202	66,4559	0,3909	0,9621	95,9713	66,2460
Staehelina dubia	0,1808	0,8148	95,2718	69,8580	0,1792	0,8922	93,2027	70,3248	0,1692	0,9530	98,2978	71,1568
Arbutus unedo	0,1604	0,7918	93,0572	73,0433	0,1175	0,8020	93,9348	79,4885	0,1053	0,8670	99,0546	80,9162
Juniperus oxycedrus	0,1229	0,8130	93,9856	78,6239	0,1056	0,7851	94,3549	81,3639	0,1031	0,9809	97,9207	81,4085
Phillyrea angustifolia	0,2561	0,7557	88,7272	60,8788	0,2252	0,7585	89,3519	64,6196	0,1962	0,9299	96,6309	67,5540
Pistacia lentiscus	0,1555	0,6565	90,7437	74,0220	0,1597	0,6715	91,0368	73,3797	0,1251	0,9250	97,3442	77,9267
Quercus coccifera	0,3411	0,9298	89,4665	51,3310	0,3070	0,9275	89,6001	54,9065	0,2425	0,9604	94,4501	61,7662
Quercus ilex	0,3433	0,9469	89,3797	51,1137	0,3099	0,8266	88,5561	54,7458	0,2498	0,9845	94,3184	60,8799
Rhamnus alaternus	0,4406	0,0833	73,7332	45,0363	0,4311	0,3175	80,0384	47,2631	0,4142	0,9298	88,6248	44,5033
Smilax aspera	0,1972	0,7958	90,3599	68,1821	0,2512	0,8636	91,4924	61,0929	0,1740	0,8983	94,9744	70,8529

Significant differences were found in **decomposition rates (k)** among different climatic treatments ($F_{2,\ 15}$ = 26.267, p < 0.001). Post-hoc differences indicated that control presented the higher *k*-values followed by warming and with drought treatment having the lower values (Figure 2). There were not differences among post-fire regenerative groups (resprouters, non-resprouters) ($F_{1,15}$ = 0.028, p = 0.87) and neither in the interaction between these two factors ($F_{2,15}$ = 0.684, p = 0.513). When considering life-form type and species nested within families as explicative factors, differences between climate treatments remained ($F_{2,15}$ = 26.833, p < 0.001). There were also significant differences among families ($F_{11,15}$ = 62.218, p < 0.001). But there were not significant differences among life-forms ($F_{3,15}$ = 0.057, p = 0.644) and neither in post-fire regenerative strategies ($F_{1,15}$ = 0.025, p = 0.877).

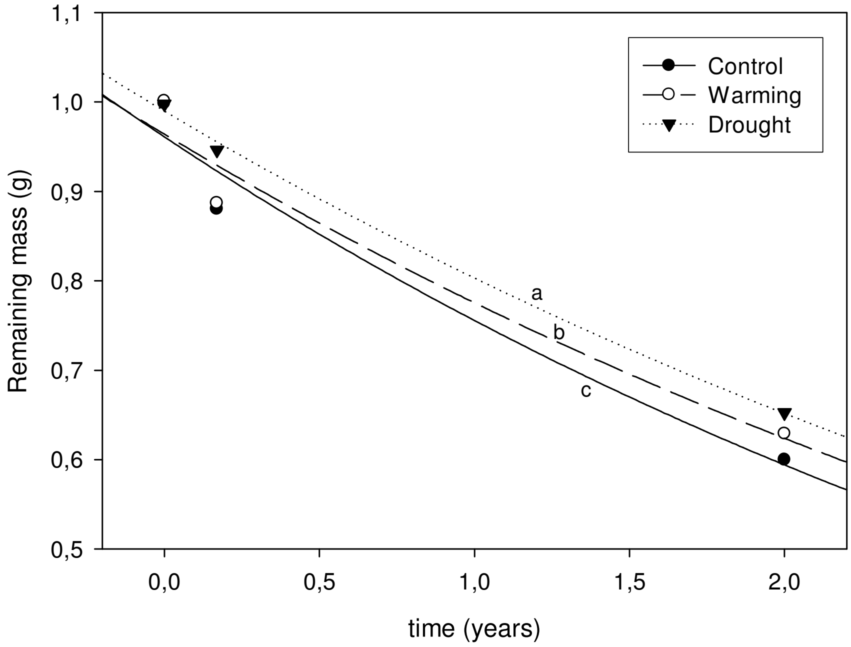


Figure 2. Mass loss average of the 19 study species for each climatic treatment and collection time. Representation of the mass loss among time following an exponencial decay model ($\ln(x_0/x_t) = kt$; (Olson 1963). Curves show differences in decomposition rate (k) under the different climatic treatments. *K* is significally different between climatic treatment and letters indicate Bonferroni's post-hoc differences.

When analyzing decomposition rate for non-treated litter bags (with 4 collection times) there were marginally significantly differences among post-fire regenerative groups (resprouters and non-resprouters) ($F_{1,16}$ = 4.172, p = 0.05). When considering taxonomical affiliation and life-form effects differences among post-fire regenerative strategies get weaker ($F_{1,16}$ = 5.989, p = 0.07) but there were not differences among taxonomical affiliations ($F_{12,16}$ = 1.926, p = 0.275) and neither among different life-forms ($F_{3,16}$ = 0.710, p = 0.595).

The analisis of the percentage remaining mass in climatic experiment is in agreement with patterns obtained for k-values since litter under drought decomposed slowly as shown by higher percentage of remaining mass while warming had no effect (Table 4, Figure 3a). This effect is particularly important during the first two months. After 2 years, the differences between treatments tend to decrease (Figure 3a).

Table 4. Repeated measures ANOVA for the remaining mass (%) and litter quality (coordinates of each species over the first axis of the PCA). Time (0,17 and 2 years) was the within-subject factor. Climatic treatment and regenerative strategy were also considered as between-subject factors. * indicates significant results ($p < 0.05$).

	Remaining mass		Litter quality	
	F	p	F	p
Climatic treatment	4,599	0,015*	0,023	0,977
Regenerative strategy	0,839	0,364	1,573	0,216
Time	1017,180	< 0,001*	4,636	0,036*
Climatic treatment x Regenerative strategy	0,004	0,996	0,081	0,922
Time x Climatic treatment	15,823	< 0,001*	0,088	0,916
Time x Regenerative strategy	4,746	0,034*	16,541	< 0,001*
Time x Climatic treatment x Regenerative strategy	0,276	0,760	0,314	0,732

The percentage of remaining mass did not differ significantly among post-fire regenerative groups (resprouters and non-resprouters) along the 2-year experiment when considering litter bags from the climatic treatments experiment, but there was a significative interaction between time and post-fire regenerative strategy (Table 4). Also, when analyzing the percentage of remaining mass along time in non-treated data, there was a significative interaction among regenerative strategy and time ($F_{3,19} = 4.19$, $p = 0.001$), so that resprouters have a slower decomposition than non-resprouters (Figure 3b). The interaction between climatic treatment and post-fire regenerative strategy was not significant, so that climatic treatment did not affect post-fire regenerative litter decomposition patterns. Life-form and taxonomical affiliations showed that besides differences between treatments and post-fire regenerative groups, there were also differences among taxonomical affiliations but not among life-form types (Table 5).

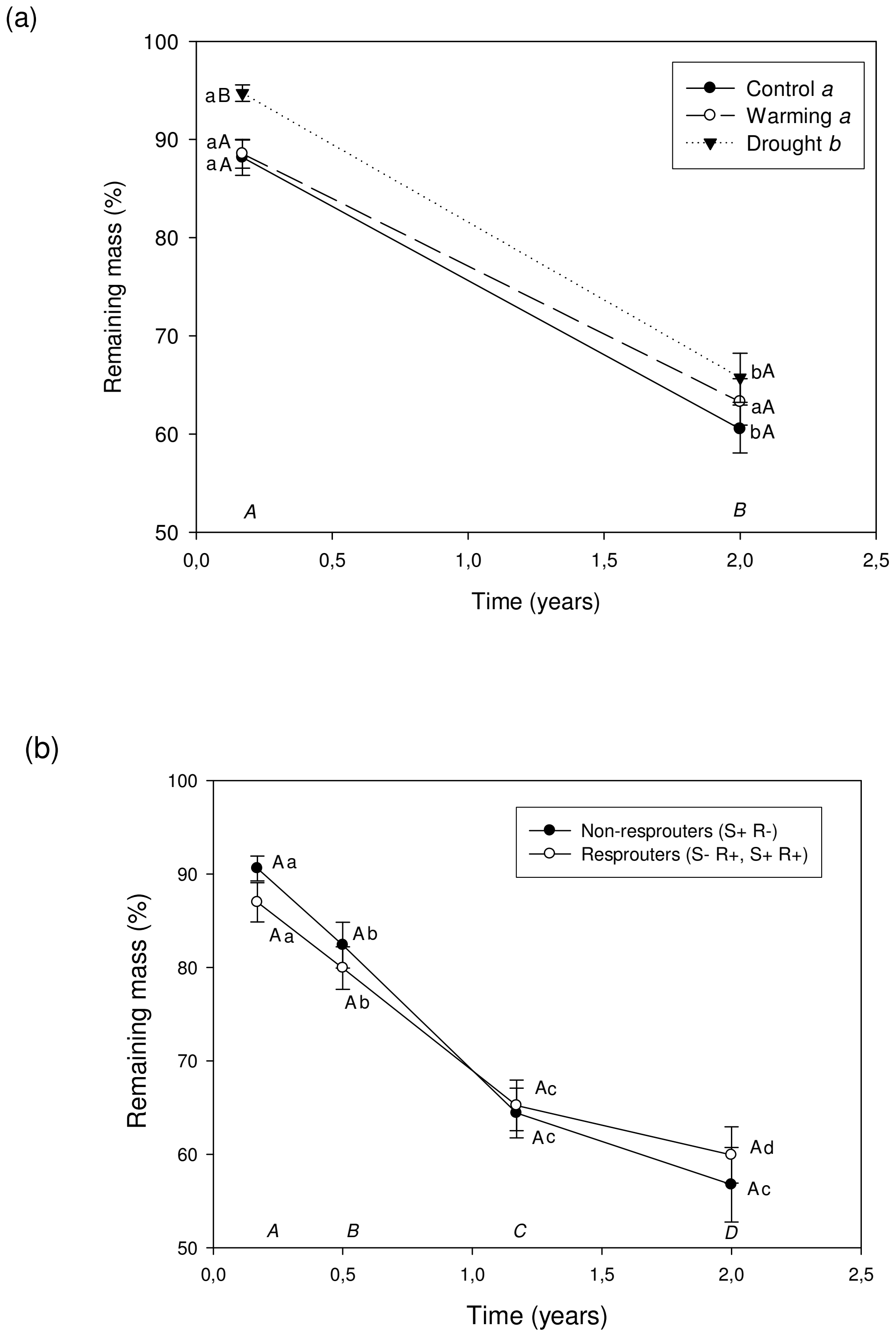


Figure 3. (a) Mean of the remaining mass (%) for each climatic treatment in the two collection times. (b) Mean of the remaining mass (%) for each post-fire regenerative strategy in the non-treated experiment (with 4 collection times).

Vertical bars denote standard errors. Post-hoc Bonferroni's significant differences ($p < 0.05$) are indicated with different letters. Upper case letters (A, B) indicate differences between treatments (3a) or between regenerative strategies (3b) for a given collection time. Lower case letters (a, b) indicate differences among collection times for a given climatic treatment (3a) or between post-fire regenerative strategies (3b). Italic upper case letters (*A, B*) indicate differences among collection times, italic lower case letters (*a, b*) in the legend box indicate differences among treatments (3a).

Table 5. GLMM (General linear mixed model) for the remaining mass (%) and the litter quality (coordinates of each species over the first axis of the PCA) at different collection times (0,17 and 2 years). (a) Climatic treatment and regenerative strategy were the fixed factors and species was a random factor. (b) The same GLMM with two more factors, life-form as another fixed factor and species (as a random factor) nested among families. * Indicates significant results ($p < 0.05$). Life-form types and families were considered following Table 1. ^{a} means that post-hoc Bonferroni differences are D^{a} W^{b} C^{b}.

	Remaining mass (t = 0.17)		Remaining mass (t = 2)		Litter quality (t = 0.17)		Litter quality (t = 2)	
	F	p	F	p	F	p	F	p
Climatic treatment	84,340	< 0,001*	21,481	< 0,001*	0,000	1,000	0,000	1,000
Regenerative Strategy	0,713	0,412	0,010	0,922	0,161	0,694	2,534	0,132
Species	18,351	< 0,001*	57,685	< 0,001*	30,089	< 0,001*	90,867	< 0,001*
Life-form	2,831	0,083	1,345	0,306	0,439	0,729	1,437	0,281
Climatic treatment	84,340	< 0,001*^{,a}	21,481	< 0,001*^{,a}	0,000	1,000	0,000	1,000
Regenerative Strategy	0,973	0,343	0,011	0,920	0,143	0,712	2,755	0,123
Family (species)	13,433	< 0,001*	53,958	< 0,001*	33,891	< 0,001*	83,569	< 0,001*

Litter composition

The results of the chemical analyses of the initial litter samples are shown in Table 6. There were not significant differences among post-fire regenerative strategies in relation to to the initial litter quality (N: $F_{1,19}$ = 0.018, p = 0.894; P: $F_{1,19}$ = 0,475, p = 0.499; Ca: $F_{1,19}$ = 2.193, p = 0.157; K: $F_{1,19}$ = 0.016, p = 0.900; Na: $F_{1,19}$ = 0.074, p = 0.789; Mg: $F_{1,19}$ = 0.276, p = 0.606; N:P: $F_{1,19}$ = 2.905, p = 0.107).

Table 6. Initial chemical composition (nutrient per leaf dry mass) of leaves incubated in litter bags for each of the study species

Species	N (mg g^{-1})	P (mg g^{-1})	Ca (mg g^{-1})	K (mg g^{-1})	Na (mg g^{-1})	Mg (mg g^{-1})	N:P
Cistus albidus	8,48	0,609	25,70	7,33	0,490	1,677	13,92
Cistus monspeliensis	6,43	0,347	15,50	5,10	0,892	1,074	18,51
Fumana thymifolia	8,17	0,490	32,96	3,86	0,199	2,561	16,68
Lavandula latifolia	13,84	0,587	27,73	1,38	0,050	1,841	23,57
Rosmarinus officinalis	6,33	0,207	20,71	9,41	0,625	1,346	30,62
Cistus salviifolius	6,42	0,184	24,85	3,04	0,179	2,666	34,91
Dorycnium hirsutum	15,17	0,474	22,80	9,91	0,751	3,000	32,00
Dorycnium pentaphyllum	5,36	0,254	17,55	6,43	0,254	2,303	21,12
Globularia alypum	8,79	0,342	19,38	4,01	1,236	1,199	25,68
Staehelina dubia	12,3	0,414	20,44	1,44	0,050	1,499	29,69
Arbutus unedo	3,65	0,282	18,23	3,80	0,050	1,211	12,94
Daphne gnidium	8,14	0,316	13,77	8,03	0,207	1,013	25,75
Juniperus oxycedrus	4,04	0,148	28,72	1,72	0,283	0,462	27,30
Phillyrea angustifolia	7,96	0,247	17,60	4,47	0,409	1,487	32,22
Pistacia lentiscus	4,42	0,160	16,64	3,38	0,469	1,425	27,65
Quercus coccifera	15,96	0,904	8,29	6,52	0,315	1,414	17,65
Quercus ilex	17,3	0,935	8,34	6,06	0,297	1,338	18,50
Rhamnus alaternus	8,22	0,225	32,97	9,12	0,358	1,260	36,49
Smilax aspera	7,51	0,195	20,25	5,40	0,808	0,998	38,46

The results of the multiple regression analyses of *k* (from samples outside the climatic treatment plots) in relation to initial chemical concentration suggested that 48 % of the variance (R^2) (F = 4.546, p = 0.019) was explained, basically by few of the litter composition variables. The nutrients that best fitted the model were: Nitrogen (t = 3.154, p = 0.007), Calcium (t = 1.961, p =0.069) and Sodium (t = 1.961, p = 0.139) (leaf litter concentration = -0.208 + 0.172 (ln(N)) + 0.007 (Ca) + 0.119 (Na)).

When exploring the overall relationship between the leaf nutrient concentrations through PCA for each climatic treatment and collection time, we observed that N, P and K were positively correlated in all cases, while the correlations of the others variables depended on the treatment and the time (Figure 4). First PCA coordinates can be interpreted as the concentration of nutrients of the leaf litter so that the higher the value of the axis 1, the higher the nutrients concentration (except for Calcium in the first two months) (Figure 4). This is especially clear when the PCA at 2 yearsis considered. When I analyzed the coordinates of the obtained PCA considering climatic treatment, time and regenerative strategy, there was a significant interaction between time and post-fire regenerative strategy, while climatic treatment did not show a significant effect (Table 4). Resprouters showed lower values of PCA coordinates after 2 years of experiment, suggesting that in this group of species nutrients composition show lower concentration than in non-resprouters (Figure 5). These results did not change when including life-form and taxonomical affiliations (Table 5).

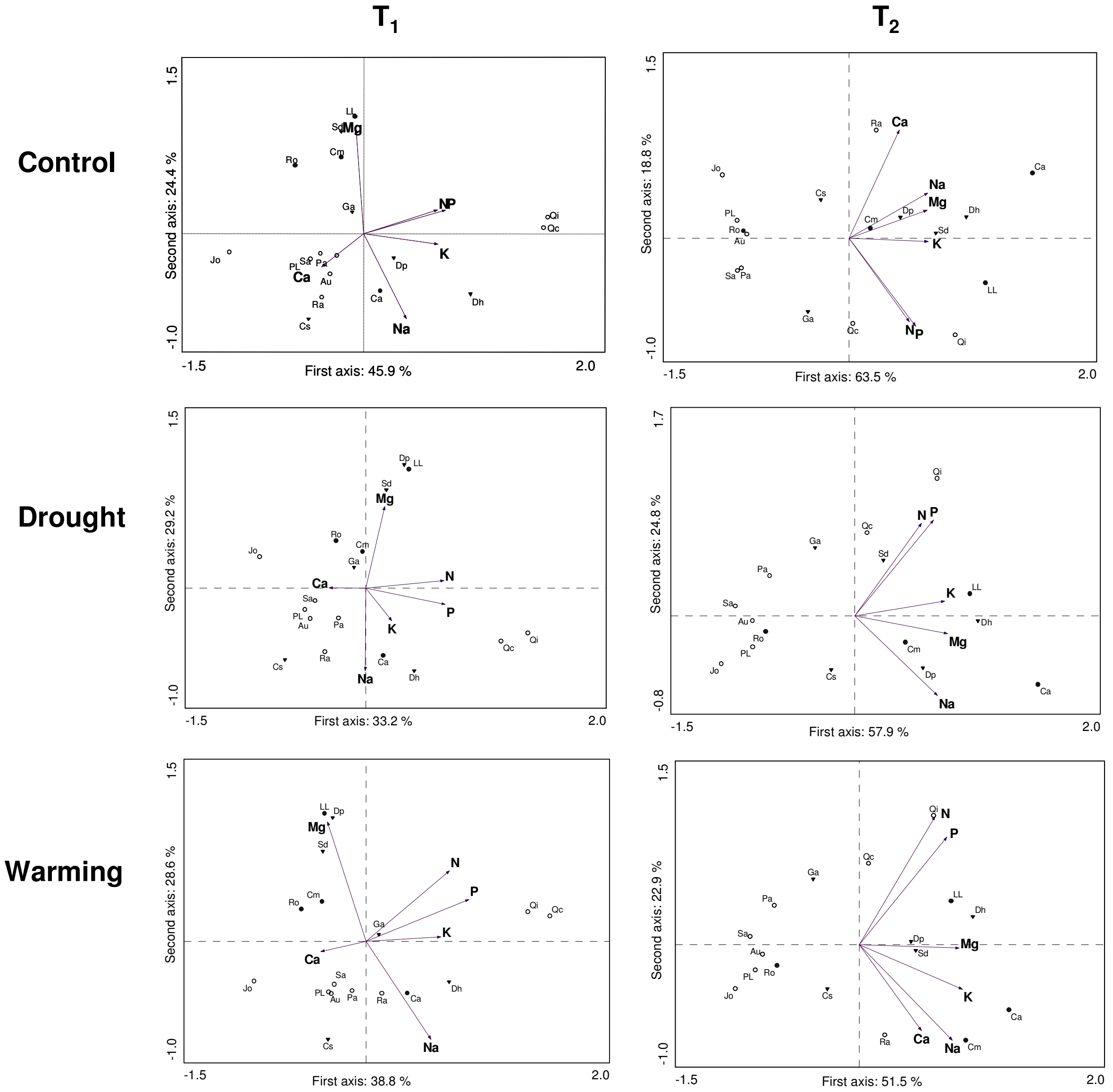


Figure 4. Principal Components Analyses (PCA) for all the studied variables: N, P, K, Ca, Mg and Na leaf litter content and for each study species. A PCA was performed for each collection time and each climatic treatment. The ● are S+ R- species, ○ are S- R+ and ▼ are S+ R+ species.

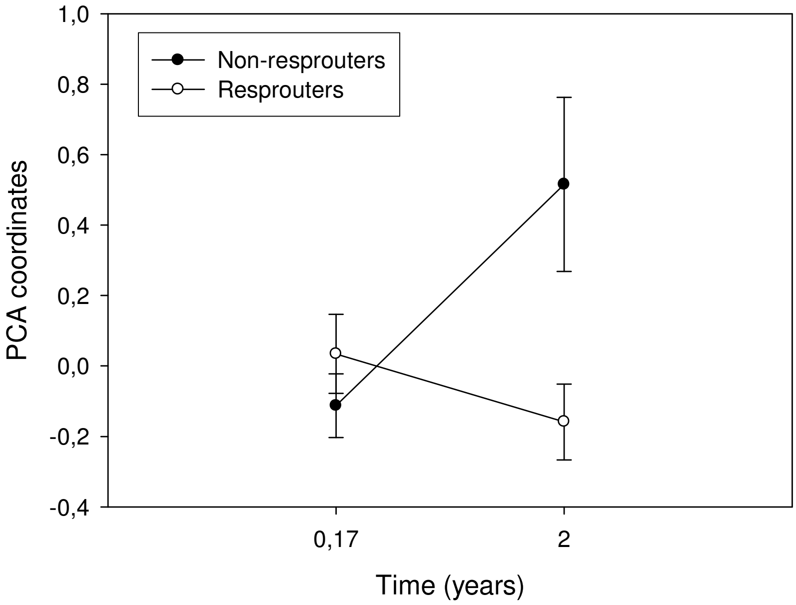


Figure 5. Mean of the PCA nutrients first coordinates for each regenerative strategy, in the two collection times. Vertical bars denote standard errors.

When analyzing each nutrient separately after two months of decomposition (Table 8), Nitrogen and N:P were lower in drought treatment while K was higher in this treatment. Other differences among climatic treatments were found in Ca, Na and Mg (Table 7 and 8). Macro-phanerophytes presented the lowest Na concentrations followed by nano-phanerophytes and chamaephytes (Table 8). Resprouters presented lower Mg and K concentrations. Finally there was an effect of taxonomical affiliation in all nutrients content.

Each one of the nutrients leaf contents were also analyzed in non-treated experiment. All groups of species tended to decrease along time ($p < 0.05$) their litter nutrients contents, especially N, P, Na and K (Figure 6). The cotent of some nutrients like Mg and Ca firstly decrease but after some time, it tends to increase again. In general, non-resprouters tend to loose less nutrients, but only N:P ratio is significantly lower in litter of non-resprouters than in resprouters ($F_{4,19} = 2.842$ $p = 0.030$, Figure 6c). These values indicate that non-resprouters litter has more proportion of P than resprouters. N:P ratio increased along time indicating that in both groups P return is more rapid than N return This is linked with results of N content and P content since resprouters tend to have higher values of N and lower of P respect to non-resprouters (Figure 6a, 6b). The litter Mg content present a significative interaction between post-fire regenerative strategy and time ($F_{1,19}$ = 2.59, p = 0.009) so that resprouters tend to loose more Mg among time that non-resprouters.

Table 7. GLMM (General linear mixed model) for remaining mass (%) and litter quality (coordinates of each species over the first axis of the PCA) at different collection times (0,17 and 2 years). Climatic treatment and regenerative strategy were the fixed factors. A hierarchical nested design of species among families was considered as well as life-form as another fixed factor. * indicate significant results ($p < 0.05$). Life-form types and families were considered following Table 1.

	N (t = 0.17)		**N (t = 2)**	
	F	p	F	p
Life-form	1,452	0,277	1,551	0,252
Climatic treatment	7,475	0,002*	14,577	< 0,001*
Regenerative Strategy	1,163	0,693	0,035	0,855
Family (Species)	133,433	< 0,001*	338,200	< 0,001*
	P (t = 0.17)		**P (t = 2)**	
	F	p	F	p
Life-form	0,502	0,688	0,808	0,514
Climatic treatment	2,913	0,069	1,056	0,360
Regenerative Strategy	0,390	0,544	0,991	0,339
Family (Species)	148,096	< 0,001*	615,402	< 0,001*
	Ca (t = 0.17)		**Ca (t = 2)**	
	F	p	F	p
Life-form	0,160	0,921	0,635	0,607
Climatic treatment	0,479	0,624	3,863	0,031*
Regenerative Strategy	0,292	0,599	0,203	0,660
Family (Species)	117,341	< 0,001*	48,718	< 0,001*
	K (t = 0.17)		**K (t = 2)**	
	F	p	F	p
Life-form	0,910	0,465	8,255	0,060
Climatic treatment	85,937	< 0,001*	1,907	0,165
Regenerative Strategy	0,055	0,818	6,334	0,027*
Family (Species)	26,585	< 0,001*	37,935	< 0,001*
	Na (t = 0.17)		**Na (t = 2)**	
	F	p	F	p
Life-form	3,691	0,043*	1,460	0,275
Climatic treatment	5,271	0,011*	1,055	0,360
Regenerative Strategy	4,263	0,061	1,702	0,217
Family (Species)	4,310	< 0,001*	30,042	< 0,001*
	Mg (t = 0.17)		**Mg (t = 2)**	
	F	p	F	p
Life-form	3,691	0,043*	2,013	0,166
Climatic treatment	24,649	< 0,001*	2,516	0,097
Regenerative Strategy	10,897	0,006*	1,962	0,187
Family (Species)	8,990	< 0,001*	92,101	< 0,001*
	N:P (t = 0.17)		**N:P (t = 2)**	
	F	p	F	p
Life-form	0,280	0,839	0,135	0,937
Climatic treatment	0,709	0,500	4,406	0,02*
Regenerative Strategy	2,561	0,136	4,129	0,065
Family (Species)	33,538	< 0,001*	90,884	< 0,001*

Table 8. Mean and standard error of litter nutrients contents (mg g^{-1}) and N:P ratio (for the two collection times) for each climatic treatment and regenerative strategy. Italic lower case letters indicate Bonferroni post-hoc differences from significant results of table 7. Life-form post-hoc differences among life-form types for Magnesium at time = 0.17 are: C^{a}, NP^{b}, MP^{c} and PV^{c}.

		N (mg g^{-1})		P (mg g^{-1})		Ca (mg g^{-1})		K (mg g^{-1})		Na (mg g^{-1})		Mg (mg g^{-1})		N : P	
	Time (year)	mean	s. e.	mean	s. e.	mean	s. e.	mean	s. e.	mean	s. e.	mean	s. e.	mean	s. e.
Control	0,17	10,167^{b}	1,065	0,392	0,054	21,707	1,835	1,893^{b}	0,274	1,158^{a}	0,129	0,288^{b}	0,083	28,339	1,905
Drought	0,17	9,585^{a}	1,089	0,372	0,055	21,555	1,684	4,489^{a}	0,627	1,187^{ab}	0,185	0,743^{a}	0,183	28,699	2,282
Warming	0,17	10,291^{b}	1,109	0,389	0,057	21,311	1,692	2,278^{b}	0,372	0,958^{b}	0,170	0,563^{b}	0,184	29,690	2,288
Control	2	11,801	1,153	0,397	0,054	37,217^{ab}	2,956	0,986	0,122	0,145	0,017	1,170	0,115	32,826^{a}	2,413
Drought	2	11,097	1,164	0,387	0,051	37,875^{a}	3,132	0,919	0,103	0,136	0,018	1,235	0,122	31,043^{b}	2,279
Warming	2	11,527	1,182	0,394	0,056	35,112^{b}	2,968	0,939	0,126	0,145	0,022	1,238	0,130	32,126^{ab}	2,390
Resprouters	0,17	10,350	0,742	0,372	0,038	21,092	1,190	2,874	0,353^{a}	1,211	0,101	0,387	0,098^{a}	308,016	13,288
Non-resprouters	0,17	8,924	1,015	0,426	0,048	22,927	1,598	2,927	0,600^{b}	0,742	0,197	1,000	0,179^{b}	227,586	21,898
Resprouters	2	11,607	0,765	0,369	0,036	36,164	2,050	0,804	0,058	0,125	0,009	1,133	0,078	345,217	15,007
Non-resprouters	2	11,046	1,359	0,470	0,051	38,590	3,050	1,415	0,150	0,198	0,031	1,480	0,126	237,975	11,847

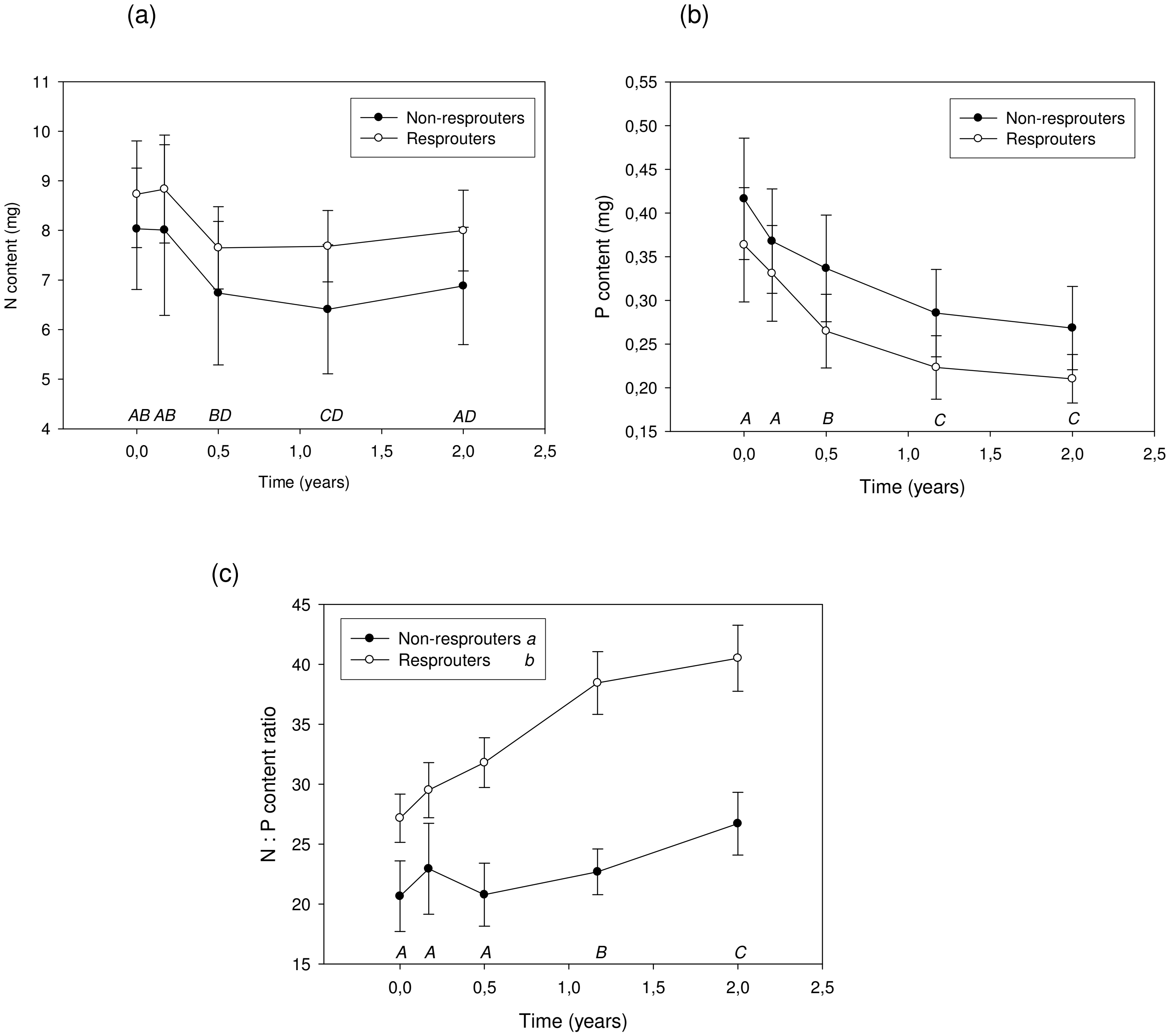
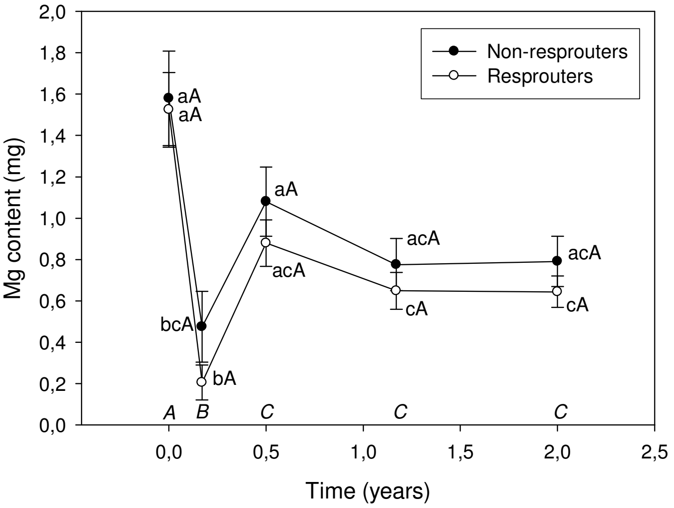
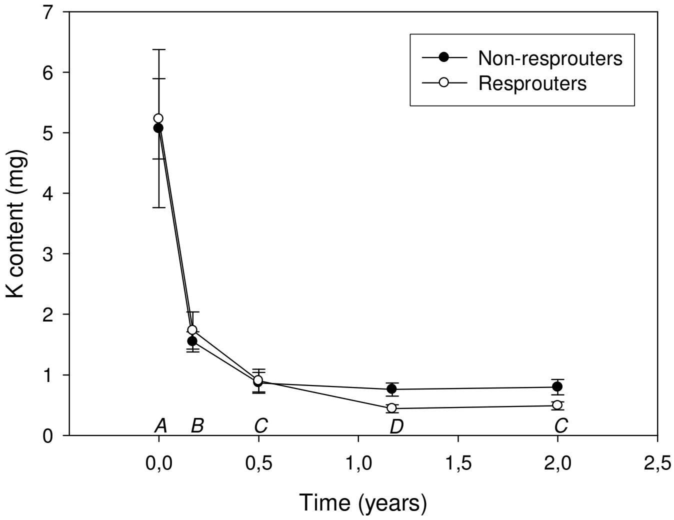


Figure 6. Mean of the different studied litter content nutrients for each regenerative strategy in the four collection times considered outside the climatic treatments. Vertical bars denote standard errors. Post-hoc Bonferroni's significant differences ($p < 0.05$) are indicated with different letters. Italic upper case letters (*A, B*) indicate differences among time. Italic lower case letters (a, b) indicate differences among regenerative strategies. Lower case letters (a, b) indicate differences among collection times for a given regenerative strategy.

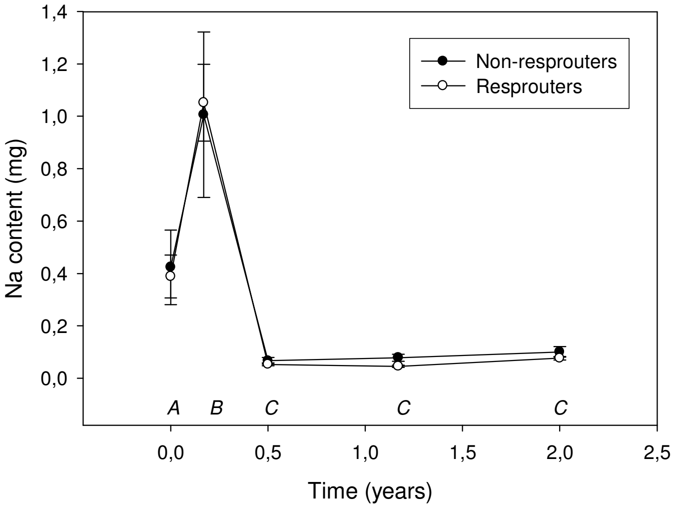
(d)


Mg content (mg)
Time (years)
Non-resprouters
Resprouters
aA
aA
bcA
bA
aA
acA
acA
cA
acA
cA
A
B
C
C
C
0,0
0,2
0,4
0,6
0,8
1,0
1,2
1,4
1,6
1,8
2,0
0,0
0,5
1,0
1,5
2,0
2,5

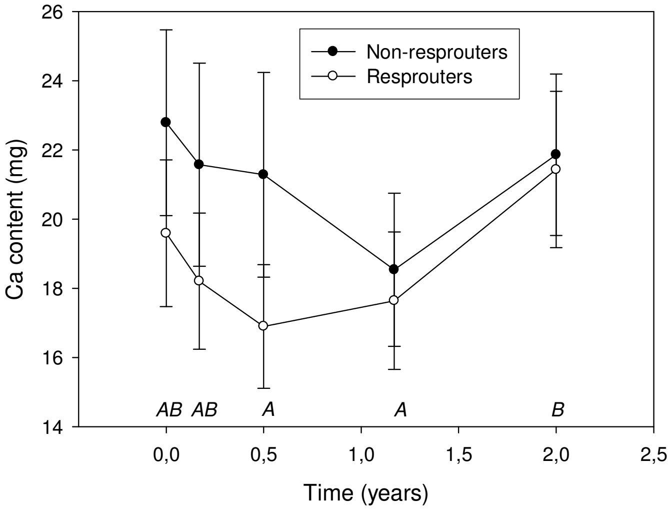
(e)


K content (mg)
Time (years)
Non-resprouters
Resprouters
A
B
C
D
C
0
1
2
3
4
5
6
7
0,0
0,5
1,0
1,5
2,0
2,5

(f)


Na content (mg)
Time (years)
Non-resprouters
Resprouters
A
B
C
C
C
0,0
0,2
0,4
0,6
0,8
1,0
1,2
1,4
0,0
0,5
1,0
1,5
2,0
2,5

(g)


Ca content (mg)
Time (years)
Non-resprouters
Resprouters
AB
AB
A
A
B
14
16
18
20
22
24
26
0,0
0,5
1,0
1,5
2,0
2,5

DISCUSSION

Soil humidity has been proposed as the main factor on decomposition rate in Mediterranean ecosystems (Cortez, 1998). Ormeño *et al.* (2006) suggested that soil moisture strongly improves leaf litter colonization by fungi in the Mediterranean ecosystems, determining the recycling of organic matter. Experimentally induced drought diminished loss of litter mass along time, leading to higher values of remaining litter after 2 years of experiment. This pattern may be explained by climatically controlled modifications on the structure of the microbial population and on the humification process (Coûteaux *et al.*, 1995). As a result, under drought conditions depleted microbial and fungus activity results in a lower decomposition rate and lower mass loss, so that nutrient cycling and functions of the ecosystem may be altered by a lower incorporation and recycling of organic matter to the soil. Warming did not affect decomposition despite a stimulation effect of temperature on the decomposition rate could be expected. Temperature is not likely to be a limiting factor for decomposition in Mediterranean ecosystems, and the relatively small increment of temperature (0.6 - 0.7ºC) induced by the experiment, may not have been enough to produce that stimulation effect. This study suggests that under the current trends of climatic change, litter decomposition in Mediterranean ecosystems would be more diminished by water depletion than increased by moderate raise of temperature. Anyway, more studies about synergies between increment of temperature and drought should be done to better understand effects of climate change.

When considering the remaining mass, the differences between climatic treatments are more evident in the first months of decomposition. This is probably because in this phase looses are mainly from easily degraded soluble compounds and celluloses. The results suggest that these soluble compounds may lixiviate with more difficulty under drought treatment. After two months, the remaining mass is mainly composed by lignified material which is not as easily degraded (Coûteaux *et al.*, 1995).

Recent studies (Saura-Mas & Lloret, 2007b) have shown that reprouters have higher Leaf Dry Matter Content in saturated conditions ($LDMC_{sat}$) (Garnier *et al.*, 2001)) than other post-fire regenerative groups. A high $LDMC_{sat}$ corresponds to a low proportion of mesophyll and epidermis (light tissues) and a high proportion of vascular tissues and sclerenchyma (dense tissues) (Dijkstra & Lambers, 1989; Niemann *et al.*, 1992; Garnier & Laurent, 1994). Kazakou *et al.* (2006) found a strong negative correlation between $LDMC_{sat}$ and decomposition rate. Thus, the physical attributes of leaves can

be one of the causes of the differences found between post-fire regenerative groups. Accordingly, resprouters are expected to show higher litter mass after 2 years of experiment. This prediction is supported by our results (Figure 3b), being the lower loss of litter mass of resprouters observed two months after the start of the experiment.
Our results show that differences on decomposition rate and litter chemical composition among climatic treatments are influenced by the taxonomical affiliation of the studied species. Taxonomical affiliation plays an important role in determining the decomposition rate, probably because the physical properties of the leaf that determine decomposition rate, such as $\mathrm{LDMC}_{\mathrm{sat}}$, are determined phylogenetically (Saura-Mas & Lloret, 2007b). Many seeders evolved during the Quaternary within a relatively low number of families while many resprouters were already present in the Tertiary in a wide range of families (Herrera, 1992; Verdú, 2000; Pausas & Verdú, 2005). Therefore, the seeder's life strategy and leaf attributes has been postulated as an adaptive response to the Mediterranean climate, which is in agreement with studies that give evidence of seeders advantages to live under climates with severe drought events (Peñuelas *et al.*, 2001; Lloret *et al.*, 2005; Arnan *et al.*, 2007).

Chemical and physical characteristics of the litter material regulate decomposition rate (Gallardo, 2001). Coûteaux *et al.* (1995) suggested that the climate would regulate decomposition rate in ecosystems under unfavorable climate, while in ecosystems with favorable climates the chemical composition of the leaf litter would be the best predictor of decomposition. The main components of the leaf litter from senescent leaves of woody species are celluloses, hemicelluloses, lignines and lipids (in order of abundance), and each one of this components decompose at a different rate (Gallardo, 2001). Furthermore, there is a positive relationship between the microbial activity and the nutrients abundance of the leaf litter limiting microbial productivity (Gallardo, 2001). Our results agree with these assumptions since species with higher initial Nitrogen concentration show higher k-values. Our study suggests that Ca and Na concentrations could also have an important role on microbial activity as well as Nitrogen, at least in soils with similar characteristics to the studied one (petrocalcic calcixerept).

Most decomposition studies have found increments in the relative concentration of nutrients along time (Kavvadias *et al.*, 2001; Allison & Vitousek, 2004). Translocation of nutrients from soil to leaf litter by fungi hyphaes have also been proposed to explain N increases (Gallardo & Merino, 1992), and Zeller *et al.* (2000) estimated that 35 % of the N incorporated to leaf litter was from fungi nitrogen. Litter under drought treatment showed lower values of nitrogen concentration, according to the described pattern of N increase in leaf litter due to fungi activity. Nitrogen deposition may also be depleted by

rain interception in the drought treatment. Since leaf litter concentration of nutrients is dependent on the remaining mass, this study also considered the absolute values of nutrients contents. Most of the litter nutrients contents tend to decay among time, which was expected because of degradation lixiviation and other decomposition processes. K and Na rapidly return to the soil, probably because of their facility to be lixiviated. This is in agreement with the fact that the litter under drought treatment was richer in K concentrations. Ca and Mg do not seem to follow this pattern of rapid return to the soil.
This study suggests that in general non-resprouters show higher nutrients concentrations in the litter fraction compared to resprouters. This trend could be explained because non-resprouters show more mass losses and the concentration of nutrient per leaf mass is likely to increase. The main difference among post-fire regenerative strategies is that non-resprouters show lower Mg loss and they tend to have a lower N:P ratio. Thus, ecosystems dominated by non-resprouters are expected to have a higher proportion of P in relation to N in the leaf litter fraction. This is probably because they do not accumulate as much N as resprouters in the leaf litter and because P concentration is higher in non-resprouter species (Saura-Mas & Lloret). What is also interesting is that both post-fire regenerative strategies loose more rapidly P than N. Lower Mg loss in non-resprouters means that communities dominated by this group of species will have slower Mg fluxes, which could be related to photosynthesis and other cell properties.

Post-fire regenerative strategies abundances can be determined in the future by new fire regimes driven by climate change increasing fire occurrence (Piñol *et al.*, 1998; Pausas, 2004). Thus, these changes may shift the abundance of resprouters and non-resprouters. Ecosystems dominated by resprouters will slow decomposition along long periods of time than non-resprouters dominated communities. Moreover, resprouters dominated communities will show a pattern of fluxes slowing down the incorporation of matter to the soil, as well as a higher proportion of N in relation to P in the leaf litter. Taxonomical affiliations have a determinant role in many of these differences, specially the ones related to the decomposition rate. Furthermore, this study suggests that the predicted decrease of precipitation and increment of drought periods by climate change, will affect ecosystem's nutrients return to the soil slowing the decomposition rates and inputs to the soil.

ACKNOWLEDGMENTS

I would like to thank M. Cabezas and A. Saperas for helping in the laboratory and A. Vila and M. Sallent for helping in the field. Special thanks are due to D. Sol, B. Shipley, M. Estiarte and J. Peñuelas for his support and suggestions. This study was funded by the Department of Universities, Research and Information Society of the Generalitat de Catalunya, the European social funds, and the Spanish MCYT projects REN 2003-07198 and CGL2006-01293/BOS.

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VIII. ROOT SYSTEM TOPOLOGY AND MORPHOLOGY

The main contents of this chapter are in preparation to be submitted as:
Saura-Mas, S., Lloret, F. Root traits of Mediterranean woody species with different post-fire regenerative strategies.

ABSTRACT

- Root topology and morphology of nine woody species with different fire-response strategy were examined in a Mediterranean shrubland. Sampling of the root system of adult individuals was done by field hand excavation helped with an air compressor.

- Results indicate that resprouters are species with longer and more branched root system. They also show higher root-to-shoot ratio supporting their greater ability to store water, starch and nutrients and to invest in the below-ground biomass. Moreover, this pattern probably allows them to explore deeper parts of the soil layers. Non-resprouters, short-living species would benefit from a higher specific root length and a less branched, overlapped root system indicating higher relative root growth and higher water uptake rates. Differences among post-fire regenerative strategies in length root traits are primarily influenced by the life-form type. Topological differences are more related to taxonomical affiliations.

- This study suggests that resprouters and non-resprouters differ on their nutrient and water uptake due to the characteristics of the root systems. Thus, proportions of regenerative strategies as a result of different fire regimes could determine functional properties of the ecosystems.

Key words: Architecture, fire, Mediterranean, resprouter, shrubland, SRL, root, structure, topology.

INTRODUCTION

In the Mediterranean Basin, trends in current fire regimes, particularly fire intensity and recurrence, are likely to determine species composition in many cases (Whelan, 1995; Lloret & Vilà, 2003; Eugenio & Lloret, 2004; Rodrigo *et al.*, 2004).

Intrinsic characteristics of Mediterranean species associated to post-fire regeneration, such as resprouting and establishment of seedlings after fire, as well as life-history traits, have been related to trade-offs involving resources uptake and storage (Paula & Pausas, 2006; Buhk *et al.*, 2007), in which root system plays a major role (Iwasa & Kubo, 1997; Pausas *et al.*, 2004). In addition, resprouter species have been described to often develop swollen organs (such as lignotubers) in the base of the shoots. They have been reported to storage resources that allow resprouting, that is, to produce new shoots after fire (Dawson & Pate, 1996; Canadell & López-Soria, 1998). In the Mediterranean basin, the group of resprouters is mostly constituted by long-lived species, typically found in late successional shrublands that often show a high percentage of individuals that survive and resprout after fire, while they do not show significant recruitment of new individuals shortly after wildfire (Bond & Van Wilgen, 1996). In contrast, non-resprouters are species without significant capacity to resprout so that individuals are killed after a fire (Pausas *et al.*, 2004). In fact, non-resprouters from the Western Mediterranean basin are species in which the population locally persists as propagules (seed or fruit) after a fire, so that they are propagule-persisters (Pausas *et al.*, 2004). In addition to high recruitment after disturbances, in the Mediterranean Basin these species usually show a shorter life-span (Pate *et al.*, 1990; Lloret, 1998; Verdaguer & Ojeda, 2002; Knox & Clarke, 2005; Schwilk & Ackerley, 2005). Thus, long-lived resprouters are expected to show a higher resource allocation to underground organs in order to sustain plant re-growth (Knox & Clarke, 2005), while short-lived non-resprouters would have shorter leaf life-span, high specific leaf area and higher photosynthetic rates (Bell, 2001; Ackerly, 2004), that is a similar syndrome to early successional species of mesic forests (Bazzaz, 1979). Studies in Mediterranean areas of Australia and South Africa have reported that, on average, resprouters have root starch concentrations four times higher than those of non-resprouters, and four to five times higher root : shoot ratios (Pate *et al.*, 1990; Bell *et al.*, 1996; Bell & Ojeda, 1999). These differences between regenerative types can be interpreted under the classical “r – K” syndromes gradient. On the “r” side there would be short-lived non-resprouters species with populations regenerating after fire by establishing seedlings which will have to produce a new root system after a fire event.

On the “K” side, there is a number of taxa that resprout from below-ground pre-existing root systems (Bond & Midgley, 2001; Keith *et al.*, 2001).

Root system performs two primary functions for plants: anchorage and resource acquisition. Both depend on architectural (topological and morphological) characteristics (Fitter, 1991). There are patterns in the distribution of architectural characteristics (distribution, angles and sizes of branches within the system) that are correlated with other important ecological attributes. For example, Rundel & Nobel (1991) suggested that competitive interactions of desert plants at the community level are strongly influenced by rooting architecture and phenological growth. Roumet *et al.* (2005) showed that annuals show root topological and morphological traits associated with enhanced resource acquisition, compared to perennials. More concretely, a herringbone-like pattern (Figure 1a) is more efficient in terms of the volume of soil explored for a given construction cost, while diffuse-branched systems (Figure 1b, 1c) are more transport-efficient and generally minimize construction costs (Fitter & Hay, 1987).

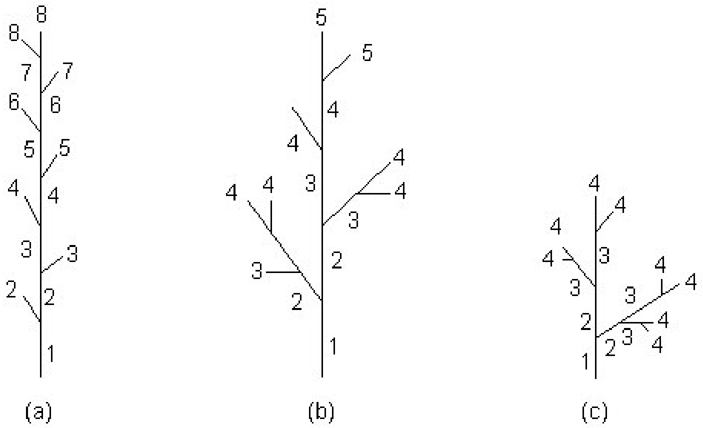

Figure 1. Diagram showing the disinction between extrem branching patterns (a, herringbone; b and c dichotomous at different levels). The altitude (A) is the longest individual path length (5, 8 and 4, respectively) and the external path lenth (P_e) is the sum of all paths to external links (33, 43 and 32 respectively). Magnitude (M) is the number of root tips of the root system (8, 8 and 8 respectively).
Adapted from Fitter, 1987.

One important challenge when studying root architecture in perennial, large, woody plants is the technical problems in extracting entire root systems (Mackie-Dawson & Atkinson, 1991). This probably the reason why most of these studies have been made with grasses (Fitter & Stickland, 1991; Arredondo & Johnson, 1999; Roumet *et al.*, 2005), or seedlings of shrubs and trees (Comas *et al.*, 2002; Clemente *et al.*, 2005; Trubat *et al.*, 2006; Padilla *et al.*, 2007). Jackson *et al.* (1996) compiled a global database of 250 root studies for terrestrial biomes, and sclerophyllous shrubland, including Mediterranean one, was described as the ecosystem with the highest root densities. However, most of the studies were made with soil cores techniques instead extraction of the root system.

Here, I provide, for a set of Mediterranean shrubs, a quantitative description of several properties of the architecture of the root systems, such as topology (distribution of ramifications within the system) and morphology (size, link lengths, weight). Root system of adult plants growing in a Mediterranean coastal calcareous shrubland was extracted. Since post-fire regenerative strategies attributes can be constrained by taxonomical affiliations and life-form type, these two factors were considered in this study. I hypothesize that post-fire regenerative properties might impose particular differences on root system structures and properties related to nutrients and water uptake so that fire regimes affecting post-fire regenerative abundances may alter ecosystem functioning. More specifically, the following question is addressed: do post-fire regenerative groups differ on topological and morphological root systems properties?

MATERIALS AND METHODS

Study site and study species

The study site was located on the Massís del Montgrí, a protected Mediterranean calcareous coastal area located in the NE of Catalonia (north-east Iberian Peninsula, 42.16ºN, 3.24ºW). The vegetation is mainly dominated by open pine forests and by Mediterranean shrublands (Polo & Masip, 1987). The soil is a *Terra rossa*, a calcareous soil in which carbonates have been extensively lost through lixiviation but a great richness of calcium has been preserved. The studied soil presented a high abundance of stones (45.7 % of the soil were elements of more than 2 mm). The area's climate is sub-humid Mediterranean, according to the Emberger classification (Emberger, 1942). The mean annual precipitation is 654.6 mm and mean annual temperature is 14.8ºC, with cool winters (mean minimum annual temperature: 4.1ºC) and warm summers (mean maximum annual temperature: 26.8ºC) (Ninyerola *et al.*, 2000; Ninyerola *et al.*, 2003).

The study was carried out on a subset of eight woody plant species growing in an area of approximately 400 m^2. The selected species were representative of the studied community and belonged to two groups, according to their post-fire regenerative strategies: resprouters (R) and non-resprouters (NR). The resprouter group is constituted by species that only resprout (S- R+, *sensu* Pausas & Verdú, 2005) and species that both germinate and resprout after fire (S+ R+). Non-resprouters are species that germinate after fire but do not resprout (S+ R-). Species were assigned to one of these two groups according to information from the literature (Cucó, 1987; Papió, 1988; Lloret & Vilà, 1997; Verdú, 2000; Alberdi & Cavero, 2003; Lloret *et al.*, 2003), and after direct field observations in a nearby area that burned in September 2004. Five species were classified as resprouters (R): *Calicotome spinosa*, *Olea europaea*, *Pistacia lentiscus*, *Rhamnus alaternus*, *Thymus vulgaris*; and three as non-resprouters (NR): *Cistus albidus*, *Helianthemum appeninum* and *Rosmarinus officinalis*. The resprouters belonged to five families and the non-resprouters to two families (Table 1). Species that neither germinate nor resprout after fire (S- R-) were not considered as none were present in the studied community.

Species life-form was described according to (Raunkiaer, 1934) classification (Table 1): C = chamaephyte: with persistent buds situated 0.2 - 0.5 m height, NP = nano-phanerophyte: with persistent buds situated 0.5 - 2 m height, and MP = macro-phanerophyte: with persistent buds situated 0.5 - 5 m height.

Table 1. Mean and standard error for each one of the studied variables and study species. Family, post-fire regenerative strategy and life-form (according to Raunkiaer classification) are also indicated.
C, Chamaephyte; NP, Nano-phanaerophyte; MP, Macro-phanaerophyte.
RL , root length; SRL, specific root length; MRL, main root length; M, Magnitude; A, Altitude; Pe, External path; LL, length between links.

			Root : Shoot		RL (cm)		SRL ($m\ g^{-1}$)		MRL (cm)		M		P_e		A		TPI		LL (cm)	
Species	Family	Life-form	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Resprouters																				
Calicotome spinosa	Fabaceae	NP	0.48	0.11	995.15	316.85	46.41	14.32	124.70	88.00	118.60	28.65	1474.60	588.64	20.00	3.39	0.20	0.04	5.25	2.05
Olea europaea	Oleaceae	MP	0.51	0.06	346.72	118.15	13.97	5.40	89.27	24.47	75.60	27.34	1046.80	442.55	23.20	4.02	0.44	0.10	2.91	0.23
Pistacia lentiscus	Anacardiaceae	MP	1.05	0.11	653.10	284.82	22.42	5.41	50.68	18.74	133.00	55.16	1887.40	901.40	30.60	6.56	0.39	0.11	2.53	0.41
Rhamnus alaternus	Rhamnaceae	MP	0.79	0.08	340.45	60.61	15.43	4.56	88.44	22.25	55.20	13.55	483.60	148.35	18.80	2.33	0.42	0.09	5.66	0.91
Thymus vulgaris	Labiatae	C	0.99	0.16	721.07	133.46	79.96	22.76	23.08	1.78	120.40	23.54	610.20	70.33	15.00	1.00	0.15	0.03	2.83	0.29
Non-resprouters																				
Cistus albidus	Cistaceae	NP	0.34	0.06	368.51	116.04	34.90	12.69	87.14	48.18	36.20	11.07	250.80	79.77	11.60	1.89	0.44	0.12	4.76	0.40
Helianthemum appeninum	Cistaceae	C	0.42	0.03	107.54	38.71	159.79	45.17	18.70	5.16	20.17	8.10	188.33	111.14	8.33	2.79	0.53	0.17	1.29	0.44
Rosmarinus officinalis	Labiatae	NP	0.18	0.03	419.14	124.54	44.87	16.94	58.62	19.18	67.20	6.38	480.60	55.93	16.80	1.02	0.26	0.03	3.71	0.67

Plant collection

Below-ground and above-ground biomass of five individuals that did not suffer any fire during the last 15 years of each species was collected in the study site during May – June 2006. No evidence of disturbance affecting above-ground or under-ground organs was observed in any selected plant.

First, above-ground biomass was clipped and weighed, and the vegetation around the individual was cleared. Sampling of the root system was done by hand excavation helped with an air compressor (Rotair – MDVS – 110P) (Photograph 1).

Photograph 1. Picture of the root extraction technique.

This technique allowed the extraction of roots ≥ 0.1 cm of diameter. The estimated root depth for each individual depended on the substrate at each sampling point. I usually had to cut the sinker roots once the bedrock was reached, in spite that some roots could penetrate into narrow fissures of the bedrock. Otherwise, all lateral roots were extracted without particular problems.

Shrubland of the study site was between 0.5 and 1 meter height. Adult plants between 20 and 50 cm (for chamaephytes), and between 40 and 100 cm height (for macro-phanerophytes and nano-phanerophytes) were considered. Roots were rinsed with water to remove adhered soil that could alter morphology measurements. Each root system was placed on a white flat plastic sheet and was hooked so that it rested in two-dimensions. The white sheet with the spread root system was immediately photographed from a perpendicular angle at a resolution of 300 dpi (Nikon Coolpix 5700).

After photographing, each root system was oven-dried at 60ºC for 72 h and weighed.

Root measurements (Root topology and morphology)

The software Miramon 5.0 (Pons, 2004) was used to determine total root length (RL) (cm), the number of tips (root ending) and the number of links (part of the root were it ramifies) (*sensu* Fitter, 1987). The topology of the root system was analyzed using the parameters proposed by (Fitter, 1987) (Figure 1). External path (P_e) is the sum of the number of links in all paths from all external links to the base link. Altitude (A) is the number of links in the longest individual path length in the system. The magnitude (M) is the number of external links of the root system (i.e. the number of root tips in the root system). Root topology was described using the ratio of A : M as a topological index (TPI). This index was suggested by (Fitter, 1987; Fitter, 1991). Its minimum value is associated with a dichotomous branching system and the maximum value corresponds to a herringbone pattern. These minimum and maximum values vary with magnitude (M), so that the slope of a plot of A (or P_e) against M describes graphically the topological index. Concretely, TPI indicates if a branching deviates from a random growth model. A TPI value of 1 indicates a random branching structure, TPI < 1 indicates a dichotomous structure and TPI >1 points to a herringbone root system structure where branching is mainly confined to a main axis. For all individuals of each species, A and M were measured on the whole extracted root system.

Specific root length (SRL) (cm g^{-1}) was measured as the ratio between total root length and root dry mass.

The root-to-shoot biomass ratio (R:S) was also estimated as the below-ground (root) biomass divided by the above-ground (shoot) biomass.

The length of the main axis of the root system (MRL) (cm) was considered as a variable since it was an indicator of the maximum depth at which it was possible to extract the root system.

Link length (LL) (cm), was estimated as the mean of the inter-branch and root-tip distances.

Statistical analyses

Differences in the root morphology and topology between the species belonging to the two regenerative strategies were tested by using general linear mixed models (GLMM), where the dependent variables were RL, P_e, A, M, TPI, SRL, R:S, MRL and LL. I considered the post-fire regenerative strategy (resprouter (R) and non-resprouter (NR)) and life-form (chamaephyte, nano-phanerophyte and macro-phanerophyte, *sensu*

Raunkiaer, 1934) as fixed effects, and species as the random factor nested within family to control the effect of taxonomic affiliations. This approach ensured that the significance tests for the fixed-effect predictors were not biased by taxonomical affiliations (Blackburn & Duncan, 2001; Garland *et al.*, 2005; Sol *et al.*, 2007). In these analyses, the replicates were the five sampled individuals of each species.

To better approximate normality, RL, P_e, A, M, TPI, SRL, Root : Shoot and LL were transformed into their Log_e (i.e. in Log_e (SRL)).

Analyses were performed using Statistica 6.0 (Statsoft) and SPSS 13.0 (SPSS).

RESULTS

The present study confirms that all studied species show typical dimorphic root morphology. It consists of a main root with one or more deeply penetrating taps (sinker) roots, and a set of lateral roots radiating out (Figure 2a, 2b). Swollen structures at the base of the upper part of the root were observed in *Calicotome spinosa, Olea europaea*, *Pistacia lentiscus* and *Rhamnus alaternus.*

Topological differences between resprouters and non-resprouters species were found. Concretely, P_e, A, and M were significantly higher in resprouters than in non-resprouters (Table 2, Figure 3a, 3b, 3c). Moreover, there were also differences among life-forms in P_e and A so that chamaephytes presented lower values than macro-phanaerophytes, M was significantly different among families (Table 2, Figure 3a, 3b, 3c). TPI also differed among families (Table 2, Figure 3d) and significant differences between resprouters and non-resprouters appeared. Although in both regenerative groups TPI was <1, indicating that all the species tended to a dichotomous root system structure, TPI was higher in non-resprouters, pointing to a less branched root system. Resprouters showed a higher dichotomous, branched system.

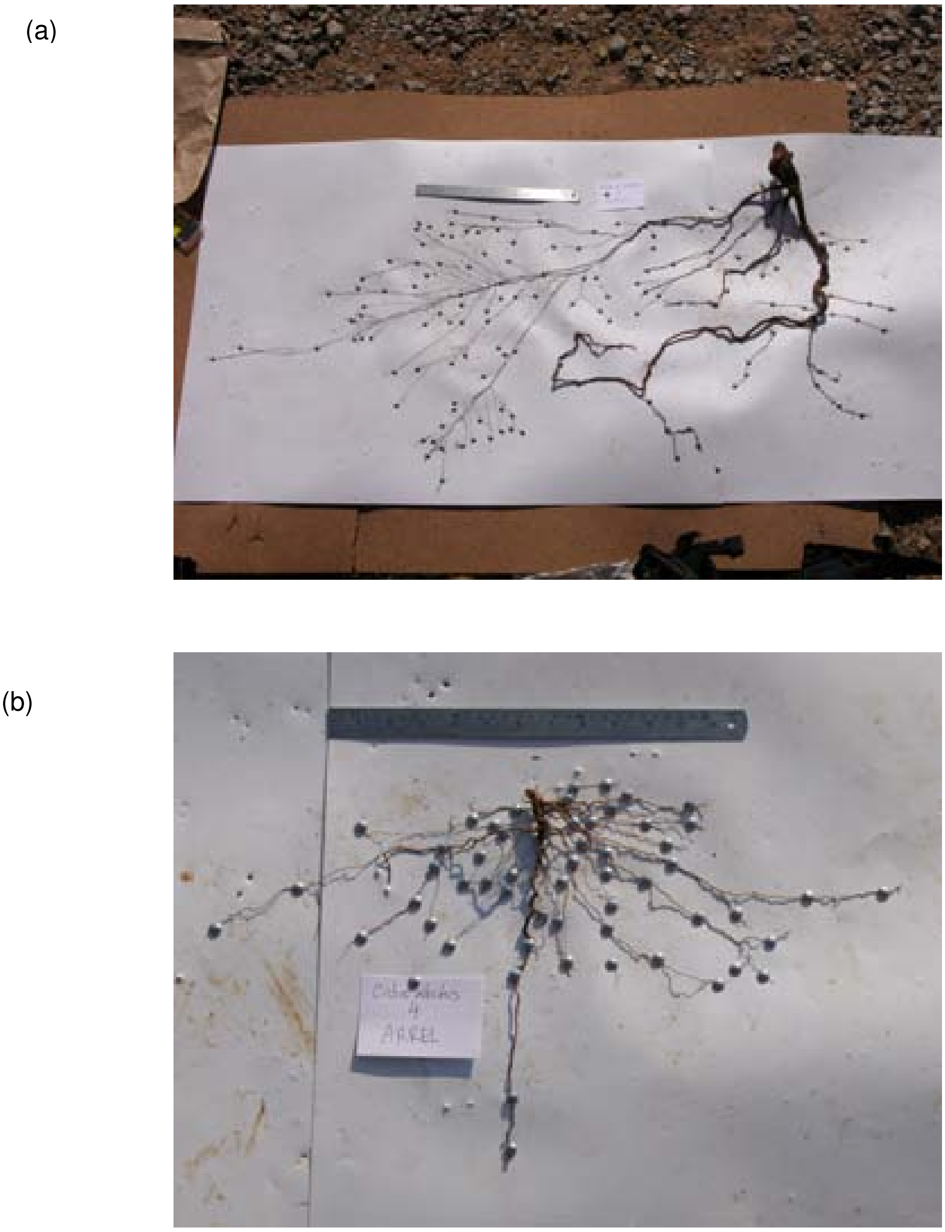

Figure 2. Examples of the dimorphic type of root system exhibited by the studied species, based on sinker roots and shallow lateral roots. (a) The resprouter *Pistacia lentiscus* shows a more dichotomous and branched root system. Note swollen lignotuber at the start of the root system. (b) The non-resprouter *Cistus albidus* shows a more herringbone-like, less branched root system.

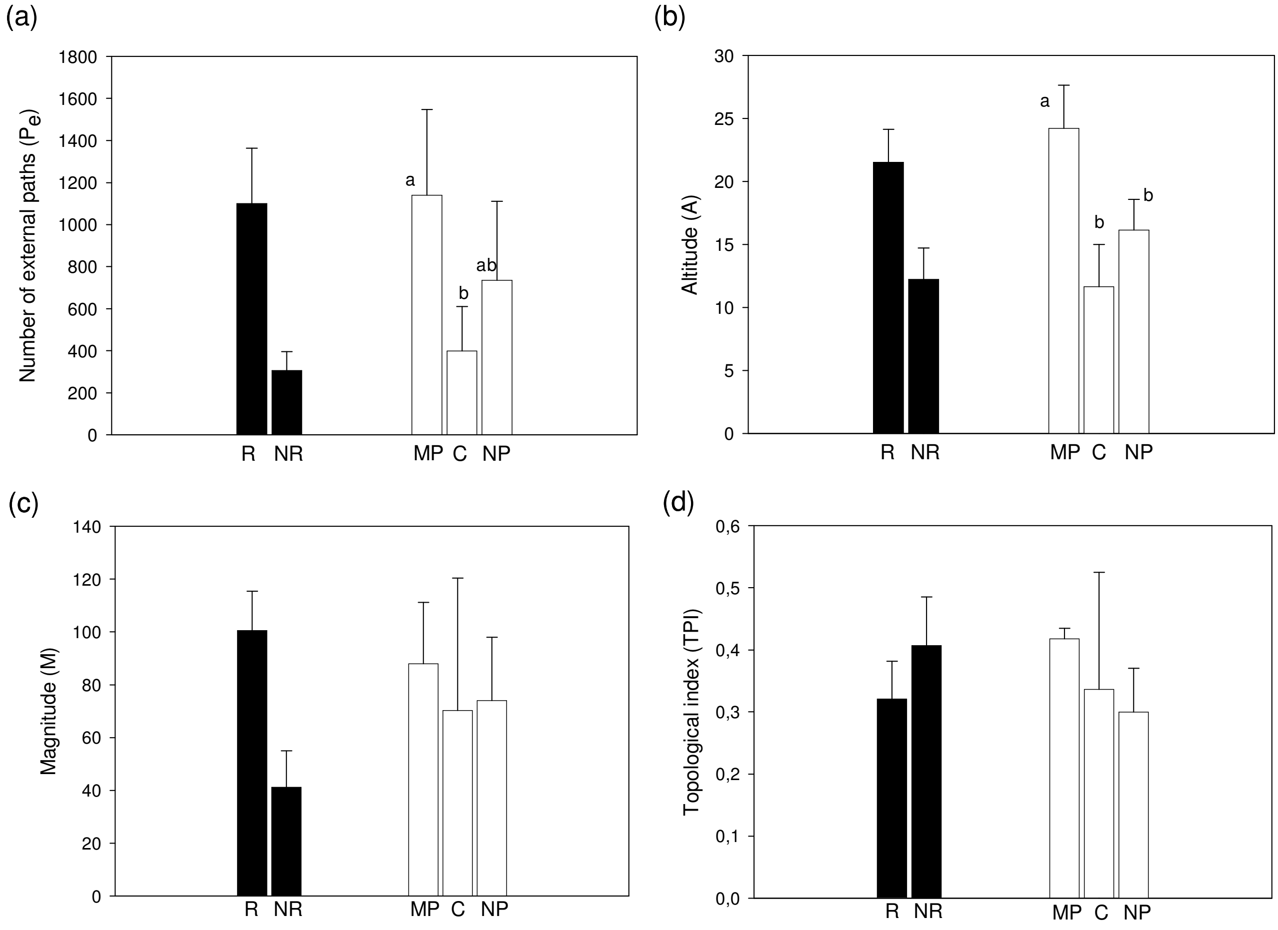

Figure 3. Mean of the External Path (P_e) (a), Altitude (A) (b), Magnitude (M) (c), the Topological index (TPI) (d) and standard errors for the different groups of species. White bars indicate post-fire regenerative groups: resprouters (R) and non-resprouters (NR); black bars indicate groups of species considering their life-form type, Chamaephyte (C), Nano-phanerophyte (NP), Macro-phanerophyte (MP). Significant differences among life-forms are indicated with letters (Fisher LSD post-hoc).

Table 2. Summary table of generalized linear mixed model (GLMM) accounting for variation in the nine variables respect to regenerative strategy factor (resprouters (S- R+ and S+ R+) and non-resprouters (S+ R-)), taxonomical affiliations and life-form (chamaephyte, nano-phanerophyte and macro-phanerophyte (*sensu* Raunkiaer, 1934). RL , root length; SRL, specific root length; MRL, main root length; M, Magnitude; A, Altitude; Pe, External path; LL, link length.** indicate significant results ($p < 0.05$).

	Post-fire regeneration		Life-form		Family (species)	
	F	p	F	p	F	p
RL	8,196	0,007**	2,926	0,097	3,114	0,021**
Root : Shoot	65,073	<0,001**	4,826	0,035**	8,361	<0,001**
M	12,550	0,001**	2,887	0,099	3,102	0,021**
P_e	9,289	0,005**	6,999	0,012**	2,249	0,072
A	6,095	0,019**	18,085	<0,001**	1,409	0,247
TPI	10,988	0,002**	2,519	0,122	3,121	0,021**
LMR	0,020	0,887	13,602	0,001**	1,196	0,332
SRL	0,022	0,882	18,274	<0,001**	1,490	0,220
LL	0,364	0,550	14,151	0,0001**	7,587	<0,001**

R : S was significantly higher in resprouters than in non-resprouters (Table 2, Figure 4). Life-form and taxonomical affiliation had a significant effect in this variable, being lower in nano-phanerophytes than in macro-phanerophytes and chamephytes (Figure 4).

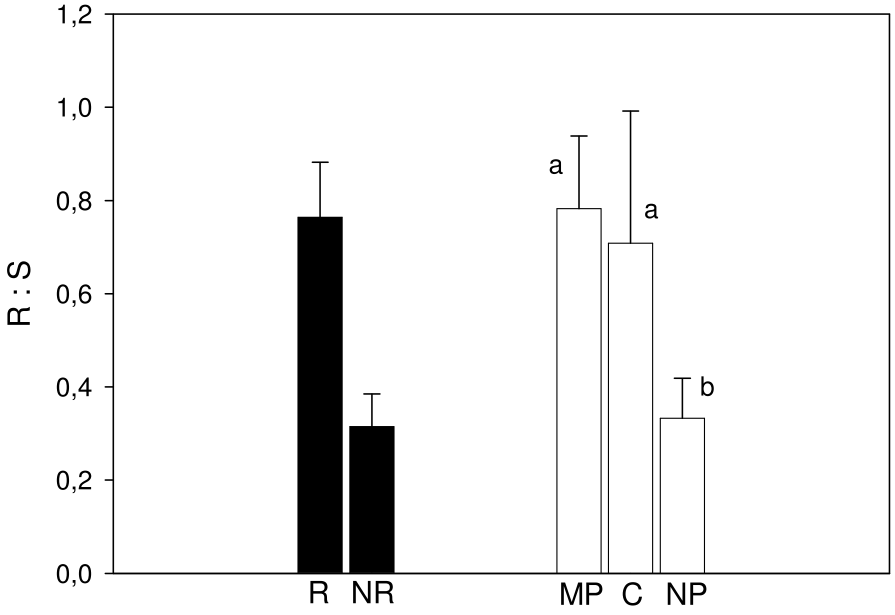

Figure 4. Mean of root-to-shoot mass ratio (R : S) and standard errors for the different groups of species. White bars indicate post-fire regenerative groups: resprouters (R) and non-resprouters (NR); black bars indicate groups of species considering their life-form type, Chamaephyte (C), Nano-phanerophyte (NP), Macro-phanerophyte (MP). Significant differences among life-forms are indicated with letters (Fisher LSD post-hoc).

There were significant differences in RL among families and between resprouters and non-resprouters (Table 2). RL was higher in resprouters (Figure 5a). MRL, SRL and LL only showed significant differences among life-form types. MRL was lower in chamaephytes than in macro-phanerophytes and nano-phanerophytes (Figure 5b). SRL was higher in the shorter species: chamaephytes > nano-phanerophytes > macro-phanerophytes (Figure 5c). Finally, LL was lower in chamaephytes than in nano-phanerophytes (Figure 5d).

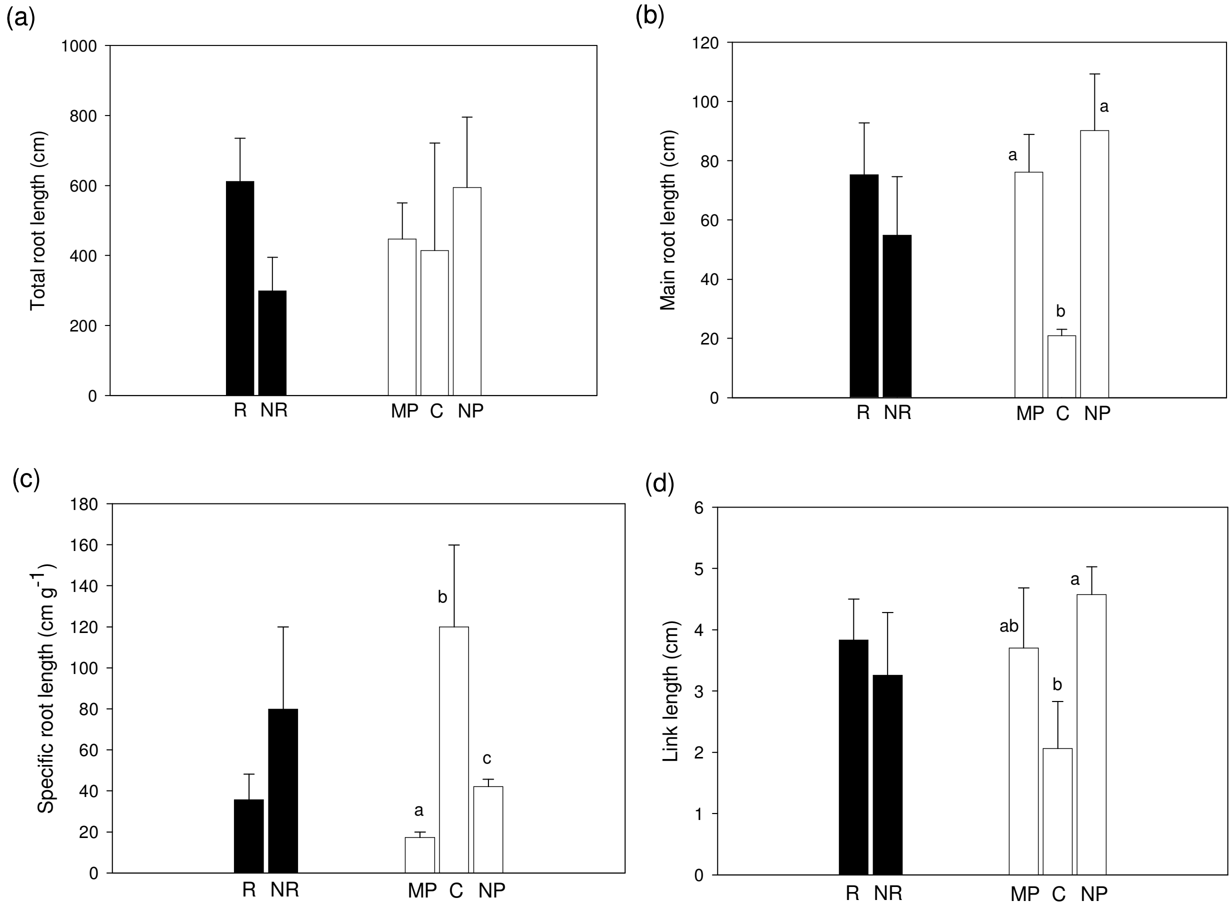

Figure 5. Mean of total root length (RL) (a), main root length (MRL) (b), specific root length (SRL) (c), link length (LL) (d) and standard errors for the different groups of species. White bars indicate post-fire regenerative groups: resprouters (R) and non-resprouters (NR); black bars indicate groups of species considering their life-form type, Chamaephyte (C), Nano-phanerophyte (NP), Macro-phanerophyte (MP). Significant differences among life-forms are indicated with letters (Fisher LSD post-hoc).

DISCUSSION

Other investigations in species from Mediterranean shrublands (Dawson & Pate, 1996; Guerrero-Campo *et al.*, 2006) support the obtained results describing a general pattern of typical dimorphic root morphology characterized by sinker and shallow lateral roots. The technique of root system extraction that was used in this study caused losses of roots with a diameter lower than 0,1 cm diameter. Therefore, there was an underestimation of some variables, such as those related to length or shoot-to-root mass ratio, but this shortcoming was assumed to have been similar for all species and individuals and not to be influential to the comparisons.

Results support the hypothesis that the capacity to resprout is related to root system structures and properties. Other linked factors such as taxonomical affiliation and life-form also have influence, but they do not change the main differences between post-fire regenerative strategies that are found in this study. TPI indicates that non-resprouters and resprouters shrubs both show a dichotomous root, instead a herringbone-like typology, that has been more often observed in herbaceous species (Fitter *et al.*, 1988; Roumet *et al.*, 2005). However, after accounting the effect of taxonomical affiliation, non-resprouters tend to have a less branched root system than resprouters. Concretely, compared to resprouters, non-resprouters have a pattern where each branch of the main root is less ramified; instead there are more roots that ramify from the main root. This pattern could be considered as intermediate between a herringbone and a fasciculate root system. However, resprouters show fewer ramifications from the main root but each one of them is highly branched and dichotomous. Root systems with higher TPI, more herringbone pattern (non-resprouters) are more effective at exploring and exploiting soil, and they are more efficient in the acquisition of nutrients over large soil volume, especially for resources of high diffusivity such as nitrate ions and water (Fitter, 1991). More branched, dichotomous systems (resprouters) have many high order laterals which typically have low growth rates and present more overlap between depletion zones (Fitter *et al.*, 1988; Dunbabin *et al.*, 2004). However, If the diffusivity is low, even the low growth rates of these root system allows it to exploit fresh soil, and the benefits of the herringbone topology are lost (Fitter & Hay, 1987). In conclusion, this study suggests that resprouters and non-resprouters show differences in the use of soil nutrients and water, likely associated of their different taxonomic affiliations.

Despite of the technical limitations, it was observed that resprouters have longer root systems than non-resprouters. Thus, the lower efficiency of its root system due to its dichotomous topology could be counteracted by length, allowing them a deeper soil exploration. A trend to grow deeper has been reported in roots from some other species with resprouting capacity (Kummerow, 1981; Clemente *et al.*, 2005), and they also tend to be thicker in order to penetrate trough soil horizons (Fitter, 1991). The longer root system as well as the observed higher root-to-shoot mass ratio in resprouter reflect an important investment in the below-ground organs, allowing the resources mobilization needed for resprouting after disturbances such as fire (Bell *et al.*, 1996; Iwasa & Kubo, 1997; Vesk & Westoby, 2004). The ability to resprout and survive fire, defoliation or drought depends on the presence of storage organs

(Bellingham & Sparrow, 2000), that provide space for nutrients and water storage (Canadell & Zedler, 1994). On the contrary, non-resprouters are defined by its high recruitment after fire, so the less branched root system may provide a better solution at the high seedling and sapling densities occurring after disturbances such as fire.

Taxonomical affiliations are very important in root topology, morphology features and R:S relationships (Guerrero-Campo *et al.*, 2006). Overall, the inclusion of taxonomical affiliation in the analyses reinforces the hypothesis of functional differentiation in relation to the use of resources among species with different response to disturbances.

Life-form is also an important factor determining ecosystem functional properties (Roumet *et al.*, 2005; Guerrero-Campo *et al.*, 2006). In the Mediterranean basin, post-fire regenerative groups of shrubs are also linked to life-form (Verdú, 2000; Pausas & Verdú, 2005) and likely to life span, with many resprouters being long-lived, macro-phanerophytes. Accordingly, the studied non-resprouters are chamaephytes and nano-phanerophytes. Macro-phanerophyte showed higher LL and MRL than chamaephytes or nano-phanerophytes, supporting that species with higher life-span develop higher root lengths. R:S followed the same pattern, that is, larger species with longer life-span showed higher root-to-shoot mass ratio.

Higher SRL is usually associated with rapid rates of root elongation (Eissenstat, 1992), high relative growth rate (Reich *et al.*, 1998; Comas *et al.*, 2002; Comas & Eissenstat, 2004) and high nutrients and water uptake capacities (Graham & Syvertsen, 1985; Reich *et al.*, 1998; Roumet *et al.*, 2005). From the point of view of the root properties, root systems can show a high SRL either because they have a small diameter or because they have a low tissue density (mass par unit of volume) (Chapin III *et al.*, 2002). Some below-ground stems and coarse roots have large diameters to store carbohydrates and nutrients or to transport water and nutrients, playing a minor role in nutrients uptake. Accordingly, SRL for chamaephytes was larger than for nano-phanerophytes, which in turn was higher than macro-phanerophytes. So, species with lower life-span tend to show lower SRL, in agreement to the expected patterns of higher resource acquisition and relative growth rate. (Craine *et al.*, 2001) suggested that both leaves and roots of slowly growing species often have high tissue density, low rates of resources acquisition but greater longevity than do leaves and roots of more rapidly growing species. This hypothesis agrees with the leaf economics spectrum, described by Wright *et al* (2004), running from species with high nutrient concentrations, short leaf life-span and low dry-mass investment per area to species with slow return of investments, long leaf life-span, high leaf construction costs, low nutrient concentrations, and high mass-based net photosynthesis and respiration. Results agree with the pattern described by Wright *et al.* (2004) because the species with a strategy of quick returns of carbon investments and nutrients (chamaephytes and nano-phanerophytes) roughly correspond to non-resprouter species. Anyway, other results of this study give evidence that non-resprouters have a root system more likely to optimize resource acquisition minimizing constructions costs (shorter, less branched and with low R:S). Since no significant differences on SRL between resprouters and no-resprouters were found, nutrients uptake and other properties related to SRL seems to be more linked to the life-form than to the capacity of resprouting itself. In fact, the SRL values of *C. spinosa* and *T. vulgaris* (which are S+ R+ species), nanophanerophyte and chamaephyte, respectively, are more similar to the values observed in non-resprouters, which have more similar life-form types.

In conclusion, the present study shows that resprouters differ from non-resprouters in terms of several key root morphological and topological properties. Topologically, resprouters are species with longer and more branched root system. They also show higher R:S relationship supporting their greater ability to store water and nutrients and to invest in the below-ground biomass. Moreover, this pattern probably allows them to explore deeper parts of the soil profile. While resprouters would benefit from a higher R:S and the presence of deeper roots, short-living species such as non-resprouters would benefit from a higher SRL and would have higher resource and water uptake properties due to the less branched root system as well as to the higher specific root length which is an indicator of higher relative root growth. As a result, this study suggests that resprouters and non-resprouters could be defined as well as different functional groups since they differ in the some of the main properties of the main resource and water acquisition plant organ, the root system. This study also suggests that the group of species that can both resprout and establish seedlings after fire (S+ R-) should be more explored to better understand their root system characteristics, which are likely to correlate to below-ground resource uptake and storage in relation to disturbances.

ACKNOWLEDGEMENTS

I would like to thank G. Calvo and Ll. Benejam for the field work, and M. Carabús for the help during the field sampling.

This study was funded by the Department of Universities, Research and Information Society of the Generalitat de Catalunya, the European social funds, and the Spanish MCYT projects REN 2003-07198 and CGL2006-01293/BOS. It also contributes to the European research group (GDRE) "Mediterranean and mountain ecosystems in a changing world" funded by the Generalitat de Catalunya and CNRS.

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IX. SÍNTESI

RESULTATS I CONCLUSIONS GENERALS

En aquest estudi s'ha mostrat com els grups regeneratius post-incendi són també grups d'espècies que funcionen de manera semblant en quant a l'ús de certs recursos (grups funcionals de resposta) com per exemple l'aigua o el fòsfor, així com també respecte a l'inflamabilitat de l'ecosistema. Com a conseqüència, d'aquest treball també se'n deriva que hi ha una sèrie de trets funcionals[8] que poden capturar les diferències entre els grups regeneratius post-incendi i per tant també alguns dels efectes dels règims d'incendis en el funcionament dels ecosistemes.

El fet que una pertorbació afecti a l'abundància d'un grup d'espècies o altres degut als seus trets de resposta en front una pertorbació com el règim d'incendis, pot provocar canvis en la composició i estructura de la comunitat, així com també pot afectar al funcionament de l'ecosistema (Figura 1). Per tant podem concloure que el règim d'incendis pot alterar el funcionament dels ecosistemes a través de canvis en les proporcions de tipus regeneratius post-incendi.

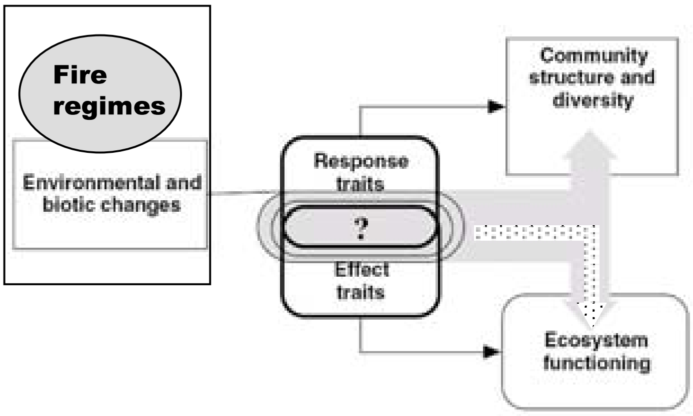

Figura 1. Adaptació del marc conceptual de relacions entre els canvis ambientals i el funcionament dels ecosistemes descrit per (Lavorel & Garnier, 2002). El règim d'incendis pot afectar a les espècies, que depenent de les seves característiques de resposta als incendis causen canvis en la composició d'espècies.

En aquest estudi s'estudien per primer cop un nombre important de trets en un gran nombre d'espècies llenyoses de la conca mediterrània en relació a la seva resposta als incendis. Per tant, aquest estudi aporta una caracterització de trets funcionals d'espècies de matollar mediterrani que pot ser clau pel coneixement d'aquests tipus d'ecosistemes i per futurs estudis sobre el seu funcionament.

Al llarg del treball s'han analitzat les diferències entre grups regeneratius post-incendi de manera separada per grups de variables relacionades. En aquest capítol, es fa una avaluació més integrada de les diferències entre grups regeneratius post-incendi

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[8] A cada capítol s'explica exactament quins són els trets i el tipus d'informació que donen.

respecte a les seves capacitats funcionals. Amb aquesta finalitat, s'han escollit 5 dels trets més rellevants per la informació funcional que proporcionen[9]. Concretament, aquests són: $\delta^{13}C$ de la fulla (C13), contingut de fòsfor foliar (LPC), contingut de matèria seca foliar (LDMCsat), percentatge de pes romanent en fullaraca després de 2 anys de descomposició (RMdec) i proporció de material fi mort (Dead fine fuel).

Després d'aplicar un anàlisi d'ordenació multivariant segons el procediment del "non-metric multidimensional scaling" (NMS), les espècies germinadores queden clarament agrupades respecte a les que pertanyen als altres grups. Segons aquesta ordinació les plantes germinadores tenen unes característiques semblants respecte a les variables considerades (l'eficiència en l'ús de l'aigua, el contingut de fòsfor foliar, la matèria seca de la fulla, la descomposició i el material fi mort de la planta) (Figura 2).

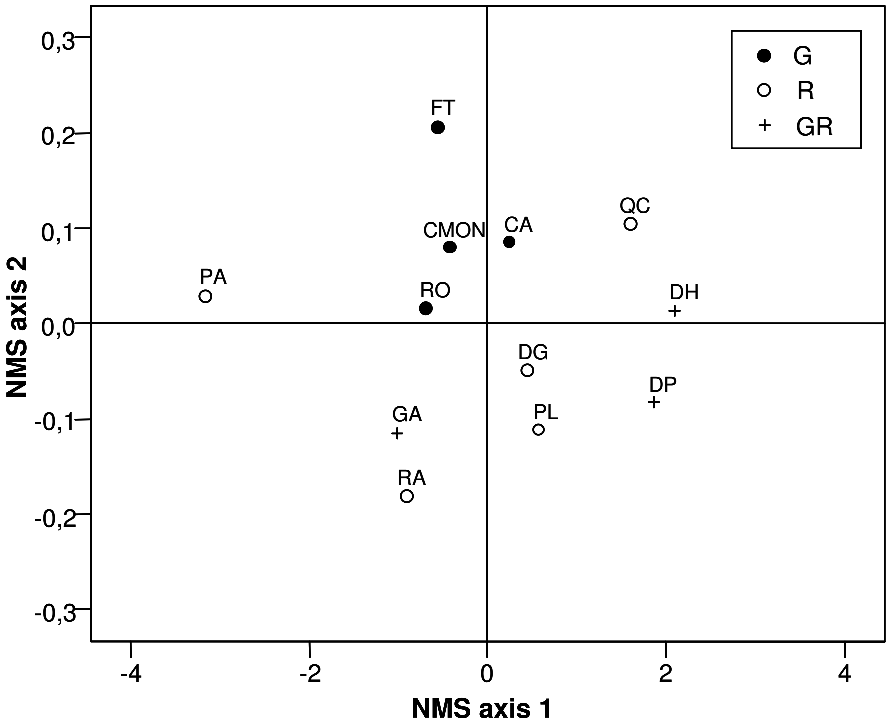

Figura 2. Espècies ordenades segons un "non-metric multidimensional scaling" (NMS), a partir d' algunes de les variables més destacades, durant l'estudi, per les seves diferències entre grups regeneratius post-incendi: $\delta^{13}C$ de la fulla, contingut de fòsfor foliar, contingut de matèria seca foliar, percentatge de pes romanent en fullaraca després de 2 anys de procés de descomposició i proporció de material fi mort de la planta. G = espècies germinadores, R = espècies rebrotadores, GR = espècies que germinen i rebroten. Les abreviacions de les espècies són les mateixes que s'han usat al llarg de la tesi.

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[9] La selecció d'un nombre petit de les variables es deu al relativament baix nombre de rèpliques (espècies) de que es disposa.

També s'ha aplicat un anàlisi de redundància (RDA) que determina el paper d'una sèrie de variables en la segregació d'un conjunt de mostres (espècies) en grups prefixats (grups regeneratius post-incendi) (Figura 3).

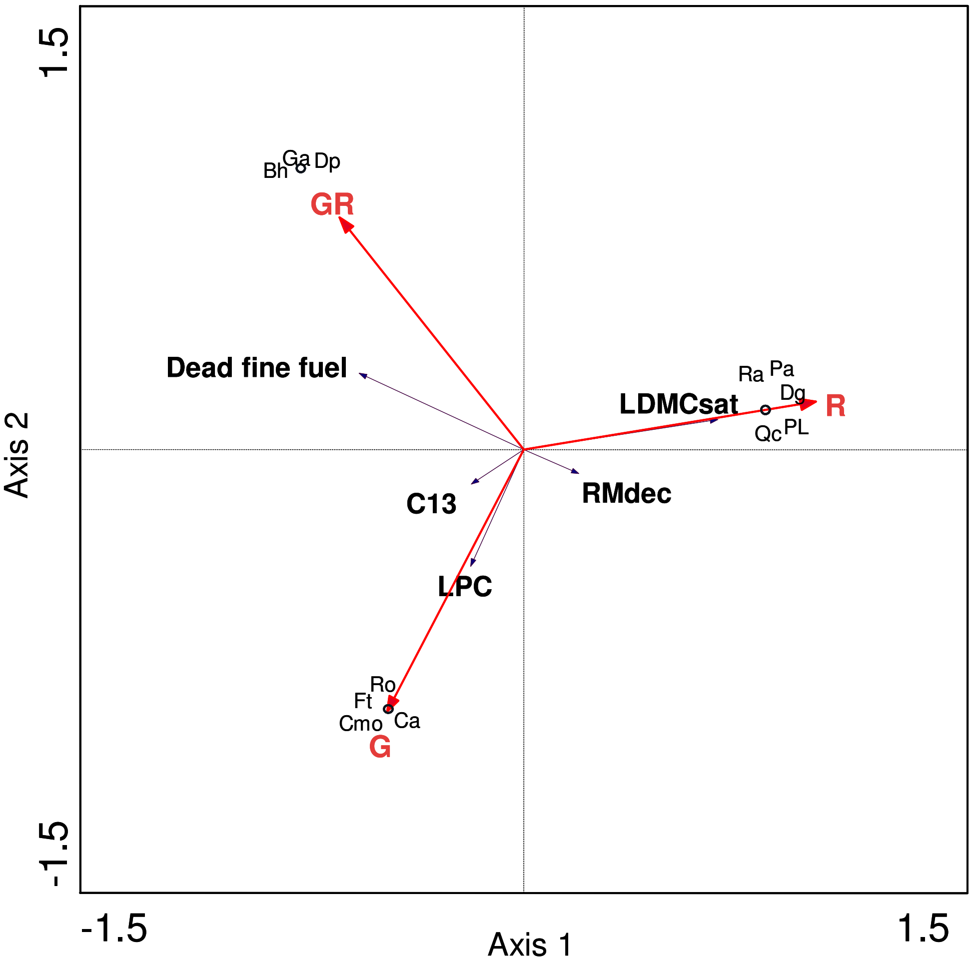

Figura 3. Ordenació de les espècies d'estudi segons la seva estratègia regenerativa post-incendi i les seves propietats d'ús de l'aigua, matèria orgànica, nutrients, descomposició i inflamabilitat. S'ha aplicat un anàlisis de redundància (RDA) on el 21.9 % de la variació total dels trets és explicada pel tipus d'estratègia regenerativa post-incendi . La correlació entre els trets i la regeneració post-incendi és de 72.9 % i l'axis 1 explica el 76.8 % de la variació en la relació trets-regeneració post-incendi, i l'axis 2 la resta, 23.2%. L´axis 1 explica el 16.8 % de la variació entre els trets i l'axis 2 el 5.1 %. El test de Monte Carlo revela relacions marginalment significatives entre els trets i la variable ambiental *germinador-no germinador* (F= 1.98, p=0.08). Els valors de C^{13} estan en positiu, per tant, en la figura cal llegir, a més C13, menys eficiència en l'ús de l'aigua.

El resultat de la RDA indica que les rebrotadores es poden considerar un grup funcional definit per alts valors de contingut de matèria seca foliar i per tant per unes fulles que triguen més a descompondre's, una major eficiència en l'ús de l'aigua i uns baixos continguts de fòsfor a les fulles. També presenten una baixa proporció de material fi mort i per tant una menor inflamabilitat respecte als altres dos grups. En canvi les germinadores es caracteritzen per ser un grup funcional amb poc contingut de matèria seca a la fulla, una descomposició més ràpida en les fulles, una menor eficiència en l'ús de l'aigua, uns majors nivells de fòsfor a les fulles i una major inflamabilitat. El tercer grup regeneratiu, (les espècies rebrotadores-germinadores) sembla que funcionalment seguiria patrons més semblants als de les germinadores pel que fa a l'ús de l'aigua, la inflamabilitat, i la descomposició de la fullaraca, però en canvi no pel que fa al contingut de nutrients. Tanmateix, el grup germinador-rebrotador arbustiu precisaria d'un estudi més detallat donada la variabilitat taxonòmica, de forma de creixement i de cicle de vida que presenta.

També s'han estudiat les relacions causals entre alguns trets foliars estudiats, així com les relacions causals entre aquests trets i la capacitat de regenerar-se després d'un incendi (Figura 4).

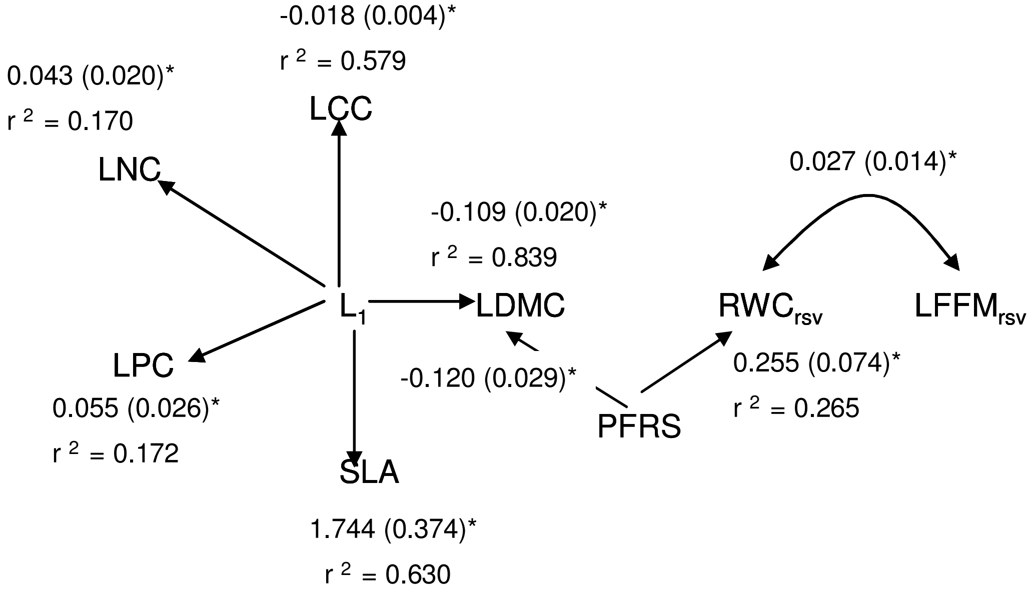

Figura 4. Relacions causals obtingudes entre l'estratègia renerativa post-incendi i els trets foliars estudiats[10]. Al model hi ha els "path coefficients", i els errors estàndards en parèntesis. * indica si el "path coefficient" és signficatiu. Els valors de r^2 també estan al model. L_1 és la variable latent proposada i que representa la ratio del volum ocupat pel citoplasma respecte al volum ocupat per les parets cel.lulars.

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[10] Per a més informació sobre la metodología emprada en l'anàlisis causal i la seva interpretació, mirar el capítol IV

Aquest anàlisi apunta que el fet de pertànyer a una estratègia post-incendi o a una altra determina els continguts de matèria seca de la fulla, així com també les variacions del contingut foliar d'aigua entre estacions. El fet que una espècie tingui una estratègia regenerativa post-incendi o una altra pot estar lligat a l'adaptació de les espècies al foc així com també a d'altres factors relacionats amb l'evolució de les espècies, com ara el clima. Per exemple, les germinadores són espècies que mostren una baixa eficiència en l'ús de l'aigua així com una estratègia de tolerància a la sequera. Per tant, aquestes particularitats podrien tenir una estreta relació amb el dèficit hídric típicament mediterrani. Així doncs, ja sigui per qüestions evolutives relacionades amb el clima o bé amb el foc[11], el fet de tenir un tipus de regeneració pot determinar les característiques dels seus trets funcionals.

L'àrea específica foliar[12] (SLA) i el contingut de matèria seca de la fulla[13] (LDMC) reflecteixen un "trade-off" fonamental en el funcionament de les plantes entre una ràpida producció de biomassa (espècies amb alt SLA i baix LDMC) i una eficient conservació de nutrients (espècies amb baix SLA i alt LDMC) (Poorter & Garnier, 1999). En aquest estudi es conclou que les espècies amb capacitat germinadora tendeixen a tenir menys LDMC i les no-germinadores més LDMC (Figura 4)[14], de manera que les germinadores tindrien una producció de biomassa més ràpida i una menor eficiència en la conservació de nutrients, així com probablement també una major fracció de volum de la fulla ocupada per mesòfil[15] (Garnier & Laurent, 1994; Garnier *et al.*, 2001a). Per tant, tot sembla indicar que les germinadores són espècies de creixement més ràpid tal i com altres estudis suggereixen (Paula & Pausas, 2006). En el grup de les rebrotadores es segueix una relació negativa entre el SLA i el LDMC, d'acord amb el patró esperat. Però no succeeix així en el grup de les germinadores i en el de les germinadores-rebrotadores (Figura 5). S'esperaria que les germinadores, que tenen menys matèria seca foliar (LDMC), tinguessin un major SLA (Figura 5). Els resultats semblen apuntar cap al fet que les germinadores tinguin baixos valors d'àrea foliar respecte al seu pes sec en comparació a les rebrotadores, fet que podria estar lligat amb l'estratègia d'aquestes espècies de ràpid creixement i poca producció de biomassa i poca eficiència en l'ús de recursos. Els baixos valors de SLA de les espècies estudiades (germinadores: 7.1 m^2 kg^{-1}, Taula 1) també poden explicar la manca de relació entre SLA i LDMC. Garnier *et al.* (2001b) van descriure que quan el

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[11] Encara avui no hi ha cap estudi que hagi pogut concloure una o altra força.
[12] La ratio entre l'àrea foliar i el pes sec de la fulla.
[13] La ratio entre el pes sec de la fulla i el pes fresc d'aquesta.
[14] Veure també el capítol II.
[15] El teixit on té lloc la fixació de CO_2.

SLA és baix (per sota dels 6-7 m^2 kg^{-1}), aquest és relativament independent dels canvis en el LDMC. però aquest dependència es torna substancial en fulles amb un SLA major que 10-15 m^2 kg^{-1}. Per tant, aquest estudi dóna suport a la idea que en espècies llenyoses, en les que normalment la seva SLA és baixa, no té perquè complir-se sempre la relació entre LDMC i SLA. Estudis fets amb més nombre d'espècies llenyoses així com també anàlisis més detallats dels teixits foliars podrien aportar més informació sobre aquesta relació.

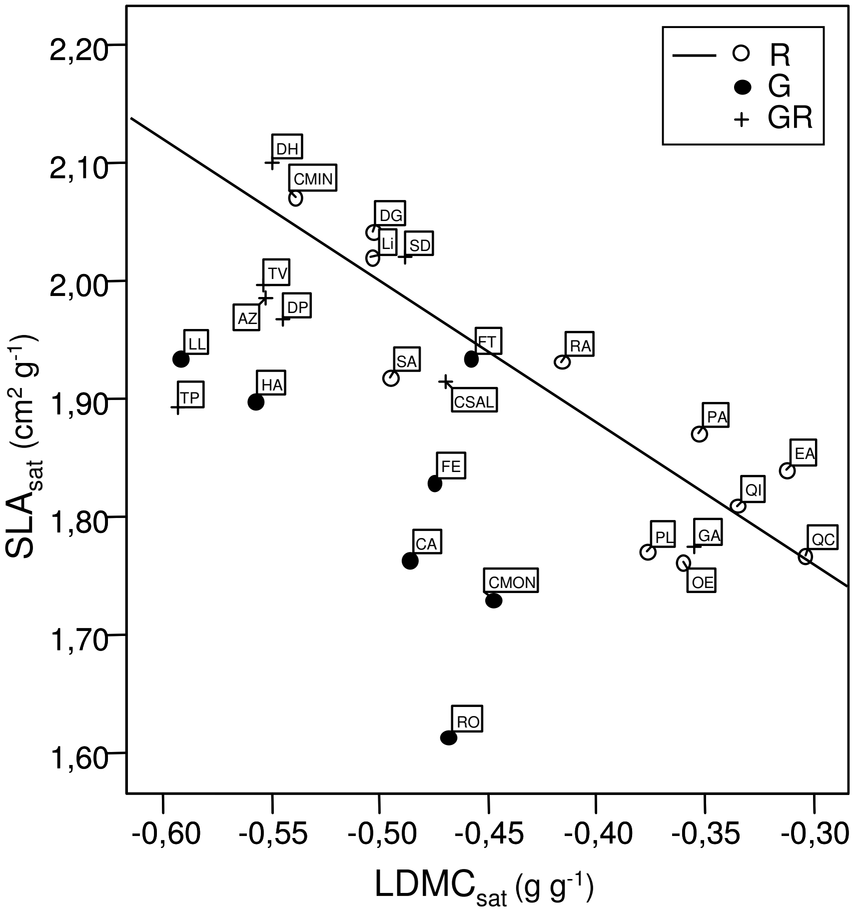

Figura 5. Regressió linear entre el log(x) de la superfície específica foliar (SLA_{sat}) i el contingut de matèria seca de la fulla saturat ($LDMC_{sat}$)[16]. R = rebrotadora, G = Germinadora, GR = Germinadora-rebrotadora.
Les espècies rebrotadores presenten una relació negativa (y = 1.412- 1.172 (x)) i significativa (R^2 = 0.80, $p < 0.001$) entre les dues variables, de manera que a menys SLA_{sat}, més LDMC. Els altres dos grups, germinadores i germinadores-rebrotadores no segueixen una relació clara ni significativa entre els dos trets foliars (germinadora: R^2 = 0.31, p = 0.19; germinadora-rebrotadora: R^2 = 0.39, p = 0.10) .

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[16] Per a més informació sobre la definició de les variables, mirar el capítol IV.

Taula 1 Valors del SLA$_{sat}$ per a les espècies d'estudi. La família i l'estratègia regenerativa de cada espècie estan indicades.

		Regenerative strategy		
Study Species	**Family**	**Seeding**	**Resprouting**	**SLA (m^2 Kg^{-1})**
Argyrolobium zanonii (Turra) P. W. Ball	Leguminosae	+	+	9,667
Cistus albidus L.	Cistaceae	+	-	5,811
Cistus monspeliensis L.	Cistaceae	+	-	5,378
Cistus salviifolius L.	Cistaceae	+	-	8,221
Coronilla minima L.	Leguminosae	-	+	11,798
Daphne gnidium L.	Thymelaeaceae	-	+	11,011
Dorycnium hirsutum (L.) ser. In DC.	Leguminosae	+	+	12,611
Dorycnium pentaphyllum Scop.	Leguminosae	+	+	9,265
Erica arborea L.	Ericaceae	-	+	6,925
Fumana ericoides (Caav.) Gandg.	Cistaceae	+	-	6,757
Fumana thymifolia (L.) Spach.	Cistaceae	+	-	8,607
Globularia alypum L.	Globulariaceae	+	+	5,959
Helianthemum appeninum (L.) Miller	Cistaceae	+	-	7,928
Lavandula latifolia Med.	Labiatae	+	+	8,610
Lonicera implexa Aiton	Caprifoliaceae	-	+	10,478
Olea europaea L.	Oleaceae	-	+	5,792
Phillyrea angustifolia L.	Oleaceae	-	+	7,444
Pistacia lentiscus L.	Anacardiaceae	-	+	5,908
Quercus coccifera L.	Fagaceae	-	+	5,859
Quercus ilex L.	Fagaceae	-	+	6,461
Rhamnus alaternus L.	Rhamnaceae	-	+	8,551
Rosmarinus officinalis L.	Labiatae	+	-	4,110
Smilax aspera L.	Liliaceae	-	+	8,301
Staehelina dubia L.	Compositae	+	+	10,466
Teucrium polium L.	Labiatae	+	+	7,811
Thymus vulgaris L.	Labiatae	+	+	9,928

Així doncs, el fet que en una comunitat hi dominin espècies amb una capacitat regenerativa post-incendi o una altra, com per exemple les germinadores, determinarà que a l'ecosistema hi dominin espècies amb una taxa de creixement ràpid però una baixa eficiència en l'ús de recursos.

Els resultats obtinguts per a cada grup regeneratiu depenen, òbviament, de les espècies que el formen. Així, la història evolutiva lligada al clima, als incendis i a altres factors adaptatius han estat claus al determinar molts dels patrons obtinguts pels diferents trets funcionals.. Això queda palès al llarg de la tesi ja que es veu com hi ha certs trets funcionals estretament lligats a les afiliacions taxonòmiques o bé al tipus de forma de vida. Concretament, l'afiliació taxonòmica és clau per explicar les variables més intrínseques de les plantes, és a dir, aquelles que són menys influenciades per factors ambientals, com per exemple el contingut de matèria seca de la fulla, el contingut foliar de nutrients, la descomposició foliar, o algunes característiques del sistema radicular. El tipus biològic té una forta influència en el contingut i eficiència en l'ús de l'aigua, així com també en alguns paràmetres de descomposició foliar i en les característiques dels sistemes radiculars.

A més, aquest treball suggereix que el fet que les espècies s'originessin durant el Terciari o el Quaternari pot ésser clau per entendre les característiques regeneratives, així com també els trets relacionats amb el cicle de vida. Segons aquesta hipòtesi, el clima en el que van aparèixer les espècies pot ser la principal font d'explicació dels patrons funcionals i regeneratius observats.

No és estrany, doncs, que els resultats de la caracterització funcional dels grups regeneratius post-incendi d'espècies llenyoses variïn en les diferents regions mediterrànies del món, ja que els tipus biològics i la taxonomia de les espècies germinadores i les rebrotadores varien segons la regió. Aquesta conclusió està en concordança amb el treball de Pausas *et al.* (2004) on s'estudia la relació entre els trets de regeneració post-incendi i altres trets de les plantes a escala global[17]. Una de les conclusions principals d'aquest estudi és que la relació entre el tipus de regeneració post-incendi i els trets de les plantes varia entre continents i entre ecosistemes. Els autors proposen que, per exemple, no totes les rebrotadores responen de manera similar a tot arreu perquè els trets associats a les espècies rebrotadores poden variar en llocs diferents. Un exemple més concret el trobem a Sud-àfrica, on les espècies germinadores pertanyen a tàxons molt diferents als d'aquí i en general són més altes que les rebrotadores (Midgley, 1996), al contrari del patró que predomina en el matollar de la conca mediterrània, on les germinadores són en general més baixes (nanofaneròfits i camèfits) que les rebrotadores (macro-faneròfits).

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[17] Comparant dades de plantes de les 5 regions mediterrànies del món.

ALGUNES FUTURES LÍNIES DE RECERCA

Moltes de les conclusions d'aquesta tesi porten a tot un món nou on investigar i a possibles hipòtesis, principalment en dos camps de l'ecologia: l'ecologia funcional i l'ecologia del foc.

Alguns dels trets funcionals utilitzats durant l'estudi i la seva repercussió en el funcionament de les plantes ja han estat força estudiats[18] (Cornelissen *et al.*, 2003). En alguns casos també s'han aplicat per estudiar el funcionament de comunitats i la seva relació amb pertorbacions com la pastura (Garnier *et al.*, 2004; Shipley, 2006; Quétier *et al.*, 2007). Però els efectes que pot provocar en l'ecosistema el fet de tenir valors més alts o més baixos d'alguns dels trets estudiats (com ara el contingut de $\delta^{13}C$, els trets d'inflamabilitat o els de nutrients com el fòsfor o altres micronutrients) encara no han estat gaire descrits.

Les conclusions d'aquesta tesi són conclusions per a espècies i grups d'espècies i permeten extreure'n hipòtesis i idees, però és difícil fer l'aproximació dels efectes a nivell de comunitat només amb les dades obtingudes. L'aplicació a nivell de comunitat dels trets descrits per les espècies pot ser merament additiva, però probablement les múltiples interelacions que es produeixen en realitat dins dels ecosistemes donen peu a nous escenaris i relacions.

Ara bé, s'estan fent avenços en aquest sentit i les dades d'aquest estudi podrien col.laborar en el "scaling up" des dels trets de les espècies al funcionament de les comunitats vegetals. Shipley *et al.* (2006) han elaborat un model en el que, a partir de trets de les plantes[19] com els que s'han estudiat en aquesta tesi, i usant models matemàtics predictius, han establert un model que permet determinar l'evolució d'una comunitat vegetal al llarg del temps[20].

La majoria d'estudis en aquest camp de l'ecologia funcional s'han dut a terme amb bases de dades a nivell global o amb bases de dades on predominen les espècies herbàcies (Reich *et al.*, 1997; Garnier *et al.*, 2001a; Wright *et al.*, 2004). Aquest treball ho fa amb un grup nombrós d'espècies llenyoses del matollar mediterrani, i obre les portes a continuar explorant els trets funcionals en ecosistemes dominats per llenyoses per tal de comprovar si les hipòtesis desenvolupades a altres escales i amb

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[18] Com per exemple el LDMC, SLA o LNC.

[19] El que a la bibliografía es coneix com a "plant trait", alguns d'ells estudiats en aquesta tesi.

[20] Model que prediu el 94 % de la variancia en les abundàncies relatives

altres grups d'espècies ocorren també en altres grups com les espècies llenyoses de matollar mediterrani.

Des d'un punt de vista de l'ecologia del foc, una de les principals línies que en podrien derivar d'aquesta tesi està relacionada amb les espècies facultatives, és a dir, que poden rebrotar i germinar després d'un incendi. Aquest grup, a nivell funcional sovint es comporta com a germinadora però de vegades com a rebrotadora. Així doncs estudis més detallats sobre la seva biologia i la seves capacitats regeneratives podrien ajudar a concloure si es poden considerar un grup funcional a part dels altres dos grups regeneratius o bé si caldria considerar-les dins d'un dels dos grups d'espècies (germinadores o rebrotadores).

El capítol d'inflamabilitat aporta més dades al coneixement de les capacitats inflamables de les espècies llenyoses mediterrànies. En aquesta tesi s'han pogut valorar alguns aspectes relacionats amb les característiques foliars i de les diferents fraccions de combustible, però d'altres propietats lligades amb la inflamabilitat podrien ser estudiades amb més profunditat.

A la conca mediterrània es fa difícil intentar estudiar si les capacitats de regeneració post-incendi (rebrotar o germinar) són fruit d'una adaptació al foc de manera que hi pugui haver[21] espècies nascudes per morir". La dificultat rau principalment en dues raons: és difícil discernir la possible adaptació al foc de l'adaptació al clima, i no hi ha cap espècie llenyosa que depengui exclusivament del foc per a reproduir-se[22]. Per tant, més estudis per intentar esbrinar l'origen adaptatiu de les capacitats regeneratives després d'un incendi a la conca mediterrània aportarien avenços en aquest camp.

Una altra aproximació interessant seria fer comprovacions empíriques de camp de com aquesta diferència de trets repercuteix en el funcionament de l'ecosistema quan domina un tipus o altre d'estratègia regenerativa, així com també relacionar aquests patrons amb la història passada dels règims d'incendis.

Pel que fa al contingut de nutrients, aquest treball apunta a una major acumulació de fòsfor en les fulles de les germinadores. Estudis sobre l'eficiència en l'ús del fòsfor i el

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[21] El que a la bibliografía es coneix com "species that are born to burnt" **Zedler PH. 1995.** Are some plants born to burn? *Trends in Ecology and Evolution* **10**(10): 393-395.
[22] En referència a la zona estudiada, a la conca mediterrània Oest.

paper que juga en el cicle de vida de les germinadores podria ser de gran interès per tal d'entendre la biologia d'aquestes plantes així com també aprofundir en el cicle del fòsfor en els ecosistemes mediterranis en relació als incendis.

APORTACIONS PER A LA GESTIÓ D'ECOSISTEMES AMB RISC D'INCENDI

Els models de comportament d'un ecosistema basats en les propietats funcionals de les espècies sota diverses situacions, com el règim d'incendis, poden ser útils pels gestors del territori, al permetre entendre millor les dinàmiques dels ecosistemes (Keane *et al.*, 2004). Lluny d'intentar gestionar els ecosistemes merament com a llistats d'espècies i tàxons, entendre el seu funcionament i tractar-los a través dels grups funcionals d'espècies també pot permetre avançar molt en la gestió dels ecosistemes com a conjunt.

A partir dels resultats obtinguts en aquesta tesi, com per exemple el contingut de nutrients foliar de les espècies, es podria extrapolar la quantitat de nutrients foliars que hi ha en un ecosistema de matollar mediterrani. Per tal de fer això caldria desenvolupar un sistema adequat on es tinguessin en compte , l'abundància de cada espècie i el contingut de nutrients. D'aquesta manera el gestor/a podria tenir informació sobre la riquesa en nutrients de la comunitat. Aquesta aproximació es podria aplicar a d'altres trets funcionals estudiats com ara la quantitat d'aigua foliar o la descomposició i aportació de nutrients al sòl.

El règim d'incendis pot determinar les proporcions de grups regeneratius. Per exemple, altes recurrències d'incendis poden fer baixar la capacitat rebrotadora o la germinadora, i per tant canviar també les proporcions presents. S'ha demostrat que com que els grups regeneratius són grups funcionals diferents el règim d'incendis pot afectar les propietats funcionals de l'ecosistema en qüestió a través de la seva influència en la composició de la comunitat. Per exemple, si en una zona, com ara el massís del Montgrí, hi ha molta abundància d'espècies de matollar germinadores, voldrà dir que la comunitat vegetal tendirà a tenir un baix contingut de matèria seca a la fracció foliar, una descomposició més ràpida de les fulles, una menor eficiència en l'ús de l'aigua, majors nivells de fòsfor a les fulles i una major inflamabilitat[23]. En canvi, una comunitat dominada per rebrotadores tendirà a tenir un patró oposat respecte aquests trets de les plantes.

Així doncs, si amb un tipus de gestió[24] es promou més un grup regeneratiu d'espècies o altre, es promouran també grups funcionals diferents i per tant això pot provocar canvis en el funcionament de l'ecosistema, a més dels canvis que pot implicar el simple fet de canviar la composició i estructura de la vegetació.

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[23] Mirar el capítol VI per veure més en detall quines diferències hi ha entre grups regeneratius respecte al risc d'incendi, ja que d'altra banda les germinadores tenen menys biomassa combustible.

[24] Ja sigui estassada, crema controlada, pastura, o abandonament.

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X. CONCLUSIONS

CONCLUSIONS

A continuació s'enumeren les conclusions principals obtingudes en cada capítol d'aquesta tesi doctoral:

II. LEAF AND SHOOT WATER CONTENT AND LEAF DRY MATTER CONTENT

- Aquest estudi revela diferències importants en alguns trets foliars relacionats amb l'aigua i el contingut de matèria seca en espècies amb diferents estratègies regeneratives post-incendi durant diverses estacions de l'any.

- Les variables foliars relacionades amb el contingut d'aigua (LM, LFFM i RWC[25]) presenten variacions estacionals (el menor contingut és a l'estiu i el major entre l'hivern i la tardor) mentre que no ho fa el contingut en matèria seca de la fulla ($LDMC_{sat}$).

- Les espècies rebrotadores tenen major contingut de matèria seca de la fulla, en relació al seu pes foliar saturat ($LDMC_{sat}$), que les espècies germinadores.

- Les germinadores tendeixen a guanyar i perdre aigua més fàcilment que les rebrotadores, mentre que aquestes no pateixen grans diferències en el seu contingut d'aigua al llarg de les estacions. Per tant, les germinadores tendeixen a presentar trets relacionats amb una "tolerància a la sequera", és a dir, a arribar a tenir baixos continguts d'aigua durant les èpoques d'estiu. Pel contrari, les espècies rebrotadores tendeixen a mostrar una estratègia d'"evitar la sequera", mantenint els seus continguts d'aigua més estables al llarg de l'any.

- Pel que fa a l'ús de l'aigua, el grup germinador-rebrotador tendeix a seguir una estratègia més semblant a la de les germinadores que a la de les rebrotadores.

La similitud filogenètica contribueix a explicar la variabilitat entre les espècies pel que respecta al contingut de matèria seca de la fulla, però no pel que fa a altres trets més lligats directament a la variabilitat ambiental, com el contingut d'aigua de fulles i branquillons (RWC, LM, LFFM).

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[25] Veure el capítol II per la nomenclatura utilitzada al definir els trets de les plantes.

III. LEAF NUTRIENT CONTENT

- Les espècies rebrotadores difereixen de les espècies no-rebrotadores en alguns dels seus continguts foliars de nutrients.

- Les rebrotadores tenen major contingut de C foliar que les no-rebrotadores, probablement pel fet que les rebrotadores tenen un cicle de vida més llarg i unes taxes de creixement menors que fan que hi hagi una major acumulació de matèria seca a la fulla.

- Pel que fa als altres nutrients (P, N, Ca, K, Na, Mg) les no-rebrotadores tenen valors més alts de contingut foliar excepte en el cas del N. Cal esmentar que el P, el C i el Ca són els nutrients amb diferències més evidents entre estratègies regeneratives.

- Les rebrotadores tenen major N:P ratio foliar.

- L'estudi suggereix que les rebrotadores tindran més limitació per P que les no-rebrotadores en ecosistemes de matollars calcaris mediterranis com l'estudiat.

- Per tant, les diferències observades entre grups regeneratius en el contingut foliar de nutrients impliquen que canvis en les proporcions d'estratègies regeneratives degudes al règim d'incendis, podrien causar efectes en el cicle de nutrients, especialment el del C, P i Ca.

- Les relacions taxonòmiques de les espècies tenen un paper rellevant a l'hora d'explicar les variacions trobades en el contingut de nutrients de les diferents estratègies regeneratives, especialment pel que fa al contingut foliar de Fòsfor i el de Carboni.

IV. TESTING CAUSALITY ON LEAF TRADE-OFFS IN MEDITERRANEAN WOODY SPECIES: POST-FIRE REGENERATIVE STRATEGY LINKS WATER REGULATION AND LEAF DRY MATTER CONTENT

- Aquest estudi suggereix que els trets foliars estudiats i les relacions entre ells són deguts a restriccions morfològiques i fisiològiques en la construcció de les fulles. Els resultats obtinguts concorden amb el patró descrit en altres treballs realitzats a partir de bases de dades de trets foliars d'espècies de diferents parts del món, suggerint que la resposta selectiva als gradients ambientals té un paper menor en el conjunt de relacions entre els trets foliars.

- A més, es conclou que la relació entre la variació interespecífica anual del contingut d'aigua i el contingut de matèria seca de la fulla és deguda a forces selectives associades a les estratègies regeneratives post-incendi. Donat que moltes de les germinadores van evolucionar sota un clima mediterrani, podrien haver desenvolupat una estratègia particular de tolerància a la sequera (sense causar un efecte en la relació entre el volum del citoplasma i el de la paret cel.lular) que podria ser la causa de la relació observada entre el LDMC i la RWC_{rsv}.

V. FOLIAR STABLE CARBON AND NITROGEN ISOTOPES

- Les espècies germinadores tenen una menor eficiència en l'ús de l'aigua (WUE[26]) estimada a partir de $\delta^{13}C$ que les no-germinadores i conseqüentment tindrien un major consum d'aigua per gram de biomassa produïda.

- La mida de la planta, estimada per la seva alçada, té un paper molt important a l'hora de determinar l'eficiència en l'ús de l'aigua. Una de les variables clau que explica les diferències en l'eficiència en l'ús de l'aigua entre germinadores i no-germinadores és que les germinadores són espècies més petites que les no-germinadores. Les germinadores es van originar majoritàriament en el Quaternari i les no-germinadores en el Terciari, sota condicions climàtiques

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[26] WUE significa "water use eficiency"

diferents. Aquest fet podria haver determinat els tipus biològics i les característiques funcionals de les espècies dels diferents tipus regeneratius.

- El fet de no mostrar diferències entre grups regeneratius en el contingut de nitrogen foliar (LNC) suggereix que la menor eficiència en l'ús de l'aigua de les germinadores és principalment deguda a diferències en la conductància estomàtica i no pas en l'assimilació fotosintètica.

- La major quantitat de $\delta^{15}N$ en les rebrotadores pot indicar que aquestes agafen una font de N a més profunditat que les no-rebrotadores, i que per tant tenen sistemes radiculars que arriben a més profunditat.

- Les relacions taxonòmiques no expliquen la variació trobada en l'eficiència en l'ús de l'aigua ($\delta^{13}C$) dels diferents grups regeneratius, mentre que el fet de pertànyer a una família o una altra sí que podria determinar les diferències entre estratègies en el contingut foliar de $\delta^{15}N$.

VI. FUEL LOADING AND FLAMMABILITY

- A l'estudiar el contingut d'aigua de la part viva de les plantes (humitat foliar i humitat del combustible fi viu) a l'estiu[27] no s'han trobat diferències significatives entre grups regeneratius, tot i observar una tendència que indica que les germinadores i les germinadores-rebrotadores tendeixen a tenir menys humitat en aquesta època de l'any[28]. D'altra banda hi ha altres paràmetres de combustibilitat i inflamabilitat que també s'han considerat en aquest estudi per avaluar altres paràmetres directament relacionats amb el risc d'incendis.

- Pel que fa a tota la biomassa de les espècies, les germinadores tenen més proporció de material fi mort i menys contingut d'humitat de tota la planta que les no-germinadores, i per tant una major proporció de material mort : material viu. Per tant, com que les germinadores són espècies amb un material vegetal més fi i més sec, pel que fa a aquests aspectes de la inflamabilitat, els ecosistemes dominats per espècies germinadores presentarien un major risc

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[27] Es fa referència a l'estiu ja que és l'època de major risc d'incendis a la conca mediterrània..

[28] Conclusió extreta del capítol I.

d'incendi. Les espècies no-germinadores tenen un combustible més gruixut i per tant promourien incendis més lents, però amb més alliberament de calor degut a una major càrrega de combustible.

- Les fulles de les germinadores són més inflamables i de més ràpida combustió, ja que la temperatura per arribar a la ignició i a la producció de flama[29] són menors, mentre que les espècies no-germinadores tenen majors temperatures d'ignició i producció de flama.

- El menor contingut d'aigua de les fulles és determinant per arribar a la fase de piròlisis i produir flama mentre que el major valor de la proporció S : V és més determinant per assolir la piròlisis i la ignició. Aquest patró indica que la ignició depèn més de les propietats intrínseques de les plantes com ara la morfologia foliar, mentre que el contingut d'aigua (una variable que depèn més de les condicions ambientals) és més determinant en la producció de flama.

- Així doncs, la proporció dels grups d'espècies fruit del règim d'incendis probablement determinarà les característiques dels futurs incendis.

- L'absència de diferències en les variables d'inflamabilitat entre les dues localitats d'estudi (Montgrí a Girona, i Murta a València) confirma que aquest patró de major inflamabilitat de les germinadores és degut a propietats intrínseques de les espècies i no a plasticitat fenotípica lligada a condicions locals.

- La menor biomassa de les germinadores està en consonància amb el seu cicle de vida curt i definit per un esforç reproductiu alt i un alt establiment de plançons, mentre que les no-germinadores presenten el patró oposat.

- El fet de pertànyer a una família o una altra no explica la variació trobada entre germinadores i no-germinadores per cap de les variables d'inflamabilitat estudiades.

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[29] Tal i com s'explica en el caítol VI, es tracta de testos fets amb fulles.

VII. LEAF LITTER DECOMPOSITION: RESPONES TO CLIMATE CHANGE

- La davallada de la precipitació i l'increment de períodes de sequera esperats pel canvi climàtic, poden afectar el retorn de biomassa cap al sòl fent baixar les taxes de descomposició i els *inputs* de nutrients en el compartiment del sòl.

- La pèrdua de massa durant la descomposició de la fullaraca d'espècies de matollar mediterrani (al llarg d'un període de dos anys) és menor quan és sotmesa a condicions de sequera[30] que simulen el canvi climàtic esperat en els propers anys.

- Aquesta diferència és més evident en els primers mesos de la descomposició, probablement perquè durant aquest període es degraden els compostos solubles i cel.luloses, i aquests es lixiviaran menys fàcilment sota condicions de sequera.

- Pel que fa a les diferències entre estratègies regeneratives post-incendi, la fullaraca de les espècies rebrotadores té menys pèrdues de massa al llarg del temps que la de les espècies no-rebrotadores. Pel que fa als nutrients, el resultat més notable és que les espècies no-rebrotadores tenen més nutrients en la fullaraca romanent al llarg del temps que les rebrotadores.

- No hi ha interacció significativa entre tractaments climàtics i estratègia regenerativa, indicant que probablement les diferències entre estratègies regeneratives en la descomposició de la fullaraca no es veuran alterades pel canvi climàtic.

- En general, per totes les espècies, al llarg del temps davallen els continguts foliars de Nitrogen, Fòsfor, Potassi i Sodi mentre que el Magnesi i el Calci no davallen tant amb el temps en la fracció de la fullaraca.

- La relació N:P al llarg del temps és menor en la fullaraca de les no-rebrotadores., Per tant, un ecosistema dominat per rebrotadores aportarà menys Nitrogen en relació al Fòsfor al sòl.

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[30] Aquestes condicions de sequera simulen l'esperada pel canvi climàtic en els propers anys. Mirar l'apartat de mètodes del capítol VII.

- La composició d’espècies i famílies en les comunitats vegetals mediterrànies sotmeses a incendis pot ser un factor clau pel que fa als efectes de la sequera en les característiques del procés de descomposició foliar.

VIII. ROOT SYSTEM TOPOLOGY AND MORPHOLOGY

- Les espècies rebrotadores i les no-rebrotadores presenten diferències en el seu sistema radicular en individus adults i en condicions de camp.

- Els dos grups d’espècies presenten un sistema radicular dicòtom, però les no-rebrotadores presenten un patró amb menys ordres de ramificació, i més semblant a una disposició en *opus spicatum* o espiga[31]. De fet, les espècies no-rebrotadores presenten un model radicular que es podria considerar intermedi entre un sistema radicular d’espiga i un de fasciculat, amb menor tendència a solapar-se que el de les rebrotadores.

- Aquestes diferències en la topologia dels sistemes indiquen una major efectivitat a l’explorar i explotar el sòl, una més eficient adquisició de nutrients per un determinat volum de sòl per part de les no-rebrotadores, així com també una major taxa d’absorció de nutrients. En canvi les rebrotadores presenten una topologia radicular que normalment té menors taxes de creixement i major solapament.

- Les espècies rebrotadores presenten un sistema radicular més llarg que pot contrarestar els efectes de la seva topologia, ja que a més longitud, major exploració del sòl.

- Les rebrotadores inverteixen més en la part subterrània respecte a l’aèria que no pas les no-rebrotadores, ja que les rebrotadores presenten major biomassa subterrània respecte a l’àeria.

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[31] “Sistema radicular d’espiga” està traduit de “herringbone root system”

- Les relacions taxonòmiques tenen un paper molt important a l'hora d'explicar les variacions en la tipologia i morfologia dels sistemes radiculars d'ambdós grups regeneratius.

- Els tipus biològics també expliquen gran part de la variació dels sistemes radiculars entre estratègies regeneratives, ja que les espècies de vida curta (nano-faneròfits i camèfits) presenten menors longituds radiculars, menys part subterrània respecte l'aèria i menys longitud específica radicular, i per tant, major taxa relativa de creixement radicular i d'adquisició de recursos.

- Aquest estudi també indica que el grup d'espècies facultatives que presenten els dos mecanismes regeneratius (germinar i rebrotar) s'hauria d'explorar més a fons per tal d'entendre millor les característiques del seu sistema radicular, tot i que sembla que presenten una morfologia acord amb l'emmagatzemament de nutrients de cara a possibles pertorbacions.

La teva solitud

En tant que puguis, doncs, no malbaratis
la teva solitud dedicant-la a una absurda
recerca del no-res ni et persegueixis
tossudament per corredors obscurs,
esporuguit per la llum dels preceptes.
Surt a ple dol i fixa't
en coses dures. Pensa
que el joc desmesurat de les paraules
no et servirà de res si no el recolzes
damunt allò que et volta. Hi ha les pedres
i els arbres i la gent i tantes coses
que pots tocar amb les mans! Que no t'adonis
algun dia, amb espant, que els anys et passen
i et mous només entorn de la teva ombra.

Miquel Martí i Pol