UNIVERSITAT DE BARCELONA
Divisió de Ciències Experimentals
i Matemàtiques
Facultat de Biologia

ESTRUCTURA I CONTINGUT DE NUTRIENTS A LES CAPÇADES DE *Quercus ilex* L. DEL BOSC DE LES MUNTANYES DE PRADES: INFLUÈNCIA DE LES CONDICIONS NATURALS DE CREIXEMENT I EFECTE DE MANIPULACIONS EXPERIMENTALS

CANOPY STRUCTURE AND NUTRIENT CONTENT IN A *Quercus ilex* L. FOREST OF PRADES MOUNTAINS: EFFECT OF NATURAL AND EXPERIMENTAL MANIPULATION OF GROWTH CONDITIONS

Santi Sabaté i Jorba

1993

Departament d'Ecologia
Programa d'Ecologia
Bienni (1988-89,1989-90)
Facultat de Biologia
Universitat de Barcelona

ESTRUCTURA I CONTINGUT DE NUTRIENTS A LES CAPÇADES DE *Quercus ilex* L. DEL BOSC DE LES MUNTANYES DE PRADES: INFLUÈNCIA DE LES CONDICIONS NATURALS DE CREIXEMENT I EFECTE DE MANIPULACIONS EXPERIMENTALS

CANOPY STRUCTURE AND NUTRIENT CONTENT IN A *Quercus ilex* L. FOREST OF PRADES MOUNTAINS: EFFECT OF NATURAL AND EXPERIMENTAL MANIPULATION OF GROWTH CONDITIONS

Memòria presentada per en

Santiago Sabaté i Jorba

per a optar al grau de Doctor en Biologia

Vist i Plau
Tutor del programa de doctorat:

Dr. Jordi Flos i Bassols
Professor Titular d'Ecologia
Departament d'Ecologia
Universitat de Barcelona

Vist i Plau
Director de la tesi:

Dr. Carlos A. Gracia i Alonso
Professor Titular d'Ecologia
Departament d'Ecologia
Universitat de Barcelona

Barcelona, abril de 1993

Dedicada a tota, tota, tota,... la meva família que tant llarga com diversa, ha estat un element increible de formació personal. Especialment, al meu pare que li feia moltíssima il.lussió, però fa molt poc ens va deixar, i a la meva mare

Per si de cas...

"NOTIFICARI"

Possible Director (P.D), possible doctorant (p.d.)

P.D.- *Així doncs dius que vols fer una tesi d'ecologia.*

p.d.- *Home, em sembla que sí, això de l'ecologia m'agrada. Això d'estudiar com animals i plantes es relacionen entre ells i amb el seu medi,... bé, ja saps que vull dir. Alló que expliqueu a l'assignatura.*

P.D.- *Sí, sí, però... Saps escalar? Quants quilos aixeques? Quant aguantes caminant? Com estàs d'electrònica? I de bricolage? I d'equilibris?... I com vas d'inventor?...T'encostipes fàcilment? ...*

p.d.- *Bé, bé, ... i ja està?*

P.D.- *Ah! No! ... Quants cops ets capaç de repetir el mateix sense avorrir-te? Se't dóna la cuina? I les receptes, les segueixes bé?*

p.d.- *Home de vegades, i això és tot?*

P.D.- *No,... llegeixes molt? i... què tal se't donen els pecés? Model.les? Programes? TURBO BASIC? SAS? SIGMA PLOT? QUATTRO PRO? WORD PERFECT?...*

p.d.- *Ufff, però qué és això? paraules en clau?*

P.D.- *No, aquestes ja les aprendràs quan escriguis, ... per que per cert, i els idiomes que tal se't donen? No em diguis que ets d'aquells que a trocets i només "Spanglish". I parlar en públic què?*

p.d.- *Home, faig el que puc, ... però això es paga?*

P.D.- *Home, ... això depèn, ... si tens sort,... que no deies que t'agradava?*

p.d.- *Sí, sí, però ...després d'això sabré que serè quan sigui gran?*

P.D.- *... (silenci, mirada a l'infinit... es repensa i diu) No ho sé, però seràs més gran, hauràs aprés coses, autodisciplina,... i tindràs el món al devant per... vinga home!,... que no ets aventurer?, una mica indiana?*

L'autor (... un de'ls que s'ha aventurat)

AGRAÏMENTS

A en Carles Gracia li haig d'agrair moltes coses, perquè un bon tros del que sóc científicament, parlant d'ecologia terrestre, m'ho ha ensenyat ell. I que a més de ser un bon amic, m'ha dirigit la tesi i ha confiat en mi. M'ha repetit moltíssimes vegades: Santi acaba la tesi... i ara, molt content, ja li puc dir, aquí la tens!

A en Ferran Rodà li he d'agrair també moltes coses. Penso que és un bon punt de referència per a qualsevol científic. Amb ell he compartit bones estones i un dels experiments d'aquesta tesi. S'ha llegit, molt detalladament i crítica, tota la tesi i ho ha fet amb tota la intenció constructiva d'un bon amic però també d'un bon "referee".

A en Antoni Escarré li agraeixo que directament o indirecta m'ha donat idees. Especialment recordo que, quan vaig començar, ens vàrem trobar a Alacant un dia sencer i molt intens, per discutir i contrastar la delimitació d'aquest projecte i els seus objectius. I he de dir que em va anar però que molt bé. I a en Jaume Terradas, que des del CREAF ha col.laborat tant directament com indirecta en resoldre problemes. Tots dos han estat persones clau en els estudis de l'alzinar.

Al Departament d'Ecologia, on he desenvolupat aquesta tesi, i del que he utilitzat totes les instal.lacions que he necessitat. Especialment a en Joandomènec Ros, el Cap del Departament, que m'ha facilitat qualsevol gestió que he necessitat.

Amb en Miguel Angel Mateo hem compartit la metodologia de digestions àcides i ha estat una sort de comptar amb ell (capítol 2). Espero que aviat acabi el seu projecte. Ell sap la feinada que suposa això de les anàlisis de nutrients de materials vegetals. També li agraeixo a en Javier Romero, el seu director, el suport que ens ha donat per perfilar amb èxit aquest apartat metodològic.

Amb Anna Sala hem compartit l'experiència de l'estudi de l'estructura vertical (veure apèndix i capítol 3) i ella més que ningú sap l'aventura o el repte que això ha representat. També li agraeixo la revisió del text presentat en el capítol 3. Ja vàrem compartir les experiències de fer les tesines al Garraf, i des que érem estudiants ens ha unit una bona amistat. També agreïxo a Mireia Abril la col.laboració i en el montatge de les estacions del coster i la vall.

Amb la Vicky Diego vàrem passar moltíssims dies al camp per montar l'experiment de fertilització i irrigació, sense ella aquest experiment no hagués estat possible. També en Xavier Mayor ha estat una persona clau en el seu desenvolupament. Amb tots dos ens hem repartit diferents aspectes del experiment i he d'agrair el bon enteniment i l'amistat (capítol 4).

L'experiment de pertorbació de l'alzinar (capítol 5) ha estat impulsat pel grup d'edafòlegs ja sigui de la UB, de la UAB o de l'escola de pèrits agrònoms així com geòlegs del Jaume Almera. A tots ells i elles moltes gràcies. He de destacar l'agraïment a en Ramon Vallejo perque des que era estudiant m'ha atès de forma excel.lent, ha contribuït a la meva formació i és un bon amic. També en Josep

Maria Alcañiz m'ha resolt dubtes i m'ha facilitat informació. Per altra banda, la Isabel Serrasolsas amb el seu bon humor sempre m'ha animat, a part que m'ha facilitat el que he necessitat d'aquest experiment. Espero que ben aviat acabi la seva part. Sense ànim de deixar-me a ningú, amb aquest grup de gent sempre és agradable trobar-se. Un altre esment especial l'haig de dedicar a en Pere Rovira que m'ha corregit les errades de català. I també al Canonge de la Seu perquè ha il.lustrat els capítols de la tesi donant-hi un to més agradable.

La feina de camp i de separar mostres hagués estat molt més dura o impossible, si no hagués estat pels cops de mà incondicionals i els ànims, que he rebut de Sílvia Calvet, Estíbaliz Tello i Rosa Marfà. També m'han ajudat amb el dictat, per la introducció a l'ordinador, d'alguns dels milers de dades que he hagut de treballar. Ajuts a part, he decobert persones excel.lents. A totes les altres persones que en algun moment m'han ajudat, en alguna campanya de mostreig, al laboratori, etc.. moltíssimes gràcies.

Una tesi que va de nutrients, feta a la UB, ha de passar quasi obligatòriament pel Servei d'Espectroscòpia de la Universitat de Barcelona. Agraeixo el suport rebut des de la direcció fins als treballadors de base. Les anàlisis de C i N han estat realitzades en el servei de cromatografia i tant l'Isidre Casals com la Pilar Fernàndez m'han tractat molt bé. Glòria Lacort, sempre a punt per resoldre dubtes, en Santi Mata i Maribel Prunera de (AAS) em van facilitar i assessorar en les anàlisis de cations de l'estudi del capítol 3. Tots els fòsfors d'aquesta tesi han passat pel servei de plasma (ICP) i a partir de la disponibilitat del multicanal també els cations (tots menys el del capítol 3). Tant l'Elionor Pelfort, la Eva Pelegrí com l'Enric Solanes (de ICP) han estat excel.lents per la seva preocupació en obtenir resultats fiables. Finalment, vull agrair especialment a Isidre Casals el fet d'haver-me assessorat en un munt de qüestions tècniques i a la Elionor Pelfort el mateix en el tema de les digestions àcides i la seva lectura per ICP (veure capítol 2). Només puc dir que són tan bones persones com grans professionals.

Al Pep Piñol li he d'agrair que em va introduir en el món de Prades i sempre que he necessitat quelcom d'ell m'ha ajudat. En Joan Bellot ha estat un bon amic i em va ajudar durant la meva estada a Alacant, fent-la agradable, familiar i resolent qualsevol cosa que necessités. A en Miquel Calvo li agraeixo enormement l'assessorament de la part estadística. No ha dubtat a atendre qualsevol dubte.

He d'agrair a Emilia Gutierrez i Oriol Bosch el haver compartit moltes estones al despatx (molts dies fins a molt tard) o en cursos, cursets, etc. Les interaccions sempre han estat enriquidores. A ells i als altres membres del cuarto dels terrestres del departament, també agraeixo que hagin suportat un innombrable quantitat de caixes, sobres, pots, etc al llarg de les diferents fases d'aquesta tesi. Darrerament l'arribada de Fàtima ha creat un clima molt agradable.

A la gent de l'Inventari Ecològic i Forestal de Caltalunya i de la resta del CREAF els he d'agrair que sempre que he necessitat alguna cosa m'ho han facilitat o inclús m'han ajudat (Juanjo, María, Olivia, Marc, Jordi, José Angel, Amalia, Mireia, Sol, *et al.*)

A la gent del departament (no els llistaré perque n'hi ha molta), he d'agrair haver-me trobat amb gent que dóna ànims i col.labora en qualsevol cosa que puguin resoldre. Amb en Joan Lluís Riera i la Montserrat Real (F.P.I. de la mateixa fornada) ens hem anat animant mútuament en la finalització de les "respectives" i ja ho hem aconseguit.

De la Universitat d'Alacant (a part dels esmentats) haig d'agrair a la Maria José, la Nuria, la Dori, en Juanra. *et. al* el haver-me facilitat informació dels treballs que han fet o fan a Prades o sencillament d'haver-me fet més agradable la meva estada a Alacant.

La Pam (secretària del Forestry Department Univ. of Aberdeen) em fa fer passar una estada a Escòcia increïble, tant pel que fa a l'eficiència de la tasca que anava a fer com pel que fa al terreny personal. Des de llavors ens uneix una intensa amistat. A en Roger li agraeixo el mateix i haver revisat el capítol 5. Haig d'afegir altra gent com en John, en Nigel (que feia una tesi també de nutrients), a la Deborah i a en Paul (company de la Pam) per la seva col.laboració i amistat. En Hugh Miller també li agraeixo que m'acollís en el seu departament i em facilités tot el que vaig necessitar.

A la família Specht, en Ray, la Marion, l'Alison, en Brett i la Rowena perquè em van acollir durant la meva estada a Austràlia i no van deixar d'esforçar-se en cap moment per ensenyar-me les coses importants del seu país, tant pel que fa a la ciència com pel que fa a la gent. Són un bons amics.

A en Ramón Margalef li he d'agrair la plataforma que ha muntat pel que fa als coneixements de l'ecologia, dels que he pogut disfrutar, i la seva atenció quan li li he consultat qualsevol cosa.

També he d'agrair el suport rebut dels meus pares i de la resta de la família Sabaté a la qui dedico aquesta tesi. Però a més, agraeixo al meu germà Quico l'ajut en algun mostreig i els moltíssims moments compartits al llarg del període que ha durat això, i a la meva germana Maria Antònia per l'ajut en el muntatge d'aquest document final. A tots moltes gràcies.

Finalment, per si m'he deixat algú, aprofito per agrair-li ara, i que em perdoni.

Aquest treball ha rebut l'ajut econòmic de la Comissió Interdepartamental de Recerca i Innovació Tecnològica de la Generalitat de Catalunya, de la Fundació Caixa de Barcelona, d'Icona (projecte LUCDEME) i de les Comunitats Europees (CEE). Durant la realització d'aquest treball he gaudit d'una beca de FPI concedida pel Ministeri d'Educació i Ciència.

ÍNDEX

1. INTRODUCCIÓ

1.1 Punt de sortida

Els orígens d'aquest projecte es troben a uns 15 anys enrera quan finançat pel *Comité Hispano-Americano de Cooperación Científica y Técnica*, les Universitats d'Alacant i Barcelona (UB i UAB) en col.laboració amb les Universitats de Yale i Virginia dels Estats Units, van engegar el projecte que pretenia l'estudi ecològic de la hidrologia i la biogeoquímica de petites conques forestades mediterrànies. Aquests estudis, inspirats en els treballs de Bormann i Likens (1967) i Likens *et al.* (1977) a Hubbard Brook, es van iniciar en paral.lel als alzinars del massís del Montseny i les muntanyes de Prades. Després del projecte Hispano-Nord-americà, el finançament ha anat venint de diferents programes o projectes a càrrec de la CAYCIT, ICONA (projecte LUCDEME), CIRIT i la CEE.

Des d'aquells inicis fins ara, tot un seguit de treballs de recerca s'han anat desenvolupant, ja sigui amb un enfoc sistèmic a nivell de conca o amb un enfoc a nivell de parcel.la. Terradas i Rodà (1988) van fer una compilació dels treballs realitzats al Montseny després de 10 anys de recerca on ja es veu una certa perspectiva. Un intent semblant es va fer l'any 1990 pel Grup d'Ecologia Terrestre, del Departament de Ciències Ambientals i Recursos Naturals de la Universitat d'Alacant (Escarré et. al. 1990) pel que fa als estudis a Prades. Fa poc, a finals de març de 1993, es va organitzar a València una trobada de la gent que té a veure amb projectes de Prades, ja siguin acabats, ja siguin a mitjes o que tot just comencen a fer-se o a plantejar-se. Aquesta reunió ha generat un recull més actualizat del recopilat el 1990 (Piñol i Vallejo 1993).

Deixant de banda els grups de treballs d'àrees concretes, una cita imprescindible pel que fa a l'alzinar és el volum 99-100 de la revista *Vegetatio* (Romane i Terradas -eds.- 1992) que recull els treballs, tots relacionats amb l'alzinar, presentats o adherits posteriorment, al ***International Workshop of Quercus ilex L. Ecosystems: Function, Dynamics and Management.*** En aquest volum es fa evident la presència dels grups que treballen a Prades i al Montseny. Cites d'aquests treballs o d'altres, amb els quals hem contrastat resultats, s'aniran trobant al llarg de la memòria.

Com que aquesta introducció pretén acostar al lector al punt de partida, al com s'origina i quin ha estat l'entorn de desenvolupament d'aquesta tesi, no entraré en detalls tractant de llistar tots els treballs realitzats a Prades o al Montseny; només els que he cregut necessaris d'acord a la temàtica d'aquesta tesi. Si el lector n'està interessat li recomano una ullada al volum de *Vegetatio* 99-110 i/o als reculls esmentats anteriorment. L'alzina (*Quercus ilex* ssp. *ilex*) ha estat la gran protagonista d'aquests estudis, però també el Faig (*Fagus sylvatica*) i l'avet (*Abies alba)* al Montseny i el pi roig (*Pinus sylvestris*) a Prades, han estat sota el punt de mira d'alguns treballs.

Gracia (1983) va mesurar i analitzar com la radiació, la seva extinció i la dinàmica de les clorofil.les es relacionen entre elles (veure també Piñol 1985), així com la seva relació amb l'organització dels elements que composen la capçada i les seves característiques (superfície mitjana de fulles, pes mitjà, etc). Que amb la seva integració va obtenir les primeres mesures de l'índex foliar del Montseny, superfície de fulla per unitat de superfície de sòl. Però, si bé aquest estudi el va centrar al Montseny, també hi va incloure algunes mesures de l'alzinar de Prades.

En paral.lel, altres estudis anaven en dansa. Així, en Ferrés (1984) va ser un dels pioners al Montseny en l'estudi de la composició química dels elements que composen la biomassa aèria. En aquest sentit, combinat amb l'estudi anterior va donar dades de com en el perfil vertical del bosc es donaven diferents concentracions dels nutrients. Però també va estudiar la biomassa i la producció de l'alzinar, que lligats a la composició química van oferir les primeres dades de mineralomasses. A Prades, Clemente (1983) va analitzar la composició química estacional, a més de l'alzina, de totes les espècies llenyoses més importants. A més d'aquests treballs, de referència obligada pel tema que ens ocupa, n'hi havia d'altres.

En el cas del Montseny, tenim la caiguda de virosta i la seva descomposició (Verdu 1984), la química de l'aigua de pluja i la seva transformació al interaccionar amb els elements que composen l'ecosistema (Rodà 1983). De manera que ja començàvem a disposar de dades de conjunt per començar a establir cicles de nutrients. Però també de l'ús de l'aigua, gràcies a treballs com els de Comin (1985) i Savé (1986). A més, el treball de Canadell (1988) va oferir un important avenç en el difícil i misteriós món de la biomassa subterrània, del qual tots hi anem estirant, i de la biomassa aèria. A una altra escala, Avila (1988) va estudiar els balanços d'aigua i de nutrients de l'alzinar a nivell de conca.

En el cas de Prades, encara que un xic més endarrerit perquè hi treballava menys gent, també s'anava avançant en la monitorització i recollida bàsica de dades. A més del treball esmentat de Clemente (1983), Lledò (1990) va fer un recull de dades de caiguda de virosta, de la biomassa i la producció de l'alzinar de Prades, i també analitzà els balanços d'aigua i nutrients a la conca de L'Avic. Bellot (1989) va determinar la química de la pluja i la seva modificació en travessar les capçades (veure també Lopez 1989), així com la distribució quantitativa d'aquests fluxos d'aigua.

Piñol (1990) va continuar amb els estudis de l'aigua de pluja i la monitorització a nivell de conca. Va quantificar els balanços d'aigua i nutrients a quatre conques de Prades, entre elles L'Avic i la Teula. En aquestes dues, va model.lar l'heterogeneïtat de la disponibilitat hídrica dins de la conca, i va establir zones de baixa disponibilitat i zones d'alta disponibilitat. A més va obtenir que l'evapotranspiració de l'alzinar en aquestes conques representa un 86% i un 92 %

respectivament de les entrades en forma de pluja. També va posar de manifest que el nitrogen i el potasi són retinguts a la conca, presumiblement incorporats a la vegetació.

En el cas dels nutrients, Escarré *et al.* (1987), relacionant les dades de Ferrés (1984), Rodà (1983) i Verdú (1984), van fer una composició de l'estratègia de l'alzina en l'ús dels nutrients. Comín *et al.* (1987) ho van fer per l'ús de l'aigua. D'aquesta manera, i en un marc més ampli que el d'una parcel.la, es van començar a configurar una sèrie de qüestions: quines són les respostes de l'alzinar davant de diferents condicions de disponibilitat d'aigua i de nutrients? Quin és el control que exerceixen les plantes davant d'aquestes diferents disponibilitats? Quin és el paper dels nutrients com a factors limitants de la producció primària?

Sobre la importància del control dels nutrients que exerceixen les plantes, els darrers anys han aparegut a la premsa científica una sèrie de treballs que posen en evidència la preocupació, o si es vol la moda d'aquest tema, girant al voltant de la qüestió: és una major eficiència en l'ús dels nutrients un mecanisme adaptatiu davant de condicions de baixes disponibilitats de nutrients? Resultats contradictoris han sovintejat les publicacions (vegi's per exemple Shaver i Melillo 1984, Nambiar i Fife 1987, Lajtha 1987, Chapin 1988, Jonasson 1989, Schlesinger *et al.* 1989, Del Arco *et al.* 1991). Entre els mecanismes conservatius, que poden incrementar l'eficiència, la reabsorció o retranslocament ha estat un dels que ha rebut més atenció en aquests treballs - que nosaltres referirem com a *Resorption* seguint les recomanacions de Killingbeck (1986) -. Aquest mecanisme permet que nutrients ja utilitzats en unitats funcionals més velles (ja existents) puguin ser reutilitzats en la construcció i funcionament d'unitats funcionals més joves, accentuant així el reciclatge intern i alleugerint la demanda de nutrients per la nova producció, de la dependència de les disponibilitats de nutrients al sòl en el moment que es necessiten. D'aquí han aparegut també discusions sobre la definició del concepte d'eficiència en l'ús dels nutrients i el paper relatiu del temps de residència dins la planta i de la productivitat dels nutrients com a termes que el composen, i que a més no sempre van en la mateixa direcció (Berendse i Aerts 1987, Aerts 1990).

Pel que fa a l'ús de l'aigua, i a partir de l'heterogeneïtat a nivell de conca, posada en evidència per Piñol (1990) a l'alzinar de Prades, Sala (1992) va estudiar les relacions hídriques en el cas de l'Avic per esbrinar el paper de la vegetació en el control dels fluxos d'aigua, comparant la part alta de la conca (coster) amb la part baixa (vall) que té més disponibilitat d'aigua. Per altra banda, Mayor (1990) va abordar a partir d'un enfoc correlacional com la producció dels alzinars del Montseny està o no limitada per la disponibilitat de nutrients, estudiant parcel.les situades a diferents posicions dins de la conca del Torrent de la Mina (diferents orientacions i altituds).

Un altre tema d'interès voltava l'àmbit de l'efecte i la resposta a les pertorbacions, que modifiquen de forma dràstica l'estructura i la disponibilitat de nutrients dels sistemes forestals, tan freqüents en els sistemes mediterranis (vegi's Terradas -ed- 1987). De manera que gestions com la tallada arreu i els incendis forestals, aquests molt més importants els darrers anys, han posat en evidència la necessitat de quantificar els seus efectes per respondre a la qüestió: quina és la gestió més adequada que s'ha de fer a la zona pertorbada? Estudis dirigits per Ramon Vallejo i Carles Gracia, sobre la capacitat de regeneració de la garriga al Garraf havien començat a aportar dades sobre la regeneració de *Quercus coccifera* i els efectes dels incendis en els nostres sòls forestals (Abril *et al.* 1987), així com altres estudis, alguns recollits en el treball esmentat coordinat per Terradas (1987). Incendis com els de Montserrat i Sant Llorenç de Munt van accentuar la polèmica a nivell popular, però també a nivell científic, perquè hi havia poques dades de l'alzinar, i menys originades a partir de condicions de pertorbació controlades. És a dir, sabent què hi havia abans.

1.2 Objectius

L'objectiu general d'aquesta tesi, queda emmarcat dins del coneixement del bosc mediterrani i en concret de l'alzinar. El que s'ha pretès és analitzar en el cas de l'alzina (*Quercus ilex* L.)

- com la disponibilitat d'aigua i nutrients es relaciona amb les característiques estructurals i el contingut de nutrients dels elements que composen la capçada,

- quins patrons de variació temporals presenten,

- com aquests patrons temporals es poden relacionar amb la utilització dels nutrients, la seva reabsorció o retranslocament i l'eficiència en el seu ús.

Aquestes anàlisis les hem conduïdes sota diferents situacions de disponibilitat d'aigua i nutrients, ja sigui en un gradient present en condicions naturals, ja sigui per manipulació experimental. Concretament ens hem centrat en tres casos que presentem a continuació, la ubicació dels quals és a les muntanyes de Prades i queda recollida en el mapa que s'adjunta de la zona (Figura 1):

1^{er} cas: Seguiment a la part alta (coster) i baixa (vall) de la conca de L'Avic.

Entre aquests dos extrems trobem un gradient de disponibilitat dins del qual la vall reb menys radiació, té sòls més profunds i, a més de la pluja, reb aports laterals d'aigua per drenatge de les parts més altes de la conca. A més d'aquests dos extrems dins de la conca, hem analitzat quines diferències apareixen en el perfil vertical de les capçades i ho hem seguit en diferents moments de l'any. Com que per quantificar la transpiració, Anna Sala necessitava mesures d'índex fol.liar, i així poder extrapolar des de les mesures fetes a nivell de fulla a una escala de capçada per unitat de superfície de sòl, i després a nivell de conca; i aquestes mesures d'índex foliar, també eren del nostre interès per poder quantificar els nutrients a nivell de capçada, la part estructural la vàrem assumir plegats (veure annex). Així doncs, els factors de variació analitzats han estat: *La situació dins la conca (coster o vall), la posició en el perfil vertical (quatre nivells de dalt al terra) i el temps (mostratge estacional: primavera abans de la brotada, mig estiu i final de tardor, pels anys 1988 i 1989).* En aquest cas els individus estudiats en cada situació, s'han desenvolupat en condicions de disponibilitat diferent (coster o vall) al llarg de la seva vida, de manera, que deixant de banda possibles diferències genotípiques, aquests també posen de manifest diferències estructurals fenotípiques després d'adaptar-se a condicions de creixement ben diferents.

$2^{\text{òn}}$ cas: Manipulació experimental a partir de la irrigació i la fertilització.

Aquest experiment va néixer en la línia d'esbrinar quins són els principals factors que poden limitar la producció primària dels alzinars xèrics i densos; així com quines són les respostes de l'ecosistema a l'augment de les disponibilitats. L'alzinar manipulat és relativament homogeni i se situa a uns 900 m d'altitud i en el vessant d'orientació E-SE del Barranc dels Torners; amb alzines d'uns 6 m d'alçada i una densitat mitjana de 18500 peus/ha (condicions més properes a la part alta de la conca de l'Avic -coster-, esmentada anteriorment, que la part baixa -vall-). *Es van escollir, com a possibles factors limitants, l'aigua, el nitrogen i el fòsfor i es va dissenyar un experiment factorial que ens permetés analitzar el paper d'aquests factors i les seves interaccions. Per la qual cosa es van delimitar 24 parcel.les de 8mX8m, agrupades en tres blocs de 8 parcel.les. A cadascun dels blocs es van aplicar a les parcel.les, un dels vuit tractaments resultants de la combinació factorial de l'adició d'aigua, nitrogen i fòsfor amb dos nivells per cada factor (presència o absència).*

El fertilitzant es va aplicar de forma sòlida el març de 1989 i en una sola dosi. Dosi que consistí en 250 kg de N/ha en forma de nitrat amònic en els tractaments amb nitrogen i 125 kg de P/ha en forma de superfosfat càlcic en els tractaments amb fòsfor. L'aigua es va proporcionar amb reg per goteig, amb un aport setmanal de 20-30 mm durant les èpoques més càlides de 1989, 1990 i 1991. En aquest experiment ens hem vist implicats més d'un investigador. A la meva tasca recollida en els objectius ja esmentats (treball a nivell de capçada), s'hi han d'afegir la feïna complementària, dirigida per Ferran Rodà, de Maria Victòria Diego (Vicky pels companys) i Xavier Mayor. La primera ha treballat bàsicament amb la caiguda de virosta i els nutrients que la composen, quimisme de la sol.lució del sòl, dinàmica del N edàfic (mineralització neta i nitrificació) i dinàmica de les arrels fines. El segon bàsicament s'ha centrat en el creixement diametral de les alzines. De totes maneres és obvi que l'interès d'una visió global i lligada ens ha portat a la interacció i la complementació d'informació entre els uns i els altres. El període d'estudi que presentem va des de la tardor de 1988 (abans de la manipulació) fins l'estiu de 1990. Més recentment, i més enllà del període de dades recollit per aquesta tesi, s'hi han afegit altra gent i mesures, com les quantitats i el quimisme del aigua del trascol a les parcel.les fertilitzades amb nitrogen (treball conduït per l'Anna Avila).

En aquest experiment, assumim que els individus estudiats presenten menys marge de diferenciació fenotípica que els comparats en les situacions anteriors (coster o vall a l'Avic) donat que es comparen individus que han crescut, al llarg de la seva vida, en condicions més homogènies, les quals nosaltres hem modificat de forma circumstancial i dirigida.

3er cas: Manipulació experimental a partir de pertorbacions: efecte del foc i la tallada arreu.

Aquest experiment va néixer de la necessitat de quantificar els efectes de les pertorbacions a l'alzinar mediterrani i la seva capacitat per a respondre. El marc més general on s'insereix la nostra aportació consisteix en l'estudi de l'efecte del foc i de la tallada arreu en el sòl forestal, estudi conduït pels equips dirigits per en Ramon Vallejo, Josep Maria Alcañiz, Ramón Josa, Albert Sole, Francesc Gallart i Maria Sala. Així doncs, les pertorbacions aplicades van consistir en el foc i la tallada arreu d'una zona d'alzinar, relativament homogènia, al costat de l'experiment anterior (en el mateix vessant d'orientació E-SE del Barranc dels Torners). Aquesta proximitat ens ha permés d'utilitzar com alzinar control de referència les parcel.les control de l'experiment anterior. A finals de l'estiu del 1988 es va fer una tallada arreu en dues superfícies (una al costat de l'altra) de 40mX20m d'alzinar. D'aquestes es van treure els troncs de més de 2 cm de diàmetre i s'hi va deixar la resta. Les restes es van distribuir homogèniament, deixant al voltant d'una d'elles una zona totalment neta per controlar el foc que a la tardor de 1988 se li va practicar.

És ben coneguda la capacitat de l'alzina de rebrotar després de pertorbacions com el foc i la tallada arreu; així que els individus o soques que, en principi, havien crescut en condicions relativament homogènies ara havien de reconstruir les seves capçades davant de situacions de disponibilitats diferents, un servidor n'ha analitzat tres: *(1) tallada arreu deixant les branques, (2) tallada arreu sense deixar-hi res (tallafocs) i (3) després del foc*. El contingut de nutrients en aquestes capçades i el seu control intern poden tenir importància en un doble sentit. Per un costat altes concentracions de nutrients poden permetre altes taxes fotosintètiques i per tant una ràpida reconstrucció de la biomassa aèria, però per altra banda, encara que part del capital de nutrients tingui el seu origen en reserves acumulades a la soca i les arrels, l'obtingut del medi extern representa la seva internalització, disminuint la probabilitat de pèrdua per erosió i/o rentat en aquestes etapes inicials de la successió secundària. Com en el cas anterior, assumim que els individus estudiats abans de la pertorbació presentaven menys marge de diferenciació fenotípica que els comparats en el primer cas (coster o vall a l'Avic) ja que havien crescut en condicions més o menys homogènies. De manera que, les reserves de nutrients a les soques i els sistemes radiculars en el moment de sortida de l'experiment, malgrat no haver estat mesurades, podíem assumir que eren comparables. Per tant, és d'esperar que les diferències de resposta en la reconstrucció de les capçades es deguin principalment al tipus de tractament.

Pel que fa a les disponibilitats, en el primer cas, es provoca que hi hagi menys radiació inicial, interceptada per les branques i la fullaraca deixades, que per altra banda protegeixen de l'erosió i en descomposar-se constitueixen una font de nutrients. En el cas del tallafocs, l'empobriment de matèria orgànica i nutrients és més gran, així com el perill d'erosió. En el cas del foc, el perill d'erosió també és gran perquè a més de deixar el sòl nu, es generen substàncies hidròfobes que la poden afavorir. Per altra banda, amb el foc es pot donar una relativa fertilització inicial donat que les cendres dipositades poden aportar cations i fòsfor, encara que el nitrogen és altament susceptible de ser volatilitzat i per tant es provoca un empobriment en aquest nutrient. Per altre costat, els individus pateixen el xoc tèrmic provocat per l'impacte del foc, que pot condicionar la seva supervivència.

El seguiment fet en aquest experiment es correspon a les etapes inicials, des de la primavera de 1989 a l'estiu de 1990. Els factors de variació analitzats durant la reconstrucció de les capçades han estat el tractament (tallada amb branques, tallafocs i foc) i la data (primavera del 1989, estiu del 1989, tardor de 1989, primavera de 1990 i estiu de 1990). Aquest experiment, com ja s'ha esmentat, es va dissenyar amb objectius molt més amplis que la nostra aportació a nivell de capçada i amb els quals hem d'agrair haver-nos pogut acoblar. Isabel Serrasolses es va centrar en l'estudi de l'evolució de la matèria orgànica que juntament amb en Xavier Àries que va estudiar l'estructura física del sòl han estat l'ànima de l'experiment. Montse Soler va estudiar l'erosió i més recentment s'hi han acoblat altres estudis com per exemple els conduits per Isabel Fleck i Dolors Vidal, que han treballat en la transpiració i la fotosíntesi dels rebrots.

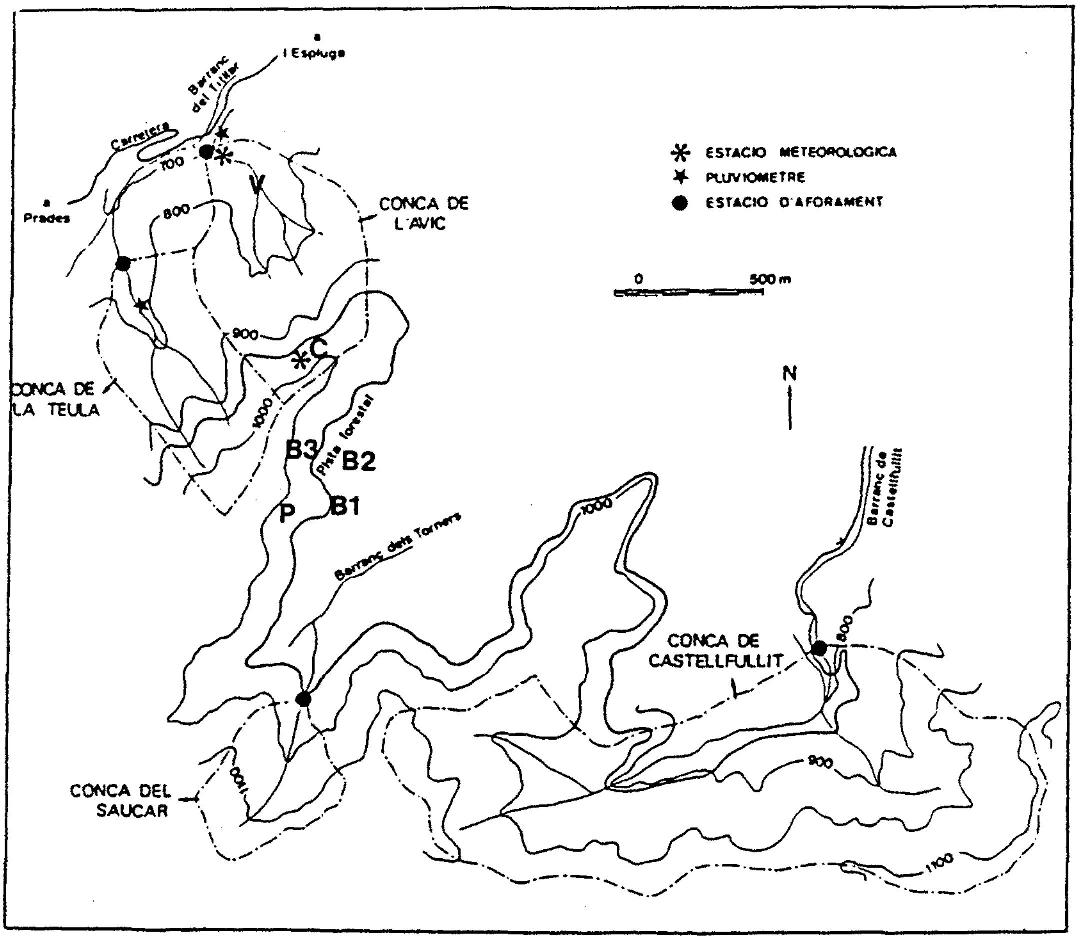


Figura 1.1. Mapa de la zona de les Muntanyes de Prades on s'ubiquen les parcel.les d'alzinar estudiades en aquesta tesi. 1. Coster (C) i vall (V) a la conca de l'Avic. 2. Experiment de fertilització i irrigació, Bloc 1 = B1, Bloc 2 = B2, Bloc 3 = B3. 3. Experiment de pertorbació (P).

1.3 Sobre l'estructura de la tesi i aspectes de formació

Finalment, per acabar aquest apartat de presentació, voldria fer uns comentaris per explicar al lector el que trobarà a continuació. Una de les característiques d'aquesta tesi és que li hem donat un caràcter modular; bàsicament al voltant dels diferents experiments analitzats. Això ens ha dut a fer referències creuades entre capítols. Malgrat aquest caràcter, l'autor desitjaria que amb el capítol 1 s'hagi produït un efecte de llaç que doni coherència al tot, si més no, que es vegi el fil conductor general; rematat amb el capítol 6 on es recullen totes les conclusions d'aquesta tesi. També aprofitarem aquest apartat per esmentar els treballs i comunicacions científiques que aquesta tesi ha generat o està en vies de generar, així com alguns aspectes de formació.

En el capítol 2, es presenta el mètode de digestions àcides utilitzat per a les determinacions del contingut de P, K, Ca, Mg i S. El seu àmbit és metodològic i, més que una resposta als objectius esmentats abans, respon a un pas previ imprescindible de millora en la capacitat analítica, donat el volum de mostres generades pels dissenys experimentals. Per això, vàrem haver d'explorar diferentes possibilitats, i finalment ens vàrem decidir per desenvolupar el mètode descrit en el capítol 2. Donat que l'anàlisi de fòsfor era d'interès per a altra gent del departament d'Ecologia (UB), em vaig associar en aquest tema amb en Miguel Angel Mateo, que si bé no estava interessat en els cations perquè treballa amb fanerògames marines (principalment *Posidonia oceànica*) tot el procediment per analitzar el fòsfor havia de ser el mateix. D'aquesta associació va néixer doncs el mètode descrit en el capítol 2 i que a més es correspon a un article que ens han acceptat per a ser publicat properament a la revista internacional ***Analitica Quimica Acta.***

En el capítol 3, es presenten els resultats de l'estudi a la conca de l'Avic. En aquest capítol s'inclouen només els resultats d'aquest estudi més relacionats amb els nutrients. La part més estructural va ser compartida amb n'Anna Sala, com s'ha dit anteriorment, i bona part de les dades ja varen ser utilitzades a la seva tesi (Sala 1992). De totes maneres, donada la nostra participació i la constant referència a la part estructural de l'estudi, hem decidit incloure, a modus d'apèndix, el manuscrit d'aquest treball que s'ha enviat a la revista ***Trees*** per a la seva publicació si l'accepten els *referees*. Del capítol 3, ha estat acceptada la seva presentació a un congrés el proper juny a Suècia (***Nutrient Uptake and Cycling in Forest Ecosystems, CEC/IUFRO Symposium, Halmstad, Sweden, June 7-10, 1993***), que després podrà ser recollit com article en un número de la revista ***Plant and Soil*** si els *referees* l'accepten.

El capítol 4 recull els resultats de l'experiment de fertilització i reg. Aquest treball ha generat un article de la part estructural publicat en el volum de ***Vegetatio*** nº 99-100, un article acceptat a la revista internacional ***Forest Ecology and***

Management, de la part del contingut de nutrients, que va ser presentat a Dinamarca en el ***International Symposium on Experimental Manipulations of Biota and Biogeochemical Cycling in Ecosystems- Approach, methodologies, findings. Copenhaguen, Denmark 18-20 may, 1992***. També es preveu una presentació sintètica i lligada amb altres aspectes estudiats per altres col.legues per ser presentat conjuntament en el congrés de Suècia esmentat anteriorment (també acceptat). Això darrer ens ha dut a tractar tot el capítol en un bloc i no separar els aspectes estructurals dels de contingut de nutrients, malgrat els treballs parcials precedents. Si els *referees* l'accepten, com en el cas del capítol 3, es preveu la seva publicació a la revista ***Plant and Soil.***

El capítol 5 recull l'estudi de la reconstrucció de les capçades d'alzina després de les pertorbacions. En aquest cas, donat que estem preparant dos manuscrits per enviar (en principi a *Oecologia*), un de la part estructural i un altre més relacionat amb la dinàmica de nutrients, hem mantingut aquests dos sub-apartats. Val a dir, que una elaboració prèvia de part de l'informació d'aquest apartat va generar una comunicació a León durant les ***III Jornadas de Ecología Terrestre, A.E.E.T. León 16-20 de septiembre de 1991***.

Durant el període de formació per l'elaboració d'aquesta tesi haig d'afegir la meva estada al *Forestry Department, University of Aberdeen, Scotland* durant 5 setmanes, juny-juliol del 1989. El grup dirigit pel Prof.HG Miller treballava en el tema del control intern dels nutrients (retranslocament, eficiència en el seu ús) i em va ser de molta utilitat. Especialment certs aspectes de la tesi de Nigel Cottam (que malauradament no m'ha arribat) però que vàrem discutir força.

Més recentment, haig d'afegir la meva estada de 8 setmanes, novembre-desembre del 1991 al *Botany Department, Queensland University, Australia* junt amb en Prof. Ray L.Specht. En aquest cas, els treballs d'en Ray pel que fa a la relació de característiques estructurals de les fulles i branquillons en relació amb característiques ambientals han influït força la meva manera de veure l'estructura de les capçades, i encara que no entri en aquesta tesi, ha generat col.laboracions científiques. Aquesta estada, a més em va oferir l'oportunitat de presentar alguns aspectes d'aquesta tesi amb el títol ***Structural characteristics and nutrient distribution in the canopy of Quercus ilex (evergreen oak) in Catalonia. Spain*** com a conferenciant convidat al ***Ecological Workshop. Lismore (NSW), University of New England, Centre for Coastal Management, Australia 11th december 1991***.

Finalment, encara que no han estat citats en els altres capítols, per temes específics o concrets, hauria d'afegir o citar que el llibre d'ecologia del professor R.Margalef (1974) i el de limnologia (Margalef 1983) han estat llibres de consulta extraordinaris per dubtes i informacions puntuals, i no només per aquesta tesi, sinó per tota la meva formació com a biòleg que treballa i estudia l'ecologia.

1.4 Cites

Abril M, Ferran A, Sabaté S, Sala A, Serrasolsas I, Gracia CA, Vallejo RV (1987) Efectes dels incendis forestals en el bosc mediterrani: repercusions al sòl i a la vegetació. Informe final dipositat a la Fundació Caixa de Barcelona (Obra Social)

Aerts R (1990) Nutrient use efficiency in evergreen and deciduous species from heathlands. Oecologia (Berlin) 84:391-397

Avila A (1987) Balanç d'aigua i de nutrients en una conca d'alzinar del Montseny. Tesi Doctoral. Universitat Autònoma de Barcelona

Bellot J (1989) Análisis de los flujos de deposición global, trascolación, escorrentía cortical y deposición seca en el encinar mediterràneo de l'Avic (Sierra de Prades, Tarragona). Tesi Doctoral. Universitat d'Alacant

Berendse F, Aerts R (1987) Nitrogen-use-efficiency: a biologically meaningful definition? Func Ecol 1:293-296

Bormann FH, Likens GE (1967) Nutrient cycling. Science 155:424-429

Canadell J (1988) Biomassa aèria i subterrània de l'alzinar de la Castanya. Treball de Mestratge. Universitat Autònoma de Barcelona

Chapin III FS (1988) Ecological aspects of plant mineral nutrition. Adv. Mineral Nutri. 3:161-191

Clemente A (1983) Componentes específico y estacional en la variación de contenidos en elementos químicos de las especies y formas biológicas del encinar mediterráneo. Tesi de Llicenciatura. Universitat d'Alacant

Comín P (1985) Balance hídrico y economía hídrica en el encinar de la Castanya. Tesi de Llicenciatura. Universitat de Barcelona

Comin MP, Escarré A, Gracia CA, Lledó MJ, Rabella R, Savé R, Terradas J (1987) Water use by *Quercus ilex* L. forests near Barcelona, Spain. In: Tenhunen *et al.* (eds) Plant Responses to stress. Functional Analysis in Mediterranean Ecosystems. Nato ASI Ser. Vol. G15. Springer Verlag. Berlin. pp 259-266

Del Arco JM, Escudero A, Vega Garrido M (1991) Effects of site charactersitics on nitrogen retranslocation from senescing leaves. Ecology 72:701-708

Escarré A, Ferrés Ll, López R, Martín J, Rodà F, Terradas J (1987) Nutrient use strategy by evergreen-oak (*Quercus ilex* ssp *ilex*) in NE Spain. In: Tenhunen *et al.* (eds) Plant Responses to stress. Functional Analysis in Mediterranean Ecosystems. Nato ASI Ser. Vol. G15. Springer Verlag. Berlin. pp:429-435

Escarré *et al.* (1990) Diez años de investigaciones en el encinar de Monte Poblet (Sierra de Prades, Tarragona). Grupo de Ecología Terrestre Dep. Ciencias Ambientales y Recursos Naturales, Universidad de Alicante

Ferrés LL (1984) Biomasa, producción y mineralomasas del encinar montano de La Castanya

(Montseny, Barcelona). Tesi Doctoral. Universitat Autònoma de Barcelona

Gracia CA (1983) La clorofila en los encinares del Montseny. Tesi Doctoral. Universitat de Barcelona

Jonasson S (1989) Implications of leaf longevity, leaf nutrient re-absorption and translocation for the resource economy of five evergreen plant species. Oikos 56:121-131

Killingbeck KT (1986) The terminological jungle revisited: making a case for use of the term resorption. Oikos 46(2):263-264

Lajtha K (1987) Nutrient reabsorption efficiency and the response to phosphorus fertilization in the desert shrub *Larrea tridentata* (DC) Cov. Biogeochemistry 4:265-276

Likens GE, Bormann FH, Pierce RS, Eaton JS, Johnson NM (1977) Biogeochemistry of a forested ecosystem. Springer Verlag. New York. 146 pp

Lòpez MV (1989) Estudio de los flujos hídricos, y la contribución de la deposición seca y lixiviación al aporte de los nutrientes a un suelo forestal, bajo encina (*Q. ilex*) y pino (*Pinus sylvestris*). Tesi de Mestratge. I.A.M.Z.

Lledó MJ (1990) Compartimentos y flujos biogeoquímicos en una cuenca de encinar del Monte Poblet. Tesi Doctoral. Universitat d'Alacant

Margalef R (1974) Ecología. Ed. Omega. Barcelona 951 pp

Margalef R (1983) Limnología. Ed. Omega. Barcelona. 1010 pp

Mayor X (1990) El paper dels nutrients com a factors limitants de la producció primària de l'alzinar de la conca del Torrent de la Mina (Montseny). Treball de Mestratge. Universitat Autonòma de Barcelona

Nambiar EKS and Fife DN (1987) Growth and nutrient retranslocation in needles of rediata pine in relation tonitrogen supply. Annals of Botany 60:147-156

Piñol J (1985) Dinàmica de les clorofil.les a un alzinar del Montseny. Tesi de Llicenciatura. Universitat de Barcelona

Piñol J (1990) Hidrologia i Biogeoquímica de conques forestades de les Montanyes de Prades. Tesi Doctoral. Universitat de Barcelona

Piñol J, Vallejo R (organitzadors) (1993) II Seminari sobre l'Ecologia de l'alzinar mediterrani. CEAM-CREAF. Alborache 29-31 Març de 1993

Rodà F (1983) Biogeoquímica de les aigües de pluja i de drenatge en alguns ecosistemes forestals del Montseny. Tesi Doctoral. Universitat Autònoma de Barcelona

Romane F, Terradas J (eds.) (1992) *Quercus ilex* L. ecosystems: function, dynamics and management. (reprinted from Vegetatio, volume 99-100). Kluwer Academic Publishers. Dordrecht

Sala A (1992) Water relations, canopy structure, and canopy gas exchange in a *Quercus ilex* forest:

variation in time and space. Ph D Thesis. Univ. of Barcelona

Savé R (1986) Ecofisiologia de les relacions hídriques de l'alzina al Montseny (La Castanya). Doctoral. Universitat de Barcelona

Schlesinger WH, DeLucia EH, Billings WD (1989) Nutrient-use-efficiency of woody plan contrasting soils in the western Great Basin, Nevada. Ecology 70(1):105-113

Shaver GR, Melillo JM (1984) Nutrient budgets of marsh plants: efficiency concepts and rel to availability. Ecology 65:1491-1510

Terradas J (ed) (1987) Ecosistemes terrestres. La resposta als incendis i a d'altres pertorbac Quaderns d'ecologia aplicada nº10. Diputació de Barcelona.

Terradas J, Rodà F (eds) (1988) Deu anys de recerca al Montseny. Unitat d'Ecologia. Unive Autònoma de Barcelona

Verdú MC (1984) Circulació de nutrients en tres ecosistemes forestals del Montseny: caigu virosta i descomposició de la fullaraca. Tesi Doctoral. Universitat Autònoma de Barcelona

2. METODOLOGIA DE DIGESTIÓ ÀCIDA:

Vegetal tissue wet digestion using a domestic microwave oven

2.1. Summary

A rapid, accurate, precise and inexpensive method for wet digestion of vegetal materials is proposed. A conventional microwave oven has been used as energy source. Total phosphorus, calcium, magnesium, potassium and sulphur have been analysed by I.C.P.-A.E.S. techniques. A varied assortment of plants (algae, seagrasses, freshwater plants and terrestrial plants) and plant parts (leaves, wood, rhizomes, roots and bark) were digested to test inter and intra-assay method precision and the effects of the characteristics of the material on its efficiency. Three standards (NBS Pine Needles, Citrus Leaves and the intercalibration sample from the Forest Research Institute of New Zealand *Pinus radiata* leaves) were also digested to test the accuracy of the method. All samples were totally digested after 20 minutes or less. Values found for standards coincided in all cases with the certified ones. Average recovery was 97.2 % and ranged from 81.3 % to 114.5 %. Variability of the method, in terms of standard error of the mean, varied from 3.025 % (Ca) to 9.721 % (K). Practical considerations such as instrument availability and purchase price, operating costs, acid volume needed and especially number of samples processed per hour, have been compared between the present method and classic methods using conventional heaters. Proper safety considerations procedures are given.

2.2. Introduction

Many plant ecology experiments involve total phosphorus, calcium, magnesium, potassium and sulphur analysis of different parts of the plant. Experimental designs usually require the processing of a large number of samples which represents one of the most time-consuming steps of the whole experiment. The plant ecologist in search of a suitable digestion procedure may find a wide range of methods in the specialized literature. However, sophisticated and often complicated laboratory routines are found. Practical considerations, such as instrument availability and purchase price, operating costs, skill or experience requirements of the analyst, number of samples processed per hour, and accuracy and precision, determine the choice (Jones and Case 1990). Hot sand baths or metal block heaters take several hours to digest a very limited number of samples. Glass digestion vessels are expensive and fragile and acid fume evacuation is always a nuisance.

Since Gleit and Holland (1962) made the first attempts at decomposing organic substances using radio frequency discharges, methods using microwave radiation have been continuously developed as an alternative to conventional heaters. Nowdays, microwave ovens are being used successfully for wet digestion purposes. Although sophisticated laboratory microwave ovens are available, simple domestic configurations can be designed. Barret and Davidowski (1978) made some practical achievements by using a pyrex box inside a commercial microwave oven vented by a Nalgene aspirator. We propose a new variation using a round domestic pyrex container with a cover, and a simple system to load up to 25 samples at a time and that minimizes dead spaces. Acid fumes are aspirated by an ordinary water vacuum pump connected to the pyrex container by teflon tubing. Samples are digested in small resistent FEP teflon bottles. Elemental analysis is performed using ICP-AES techniques.

The Standard Reference Materials (SRM), NBS 1572 Citrus Leaves, 1575 Pine Needles and a wide range of botanical samples (see table 2.3 for list of samples) have been analyzed using this configuration, obtaining satisfactory accuracy and precision levels.

2.3 Experimental

Apparatus

A domestic microwave oven Sanyo EM-840 with rotatory tray and a maximum power rating of 750 W (length and width, 35cm; height, 25cm) was used as energy source for the acid digestion.

Elemental analysis was performed at the *Serveis Cientific-Tècnics* (Scientific-Technical Services) of Barcelona University, using the inductively coupled argon plasma emission spectrometers JOBIN IVON JI-38 (3600 grooves.mm^{-1}) and multi-channel THERMO JARREL ASH POLYSCAN 61E (2400 grooves.mm^{-1}) with special channels for K, Li and Na.

Reagents

All sample dilutions were made with deionized water of 18 Mohms. cm^{-1} resistivity from a Mili-Q Water Purification System. HNO_3 60% and $HClO_4$ 60% reagent grade were used for digestion of samples.

Procedure

Samples and SRM were oven dried at 70°C for 48 hours. Next, they were milled with a Tecator CYCLOTEC 1090 Sample Mill with a 0.4 mm screen. They were then oven dried again at the same temperature for 24 hours. Samples were then allowed to cool to laboratory temperature in a dessicator, before weighing. About 0.1 g of sample was weighed on an analytical balance Mettler AE200 (0.0001 to 205 g). The material was then placed in 50 ml Nalgene FEP (fluorinated ethylene propylene) teflon bottles (Cent Tubes Oak ridge FEP 3114-0050). Some sample particles may stick the neck of the bottle. Nevertheless, appropriate reflux achieved during the digestion incorporates these particles to the rest in the bottom of the bottle. Bottles should be perfectly dry to minimize this.

From 1.3 to 2.0 ml of a mixed solution (nitric: perchloric, 10:4) was added to every 0.1 g sample using a Pressmatic 2000 dispenser 0.2-1.0 ml from J. Bibby Science Products Ltd. This proportion acid-volume/sample-weight coincided with the safety margin estimated by Abu-Samra of 10 ml for every 0.5 g of sample (Abu-Samra et al. 1975). H_2SO_4 was not used in the solution to avoid calcium-sulphate precipitation (White and Douthit 1985) and to permit sulphur analysis. Three reagent blanks were included in every digestion programme. Bottles were gently agitated to obtain an homogenous mixture between acids and materials. It is recomended that acids should react with samples for some minutes before exposing them to microwave radiation to prevent violent exothermic reactions between perchloric acid and organic matter (Jackson 1958). Insufficiently milled material may cause dangerous explosions.

Bottles were buried to about half their height in a pyrex container (heigh 15cm, diameter 25cm) containing suitable amounts of fine sand. This procedure eliminates almost all dead space thus facilitating evacuation of acid fumes. 25 samples were loaded each time, with the limit imposed by the size of the container. The container was then closed remaining the bottles opened inside it. No vacuum is created in the container as it is not airtight. Teflon tubing, 1.5 cm diameter, connected the container to an ordinary laboratory glass water vacuum pump for fume extraction purposes. The flux created efficiently removed fumes from the container and prevents leakage to the oven cavity. Although acid fumes are diluted in water occurs during the aspiration, the use of an acid fume scrubber with a 2M KOH solution is recommended to avoid piping corrosion (Barret and Davidowski 1978). Suitable holes were drilled in the middle of the container cover and on one side of the oven. Microwave radiation leakage must be checked periodically for all parts of the configuration. A 3 cm of diameter hole was checked by Barret et al. showing no significant radiation emissions (Barret and Davidowski 1978). The 1.5 cm hole and the rest of our system is exhaustively checked every month showing no significant leakage. Teflon angles and joints were used to assemble the configuration. Connection with the container was made in such a way that allowed it to rotate with the oven tray. This connection must be designed to be easily released from the cover.

Before starting digestion programmes, all interior surfaces of the oven, including electronics and lamps, were protected from possible acid fumes leakage. For this purpose, the Turbo Lube Synthetic Lubricant spray with teflon particles was used. It must be totally replaced at least every week. A pyrex vessel with deionized water must be placed in the oven to prevent it from working with little or without microwave sink. Water must be replaced every digestion programme. The two last measures will considerably increase oven life (Abu-Samra et al. 1975).

All the configuration must be placed into a fume hood to maximize safety conditions. In Figure 2.1., a simplified scheme of the configuration has been outlined. Both fume hood extractor and water pump must be running before exposing samples to microwaves. Pump water flux and microwave power allowed us to obtain a satisfactory balance between acid evaporation and fume reflux within the bottles (Abu-Samra et al. 1975). The digestion programmes used are shown in Table 2.1. Although the process requires little supervizing, it must be extreme during the first attempts. At the end of the process it is recommended to wait for some minutes to allow system cooling. After that, teflon tubes can be safetly manipulated. The content of the bottles will appear completely clear remaining very little acid (mainly $HClO_4$). A slight green-yellow colour is accepted as a normal feature (remains of HNO_3). Another exposure programme was used for incompletely digested samples, setting about 1/3 of the exposure time and adding about half the volume of the mixed acid solution if necessary. It is also recomended to add from 0.5 to 1 ml of $HClO_4$ or of mixed reagent after digestion to keep all elements in solution. The standards for elemental analysis must include the same acid proportion. Deionized water was added with a Dispensette Brand dispenser (0-10 ml) to dilute to a final volume of 20 ml, giving, for the treated samples, an appropriate elemental concentration for ICP-AES analysis.

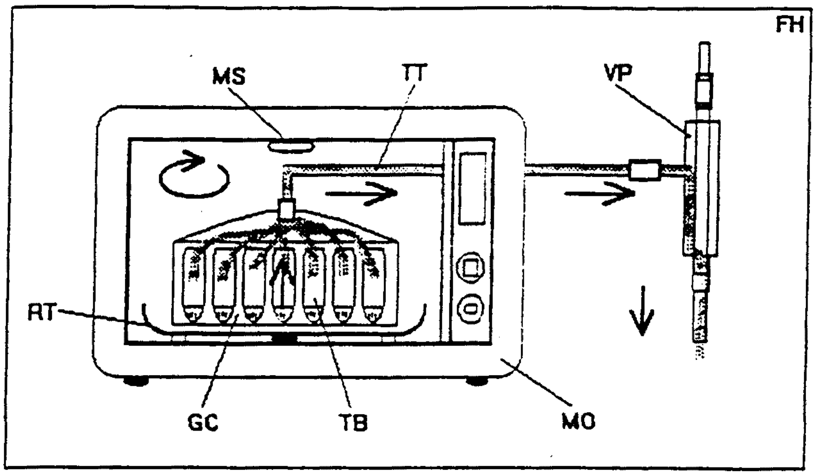


Figure 2.1. Scheme of the proposed configuration. FH: fume hood; MS: microwave source; TT: teflon tubing; VP: vacuum water pump; RT: pyrex glass rotatory tray; GC: pyrex galss container; TF:teflon bottles; MO: domestic microwave oven. The arrows show acid fume flux. Sand has been omited for clarity.

Table 2.1. Microwave digestion programmes used in the present work. 100% is a power rating of 750 W. The rest of parts of the plants includes rhizomes, roots, wood and bark. The second programme is used for samples incompletely digested after the first one

		First		Second	
		Power	Time	Power	Time
Algae		75%	15'	none	none
Spermatophyta	Leaves	100%	15'	75%	5'
	Rest of Parts	100%	25'	75%	5'

Finally, teflon bottles were tightly closed and thoroughly shaken before transferring the dilution to 50 ml polyethylene vessels for storage. The final diluted solutions, appeared to be stable for at least one month with no special storage conditions. Reproducibility of calcium values for ICP determination, seemed to be better when samples were stored in fridge at 5°C.

No more steps were required for elemental analysis. The wide sensitivity range of ICP- atomic emission spectrometers, allowed us to use the same dilution for the five elements analyzed. Wave lenghts used were (nm): 213.618 with the monochromator ICP and 178.287 with the polychromator for phosphorus. Both apparatus were intercalibrated for phosphorus determination giving identical results. The remaining elements were analyzed only with the multi-channel ICP-AES. Ca: 317.933; Mg: 279.079; K: 766.491 and S: 182.040. A high solid content nebulizer was used making the filtration of dilutions unnecessary; a high flow torch was selected. The output power was of 1150 W; auxiliary argon flow used was of 0.5 $l.min^{-1}$ and nebulizer argon pressure was set at 30 psi.

2.4. Results and discussion

All samples were digested in 20 minutes or less. High fiber content samples, such as rhizomes, roots, wood and bark needed in general to be treated with the two exposure programmes. Algae and plant leaves were totally dissolved after the first one.

Rotatory configuration totally overcame hot spot problems (Lamothe et al. 1986). The use of teflon bottles eliminated the problems of acid overheating ocurring when using pyrex glass vessels or Erlenmeyers (Wandt and Pougnet 1986). Lubricant spray with teflon particles gave satisfactory acid protection to all the oven parts representing an adventageous choice when compared to expensive or complicated designs (Lamothe et al. 1986, Alvarado et al. 1988). While classic block digestors, laboratory microwave ovens or other self-made configurations (White and Douthit 1985, Lamothe et al. 1986, Wandt and Pougnet 1986, Kingston and Jassie 1986) are usually limited to a dozen samples (Lamothe et al. 1986), from 1 to 25 samples were easily digested at a time with the proposed configuration, the pyrex container size, being the limit. Up to 150 samples were digested per person and day. Never more than 4 ml of the mixed acid solution was needed to complete the digestion representing an important reagent saving. Acid fume extraction was totally efficient with little incidence on microwave oven parts after several months.

The obtained values for NBS standards coincided with the certified ones (Table 2.2.). A *Pinus radiata* sample was used for method intercalibration between our Department and the Forest Research Institute (FRI) of Rotorua in New Zealand.

Table 2.2. Method accuracy test. Certified and found values for NBS standards and Forest Research Institute intercalibration sample; standard errors are not available. Values by White and Douthit (1985) were also obtained using a microwave oven and ICP-AES techniques. Mean±standard error. Values are in % of dry weight.

Pine needles	Found value (n=8)	NBS value	White & Douthit
P	0.120±0.002	0.12±0.02	0.12±0.01
Ca	0.470±0.006	0.41±0.02	0.42±0.01
Mg	0.110±0.002	-	0.12±0.01
K	0.320±0.004	0.37±0.02	0.39±0.02
Citrus leaves	Found value (n=7)	NBS value	
P	0.133±0.001	0.13±0.02	
Pinus radiata leaves	Found value (n=5)	FRI value	
P	0.159±0.001	0.15	
Ca	0.227±0.005	0.25	
Mg	0.130±0.003	0.16	
K	0.852±0.030	0.85	

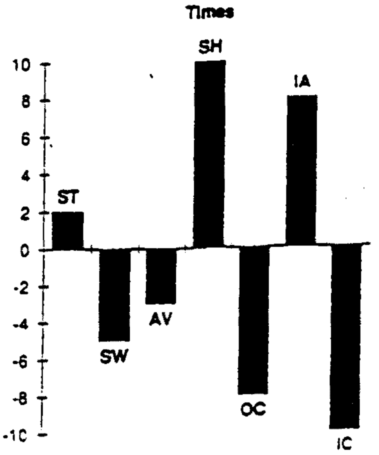


Figure 2.2. Confrontation between the present method and other methods using conventional heaters. ST: number of samples digested at a time; SW: sample weight needed; AV: acid volume needed; SH: maximum number of samples digested per hour; OC: operating costs; IA: instrument availability; IC: instrument purchase cost. Example: The number of samples digested per hour with the proposed method, is roughly 10 times higher than the number digested by other methods (see text for more details).

They analyzed this sample using dry digestion methods (Nicholson 1984). Values found using our method, showed identical or statistically equivalent values (Table 2.2). Standard errors for FRI values are not available. Intra-assay reproducibility was tested for all the samples by digesting at least five replicates within the same digestion programme. Error ranged from 3.025 % for calcium to 9.721 % for potassium depending basically on element concentration in the tissues. Errors can be considerably reduced if required, by increasing sample weight used and dilution final volume. The results obtained are sumarized in Table 2.3.

Three different standard-markers were analysed periodically with our method during more than a year by different analysts to assure accuracy and replicability constance. The results showed satisfactory inter-assay performance (Table 2.4).

In Figure 2.2., some practical parameters of the present method are compared with a rough average of the classic ones. The volume of acid needed has been reduced about three times in the present work. Usually, very little amount of sample is available. All results given in this report have been obtained by digesting about 0.1 g of sample. However, analysis attempts were successfully performed with 1/2 and even 1/4 of this weight. Sample processing speed was increased on about 10 times with respect to classic methods. Although electric energy consumption of the oven used was higher (750 W) than hot plate heaters (500 W on average), time reduction results in an 8 fold of operating costs reduction. Instrument availability is also an important factor to be taken into account especially when asking for original spare. Although no complicated calculations are needed to asses the advantages of domestic instruments in this point, some data of shipping time needed have been gathered and compared. Exactly the same comments can be made about instrument purchase price, being in most cases a decisive point when choosing a method.

We want to enphasize that working safety is the primary concern. After thousands of digestions no accidents or incidents have ocurred. The careful observation of the procedure safety considerations will prevent from any contingency. We recomend to consult the recently approved US EPA microwave methods 3015 and 3051 for sample preparation.

We conclude, after the results obtained and the reading of current literature on this topic, that microwave energy-based wet digestion systems (nuclear or internal heating), show important and conspicuous advantages over peripheral heat conduction systems. We also feel that price reduction and design improvement of laboratory microwave ovens, will definitely generalize their use for the wet digestion of all type of samples.

Table 2.3. Method intra-assay precision test. Values found for the samples used in the present work. Five replicates for each sample were digested together within the same program. Mean ± Standard error. Values are in % of dry weight. (Mean % of error; P 7.0%, Ca 3.0%, Mg 4.4, K 9.7%) (% of samples with <10% of error; P 73.5%, Ca 96.8%, Mg 90.3%, K 71.0%).

Seagrasses	Plant Part	P	Ca	Mg	K
Posidonia oceanica	Leaves	0.130±0.002	9.046±0.098	0.862±0.097	0.624±0.030
	Rhizomes	0.064±0.001	6.029±0.149	0.741±0.149	0.985±0.030
Cymodocea nodosa	Leaves	0.144±0.006	-	-	-
	Rhizomes	0.214±0.001	-	-	-
	Roots	0.172±0.002	-	-	-
Freswater plants	Plant Part	P	Ca	Mg	K
Ruppia cirrhosa	Leaves	0.180±0.002	2.000±0.065	1.195±0.004	0.804±0.015
	Roots	0.117±0.006	1.226±0.020	1.235±0.011	1.368±0.020
Ulva sp.	Talus	0.062±0.001	3.408±0.029	0.948±0.009	0.478±0.019
Oryza sativa	Straw	0.097±0.002	4.948±0.084	0.413±0.013	0.822±0.044
Isoetes lacustris	Leaves	0.187±0.001	0.926±0.030	0.237±0.010	3.220±0.153
	Corm	0.320±0.007	0.570±0.008	0.137±0.001	0.037±0.016
	Roots	0.134±0.001	1.348±0.027	0.119±0.004	1.463±0.082

Table 2.3. (Continuation)

Terrestrial plants	Plant Part	P	Ca	Mg	K
Pinus radiata	Leaves	0.159±0.001	0.227±0.005	0.130±0.003	0.852±0.030
Pinus uncinata	Leaves	0.069±0.001	0.364±0.010	0.090±0.001	0.386±0.058
	Bark	0.011±0.001	0.802±0.000	0.018±0.000	0.035±0.005
	Wood	0.006±0.002	0.210±0.009	0.021±0.001	0.030±0.004
Pinus nigra	Leaves	0.076±0.001	0.482±0.010	0.116±0.002	0.408±0.007
	Bark	0.013±0.002	0.818±0.006	0.021±0.001	0.020±0.004
	Wood	0.009±0.001	0.138±0.002	0.022±0.002	0.096±0.041
Pinus halepensis	Leaves	0.071±0.001	0.932±0.017	0.218±0.003	0.272±0.004
	Bark	0.011±0.002	2.333±0.097	0.047±0.001	0.053±0.006
	Wood	0.010±0.002	0.218±0.005	0.025±0.001	0.074±0.002
Pinus sylvestris	Leaves	0.076±0.001	0.486±0.054	0.095±0.007	0.441±0.012
	Bark	0.009±0.002	0.872±0.030	0.009±0.001	0.023±0.009
	Wood	0.011±0.001	0.120±0.009	0.021±0.001	0.066±0.004
Quercus ilex	Leaves	0.107±0.001	0.805±0.060	0.045±0.002	0.599±0.007
	Bark	0.026±0.000	6.586±0.142	0.052±0.001	0.258±0.002
	Wood	0.019±0.001	0.780±0.026	0.058±0.001	0.272±0.004
Quercus cerrioides	Bark	0.013±0.003	4.380±0.240	0.282±0.024	0.120±0.010
	Wood	0.015±0.002	0.356±0.012	0.025±0.001	0.198±0.002

Table 2.4. Method inter-assay precision test. Every replicate was digested within different programmes for several months. Standard-maker 1: *Posidonia oceanica* whole rhizomes. Standard-maker 2: *Pinus radiata* leaves. Standard-maker 3: *Quercus ilex* leaves. Values are % of dry weight.

Element	n	Mean±standard error
Standard-maker 1		
P	32	0.025±0.001
Standard-maker 2		
P	54	0.110±0.001
Ca	45	0.790±0.011
Mg	45	0.054±0.004
K	45	0.550±0.012
Standard-maker 3		
P	94	0.101±0.001
Ca	94	0.657±0.003
Mg	94	0.044±0.001
K	94	0.646±0.004
S	94	0.099±0.003

2.5 References

Abu-Samra A, Morris JS, Koirtyohann SR, (1975). Anal Chem 47:1475-1477

Alvarado J, Márquez M, León LE (1988). Analytical Letters 21:357-365

Barret P, Davidowski LJ Jrk (1978). Anal Chem 50:1021-1023

Gleit ChE, Holland WD (1962). Anal Chem 34:1454-1457.

Jackson ML (1958) Soil Chemical Analysis. Prentice-Hall, Inc. Englewood Cliffs, NJ

Jones JB Jr, Case VW (1990) Sampling, Handling, and Analizing Plant Tissue Samples. Chapter 15. In: Westerman R.L (ed.). Soil Testing and Plant Analysis. SSSA, Inc. Madison, Wisconsin, USA. 784 pp

Kingston HM, Jassie LB (1986). Anal Chem 58:2534-2541

Lamothe PJ, Fries TL, Consul JJ (1986). J Anal Chem 58:1881-1886

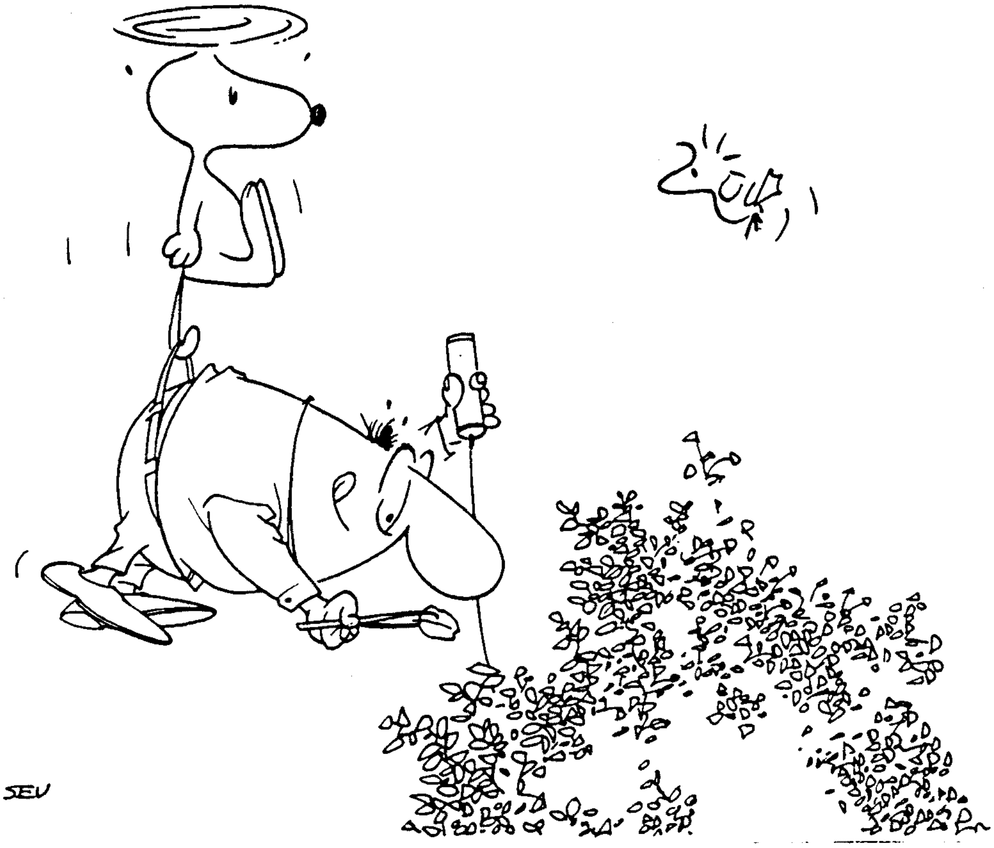
Nicholson G (1984). New Zealand Forest Service. FRI Bulletin 70

Wandt MAE, Pougnet MAB (1986). Analyst 111:1249-1253

White RT, Douthit GE (1985). Anal Chem 68:766-769

3. Contingut de nutrients a les capçades de *Quercus ilex* a la conca de l'Avic. Estudi de la variabilitat temporal, altitudinal i deguda a la posició en el perfil vertical de la capçada:

Nutrient content in Quercus ilex canopies: seasonal and spatial variation within a cathment



EL CANONGE DE LA SEU

3.1. Summary

Spatial and temporal changes in canopy nutrient content were studied in a mediterranean *Quercus ilex* forest in Catalonia (NE Spain). Destructive sampling during 1988 and 1989 was conducted in parallel at two locations within a catchment (ridge-top, at 975 m and valley bottom, at 700 m); the two loactions represented two ends of a gradient in terms of local topography, microclimate and forest structure. The purpose of this study was to compare the relative importance of canopy nutrient contents and dynamics at each site and their seasonal variation. C, N, P, K, Ca and Mg concentration (% dry weight) and mass on leaf area basis were analyzed in leaves and stems sampled at four different canopy layers, from top to bottom of the canopy.

N, P and Mg concentration (% dry weight) and N and Mg mass (μg/cm^2) in leaves were significantly higher at the valley bottom site than at the ridge top site. This may be related to a higher nutrient availability (deeper soil at the valley bottom site). In contrast K concentration (% dry weight) and mass (μg/cm^2) in leaves was significantly higher at the ridge top site. This is probably related to lower water availability, and explain the increased stomatal control of transpiration at the ridge top site as compared to the valley bottom site (Sala 1992).

Nutrient resorption, on a leaf unit-area basis, was calculated as the difference between the largest nutrient mass measured in green leaves before senescence and the nutrient mass remaining in leaf litter. N resorption from top to bottom of the canopy ranged from 73-165 μg/cm^2 at the ridge top site and 30-145 μg/cm^2 at the valley bottom site (33-55 % vs. 14-47 % of N resorption efficiency, relative to the largest nutrient mass). P resorption ranged from 8.1-14.7 μg/cm^2 at the ridge top site and 12.3-17.7 μg/cm^2 at the valley bottom site (42-57 % vs. 56-62 % of P resorption efficiency). These results showed a higher N and lower P resorption at the ridge top site where growth may be limited by decreased water and nutrient availability (steeper and shallower soils). Besides resorption prior to leaf abscission, seasonal changes of P and N concentration on a leaf area basis suggest P and, to a lesser dregree, N replenishment during periods of lower growth activity due to low temperatures, but coinciding with higher water availability (autumn-early spring period). These variations were larger at the valley bottom site than at the ridge top site.

The holm oak sclerophylly is influenced by atmospheric conditions (annual radiation load, mean annual temperatures, annual rainfall). These conditions govern leaf area index and leaf biomass, affecting nutrient canopy concentration and mass. Thus aspects other than soil nutrient status, should be considered when interpreting the extent to which differences in nutrient content, use efficiency and resorption are responses to nutrient availability.

On total canopy basis (canopy nutrient mass/canopy biomass), lower stem nutrient concentration was found at the valley bottom site, suggesting a higher production per unit of nutrient (equivalent to nutrient dilution) at this site and, so combined to resorption efficiencies, higher nutrient use efficiency in stem canopy construction. On the other hand, higher leaf nutrient concentrations, on total canopy basis, were computed at the valley bottom site except for K which was higher at the ridge top site.

3.2. Introduction

Quercus ilex L. (holm oak) is adapted to the low temperatures characteristic of high elevation sites and low soil moisture following scarce summer precipitation in the mediterranean basin (Comin et al. 1987, Sala 1992). The biogeochemistry of this species shows intermediate characteristics between coniferous and deciduous forests. Escarré et al. (1987) suggested that the high nutrient content in fine branches are an adaptation to fluctuating nutrient availability, if these reserves can be easily mobilized. For instance, the role of old leaves storing nutrients could be interpreted as an advantage of evergreenness (Chabot and Hicks 1982). In evergreen species leaves appear to be as important as roots or stems as sites of nutrient accumulation and storage (Chapin 1980). Thus seasonal nutrient storage, like luxury consumption, is essential to the success of perennial species in low-nutrient environments (Chapin 1980, 1988).

The possibility to re-use nutrients several times increases its use efficiency (Vitousek 1982). Escudero et al. (1992a) did not find this role in *Quercus ilex* ssp. *rotundifolia* (this ssp. is found on drier areas compared to *Quercus ilex* ssp. *ilex* of this study). Del Arco et al. (1991) suggested that the pattern of leaf abscission under dry conditions tends to reduce the efficiency of nutrient resorption (negative relationship between length of leaf abscission period and % of N resorption). Escudero et al. (1992b) stated that if instantaneous nutrient productivity does not vary with leaf age, resorption does not affect nutrient use efficiency decisively. Leaf longivity in evergreens could be more important in increasing retention time of nutrients than resorption from senescing leaves. So the advantage of evergreenness may be related to a possible improvement in overall photosynthetic efficiency.

Although soil fertility is a relative term, there are consistent patterns of nutritional response in plants from soils of differing fertility (Chapin 1980). Species characteristic of favourable habitats show greater plasticity in their allocation pattern than do species from stressful environments (Grime 1977), but a high root:shoot ratio is in part a phenotypic response to reduced nutrient (Chapin 1980) and water availability. This plasticity was found by Canadell and Rodà (1991) since *Quercus ilex* ssp. *ilex* from xeric sites have a significant higher root:shoot ratio than those from mesic sites. An interesting point is how different structural characteristics affect the ecological pattern of nutrient use and resorption efficiencies. There is no evidence that wild plants have adapted to infertile conditions through an increased physiological potential to produce biomass per unit of nutrient (Chapin 1988) and the particular effectiveness in nutrient resorption prior leaf abscission (Chapin and Kedrowski 1983, Pugnaire and Chapin 1993). The origin of this unclear pattern could be due to the relative role of other factors such as water availability and the mixture of genotypic and phenotypic plasticity responses to soil fertility as compared to different species (Chapin and

Moilanen 1991). Following this line, Pugnaire and Chapin (1993) conclude that nutrient resorption is not an adaptation of plants to high or low nutrient availability, but a phenotypic response by plants to variation in nutrient status. Nevertheless, May and Killingbeck (1992) found that resorption is closely linked to fitness in *Quercus ilicifolia*, a species restricted to nutrient-poor sites, but there are no experimental data to clarify this generality.

A distinct environmental gradient exists at l'Avic, with greater water and nutrient availability and reduced radiation load at the lowest valley bottom sites, and lower water and nutrient availability and higher radiation input throughout the upper slopes (Piñol 1990, Sala 1992, Alcañiz unpublished data). In this study we compare two locations within l'Avic catchment (ridge top and valley bottom) representing two ends of these water and nutrient availabilities and radiation load. The Canopy structure of this *Quercus ilex* ssp. *ilex* forest was reported in another study (Sala et al. submited manuscript). The goal of this study is to examine how these differences in nutrient and water availability affect the nutrient content and dynamics at both sites. Firstly, we analyze nutrient concentrations (% of dry weight) in leaves and stems, as well as nutrient mass in leaves (on leaf area basis), and temporal variations at each site and at different canopy levels. Secondly we report the nutrient resorption at both sites from green leaves and from leaf litterfall. Finally we compare the nutrient mass per square meter of ground contained in the whole leaves and stems system of the canopy, at each site, and with other holm oak forests growing under different environmental conditions.

3.3. Study area and Sampling sites

The l'Avic watershed (41° 15' N, 1° E) is located in the Prades Mountains (Catalonia, NE Spain). The watershed occupies 51.6 ha, ranging 680 to 1007 m in elevation. The average slope is 26° facing NNW. *Quercus ilex* ssp. *ilex* L. (holm oak) forms essentially pure stands throughout the study area. Soils are xerochrepts (USDA Soil Taxonomy, 1975) of variable depth, which tend to increase in the lower parts of the watershed (Piñol 1990). Climate is typically mediterranean, with hot and dry summers, fresh and wet springs and autumns, and mild as well as fairly dry winters. The mean annual temperature is 13.8°C and the average annual precipitation is 647 mm (period 1957-1990). Bellot (1989) did not find rainfall altitudinal differences at L'Avic. Lledò (1990) reported an average rate of foliage turnover, in *Quercus ilex* holm oak at l'Avic watershed, of about 2.4 years and the growth occurs mainly during the spring (May to June). This point was of use when considering the origin of leaf litterfall in order to calculate nutrient resorption after leaf litterfall that occurs mainly between April and August (Bellot et al. 1992).

Two sampling sites were located in l'Avic watershed at the two ends of a gradient in terms of local topography, microclimate and forest structure: 1) at the bottom of the valley, at 700 m altitude, near to the stream, sheltered by the steep valley slopes (*valley bottom site*), and 2) on the upper open slopes, approximately 30 m below the ridge of the mountain, at 975 m altitude (*ridge top site*). Some characteristics of both sites are shown in Table 3.1.

3.4. Methods

Sampling procedure and measurements

Sampling of canopy elements were conducted during 1988 and 1989 growing seasons. Sampling was done in parallel at the ridge top and valley bottom during mid-summer of 1988 (late July and early August), late autumn 1988 (late November and early December), early spring of 1989 (early April, before the new growth period), mid-summer of 1989 (August), and late autumn of 1989 (late November). Detailed description of sample harvesting procedures and structural characteristic measurements were reported in Sala (1992) and Sala et al. (submited manuscript). At each site and sampling date, leaves and stems smaller than 2 cm in diameter from three randomly located square columns (0.5 x 0.5 m^2) were collected every 0.5 m from the top of the canopy to the ground and stored in labeled plastic bags. Samples were transported to the laboratory and kept in a dark freezer (-1 °C) until analysis. Leaves from different spring growth seasons, stems supporting these leaves and stems without leaves were separated for each sample. Leaf area was measured with a leaf area meter Li-3000 (LiCor Inc.). Specific leaf weight was obtained from subsamples oven dried at 65°C for 72 h. Total dry weight was divided by the area of the corresponding subsample.

Nutrient concentration (% of dry weight) was analized at four levels along the vertical profile from the top to the bottom of the canopy: A(0 to 0.5 m), B(0.5 to 1 m), C(1 to 2 m) and D(2m to the ground). As reported by Sala et al. (submited manuscript) more than 81% of the total LAI is found in the upper 2 meters of the canopy and 60% in the uppermost meter at both sites. Carbon and nitrogen content of each fraction were analyzed using a Carlo-Erba D-700 elemental analyzer. Phosphorus and cations were analyzed using wet digestion as described in Mateo and Sabaté (in press) and values were determined for P using a JOBIN YBON JI-38 induced coupled plasma (ICP) and a PHILLIPS PU9200X spectrophotometer by atomic absorption for Ca and Mg and by emission for K.

The specific leaf weight was used to determine the nutrient mass per unit leaf area. Since leaf surface area remains approximately constant during senescence, providing an accurate frame of reference for determining net nutrient movements into or out of leaves (Woodwell 1974), variations over time of nutrient mass per unit leaf area were used to compute nutrient resorption. Resorption from leaf litterfall was calculated as the difference between the largest nutrien mass value on leaf area basis measured in green leaves produced in spring of 1987 (leaves-87) and the nutrient mass value on leaf area basis measured in leaf litterfall collected from litter traps below the canopy in June of 1989 (leaf litterfall mainly due to leaves-87). In leaves produced in spring of 1988 (leaves-88), resorption was calculated as the difference between the largest value and the next relative lowest value. The nutrient resorption efficiency was calculated as the mass of resorbed nutrient divided by the largest nutrient mass in green leaves. Biomass distributions of different fractions considered along each vertical profile were used to determine the total nutrient mass per unit of ground area.

Statistical analysis

Data were analyzed using SAS GLM procedure (SAS 1988) for a complete three-factor factorial model with *sampling date* (DATE), *sampling site* (SITE), *canopy height* (C.H.) as main effects.

3.5. Results

Nutrients in leaves and stems

Figures 3.1.1 through 3.1.5 show nutrient concentration (% of dry weight) and nutrient mass (on leaf area basis, $\mu g/cm^2$) in leaves produced in spring of 1987, 1988 and 1989, along four layers, from top to bottom of the canopy.

In general, N concentration and mass showed significant site and temporal variations (Figure 3.1.1). N concentrations were higher at the valley bottom site than at the ridge top site. These differences between sites narrowed when comparing N mass, and sometimes disappeared or even changed sign (see leaves-87). This was because specific leaf weight tended to be lower at the valley bottom site (Sala et al. submited manuscript). Similarly in addition, a significant canopy height effect was evident at both sites when comparing N mass. Since the leaf specific weight decreased from top to the bottom of the canopy (Sala et al. submited manuscript), and no substantial differences of N concentrations were found on this axis (there was only a significant decrease in leaves-88), leaves from the lower canopy layers exhibited less N mass.

In summer of 1989, especially for leaves-88, N concentration and mass twere similar at both sites. On the other hand, leaves produced in spring of 1987 and 1988 reached a higher N concentration and mass in autumn of 1988 or early spring of 1989 when low temperatures slowed growth activity. The temporal pattern of N concentration was not so clear for leaves-89 at the ridge top site as for leaves-89 at the valley bottom site, which showed lower values in summer of 1989 and higher values in autumn of 1989.

P concentration showed similar temporal patterns than N (Figure 3.1.2). In spite of this similarity, differences between sites were not significant when comparing P mass. On the vertical profile axis P mass decreased in the same way as N from top to bottom of the canopy layers.

Figure 3.1.3 shows K concentration and mass in leaves. The pattern observed is quite different from the one observed for N and P. In general, K concentration and mass were higher at the ridge top site than at the valley bottom site. The temporal variation showed significant decreases over time, but no clear replenishment processes were observed. On the vertical profile axis differences on K mass were not significant. Figures 3.1.4 and 3.1.5 show Ca and Mg concentration and mass in leaves. Ca did not show a clear pattern although some significant differences in leaves-88 were found showing lower values in spring of 1989, especially in the bottom canopy layers, and increasing again in summer and autumn of 1989. Like Ca the Mg pattern did not show clear differences, but leaves-88 had higher concentration and mass values at the valley bottom site than at the ridge top site, and also values in summer tended to be higher.

C and N concentration in stems did not change with respect to sampling date, site or canopy height (data not shown). P concentrations tended to be higher in summer and lower in autumn and spring (Table 3.2.1). This pattern was opposite to the one observed in leaves (Figure 3.1.3). K concentration in stems declined significantly over time (Table 3.2.1). No substantial differences in Ca and Mg concentration in stems were found, and the pattern of variation was not clear (data not shown).

Tables 3.2.2 and 3.2.3 show the mean for all canopy C, N, P, K, Ca and Mg concentration values of leaf-bearing fine stems and leaves. Generally, higher C and N concentrations and lower P, K, Ca and Mg concentrations were found in leaves than those found in stems. This pattern was similar to those found by other studies in the same forest (Clemente 1983) and other holm-oak forests (Ferrés 1984, Mayor 1990, Mayor and Rodà 1992, Canadell and Vila 1992). In addition, as in leaves, K concentration in stems with leaves was higher at the ridge top site than at the valley bottom site. These differences were significant for stems-88 ($P<0.005$) and stems-89 ($P<0.001$) (Table 3.2.2).

Nutrient resorption

Table 3.3.1 shows N mass in leaf litterfall on a leaf area basis and the largest value of N mass in leaves-87 before shedding. Resorption is shown for different canopy layers from top to bottom of the canopy. N resorption mass and its efficiencies were higher at the ridge top site and also in the upper part of the canopy. At the ridge top site values ranged between 52% in the uppermost layer and 33% at the lower canopy layer. The valley bottom site showed a range from 47% in the uppermost canopy layer and 15% at the lower one. P mass resorption is shown in Table 3.3.2. In this case the values of P resorption were more homogeneous along canopy layers. The values calculated at the ridge top site were lower than those calculated at the valley bottom site (between 42% to 57% and 56% to 65% respectively).

Variations in leaf nutrient mass (as Figure 3.1.1 and 3.1.2 show) suggest nutrient withdrawal and replenishment several times during leaf life-span. From these results *Quercus ilex* seems to be an evergreen species able to supply nutrients from leaves to new production, and later be replenished when growth activity decline during lower temperatures, but higher water availability, in autumn early spring period. The resorption values from retained foliage are shown in Table 3.4.1 for N and Table 3.4.2 for P. Nitrogen did not show high nutrient resorption values as compared to nutrient resorption before leaf fall. N-resorption efficiency values were between 1% to 15% at the ridge top site and 16% to 21% at the valley bottom site. On the other hand, P resorption efficiencies were larger, between 25% to 30% at the ridge top site and 33% to 40% at the valley bottom site.

Although differences between largest mass values in green leaves and mass values in leaf litter (μg/cm^2) could be calculated for K and Mg, as was done for N and P (Tables 3.3.1 and 3.3.2), K and Mg differences obtained were due to resorption and lixiviation processes (data not shown). Bellot (1989) found that about 90% of K and 60%-70% of Mg in throughfall in *Quercus ilex* were due to lixiviation. These values were on a ground area basis 1.35 g/m^2 of K and 0.10 g/m^2 of Mg. Comparing these values with K and Mg average mass in leaves per unit of ground area in this study (see Table 3.5.1), lixiviation is about 25% of K and 13% of Mg mass in leaves at the ridge top site and 27% of K and 9% of Mg mass in leaves at the valley bottom site.

Leaves and stems biomass and nutrient mineralomass

The biomass and nutrient canopy mass (leaves and leaf bearing stems) per unit of ground area, at the ridge top and valley bottom sites, are shown in Table 3.5.1. A general trait was a higher nutrient mass at the valley bottom site than at the ridge top site. In general these differences paralleled differences in leaf biomass and nutrient concentration, but only N and Mg canopy mass differences were significant. Unlike the other nutrients, K mass value in leaves was higher at the ridge top site. This agreed with the higher nutrient concentration and mass on leaf area basis at the ridge top site (Figure 3.1.3), but statistical significance disappears because the higher leaf biomass at the valley bottom site counterbalanced concentration differences. Stems K mass was higher at the valley bottom site, despite lower concentrations at this site (Table 3.2.2), again because of its higher stem biomass.

Tables 3.5.1 and 3.5.2 show how similar l'Avic is to La Castanya (Escarré et al. 1987) and Le Rouquet (Loissant and Rapp 1978, Cole and Rapp 1981). L'Avic is the driest and warmest location, followed by Le Rouquet and La Castanya. Leaf biomass and Leaf Area Index could be related to environmental conditions (Specht and Specht 1989). Higher biomass showed an inverse relation to rainfall and Leaf Area Index was parallel to radiation. These values influenced the whole nutrient canopy mass on a ground area basis counterbalancing or increasing differences produced by differences in nutrient concentrations. In the leaf canopy system as a whole, N, Ca, and K mass values were higher at l'Avic than at La Castanya or Le Rouquet (Table 3.5.1) and P and Mg mass were similar, lower concentration at l'Avic being counterbalanced by higher leaf biomass.

The average leaf nutrient concentration values were be computed as the rate between leaf or stems canopy nutrient mass and leaf or stems canopy biomass

(Table 3.5.2). Stem mean nutrient concentrations were higher at the ridge top site than at the valley bottom site. The different pattern shown by this nutrient concentration in canopy as compared to the concentrations shown in Table 3.2.2 (i.e. higher N concentration at the valley bottom site) was because the structures with lower concentrations corresponded to its higher biomass. Which leads to a relative reduced nutrient concentration in these structures. On Leaves, these averages were different. The mean canopy nutrient concentrations were higher at the valley bottom site except for K, which was higher at the ridge top site. Compared with the other *Quercus ilex* forests, l'Avic at the ridge top site showed lower leaf P and Mg concentrations than Le Rouquet and La Castanya (Table 3.5.2). The pattern of mean K concentration in leaves paralleled radiation load. The pattern of Mg, presumably related to chlorophyll content, was the reverse of the pattern of specific leaf weight as chlorophyll content in other studies showed (see Gracia 1988, Stewart et al. 1990). Differences in leaf biomass values were affected by different estimation methods, but using allometric relationships on two plots at the ridge top site estimated leaf biomass was 7.6±0.2 Mg/ha. Differences were possibly due to small canopy discontinuities. However, the ranges obtained by using the vertical profile column method and allometric relationships were close, and leaf biomass remaind higher than the other holm oak forests.

Leaf biomass production, computed as current leaves sampled in summer, is shown in Table 3.5.3. The inter-annual differences in leaf production (P=0.0110) agreed with rainfall during pre-growth period. Thus leaf production in 1988 was higher than leaf production in 1989. In addition, at the ridge top site leaf production was lower than at the valley bottom site (P=0.0595) in accordance with its lower soil water storage capacity and lower lateral water fluxes (Piñol 1990). Mean values were in the range reported by Lledó et al. (1992) at the same forest (2.7 Mg/ha/year) and lower than the 4.5 Mg/ha/year of Le Rouquet (Cole and Rapp 1981) and 3.1 Mg/ha/year from La Castanya (Ecarré et al. 1987). Nevertheless, leaf production at La Castanya was similar to the l'Avic valley bottom site, and Le Rouquet shows similar values on the basis of leaf litterfall (2.5 Mg/ha/year, Lossaint and Rapp 1978).

Figures 3.1.1-3.1.5 Nutrient concentration (% dry weight) and nutrient mass on leaf area basis (μg/cm^2) in leaves produced in spring of 1987, 1988 and 1989, along four layers from top to bottom of the canopy. (Figure 3.1.1: N, Figure 3.1.2:P, Figure 3.1.3:K, Figure 3.1.4:Ca and Figure 3.1.5:Mg). Significant differences between DATE, SITE and CANOPY HEIGHT are indicated below (*:P=0.05, **:P=0.01 and ***:P=001). Values are means ±SE, n=3.

FIGURE 3.1.1.

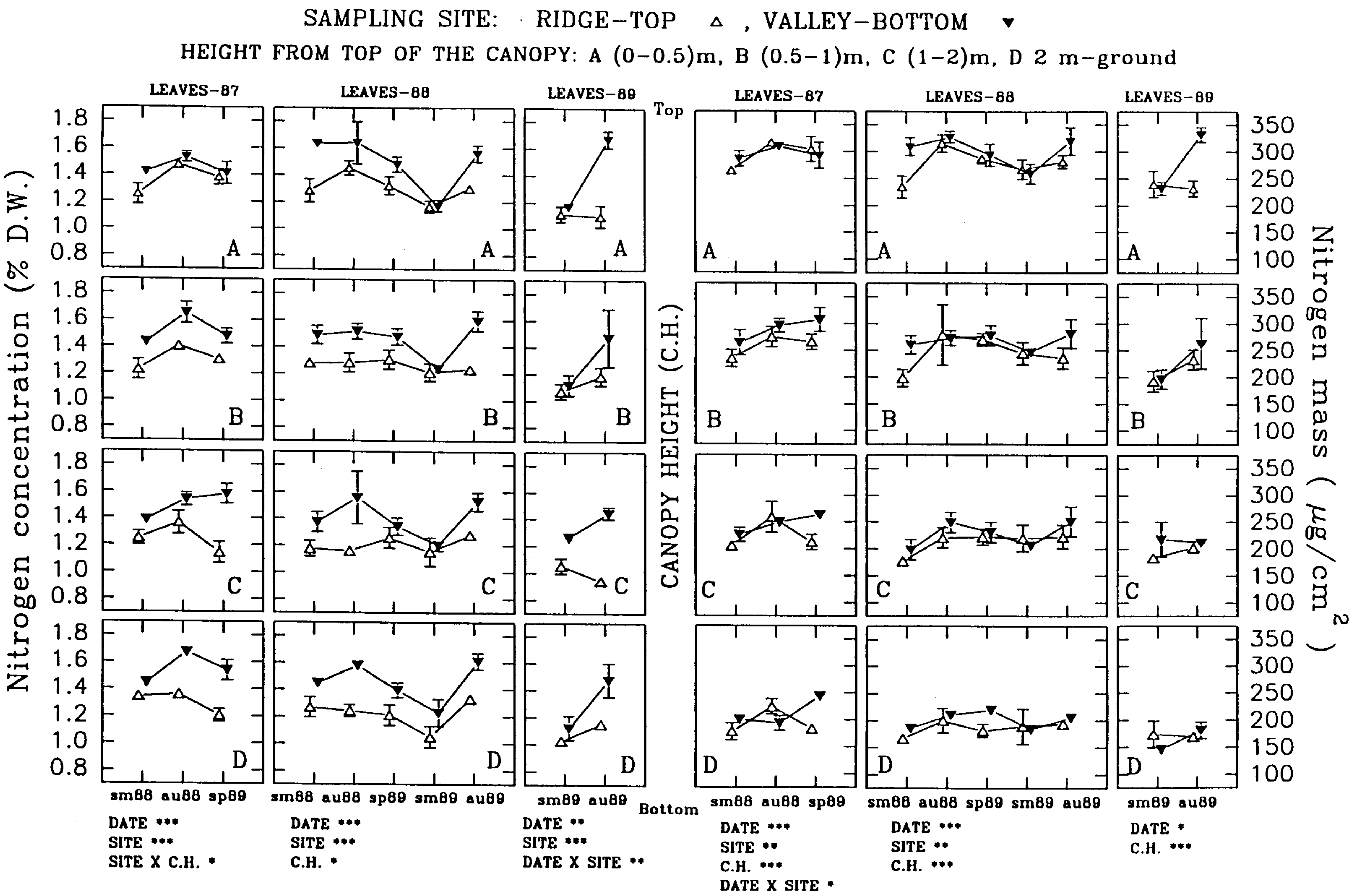

SAMPLING SITE: RIDGE-TOP △ , VALLEY-BOTTOM ▼
HEIGHT FROM TOP OF THE CANOPY: A (0-0.5)m, B (0.5-1)m, C (1-2)m, D 2 m-ground
LEAVES-87
LEAVES-88
LEAVES-89
Top
Bottom
CANOPY HEIGHT (C.H.)
Nitrogen concentration (% D.W.)
1.8
1.6
1.4
1.2
1.0
0.8
Nitrogen mass ($\mu g/cm^2$)
350
300
250
200
150
100
A
B
C
D
sm88 au88 sp89
sm88 au88 sp89 sm89 au89
sm89 au89
DATE ***
SITE ***
SITE X C.H. *
DATE ***
SITE ***
C.H. *
DATE **
SITE ***
DATE X SITE **
DATE ***
SITE **
C.H. ***
DATE X SITE *
DATE ***
SITE **
C.H. ***
DATE *
C.H. ***

FIGURE 3.1.2.

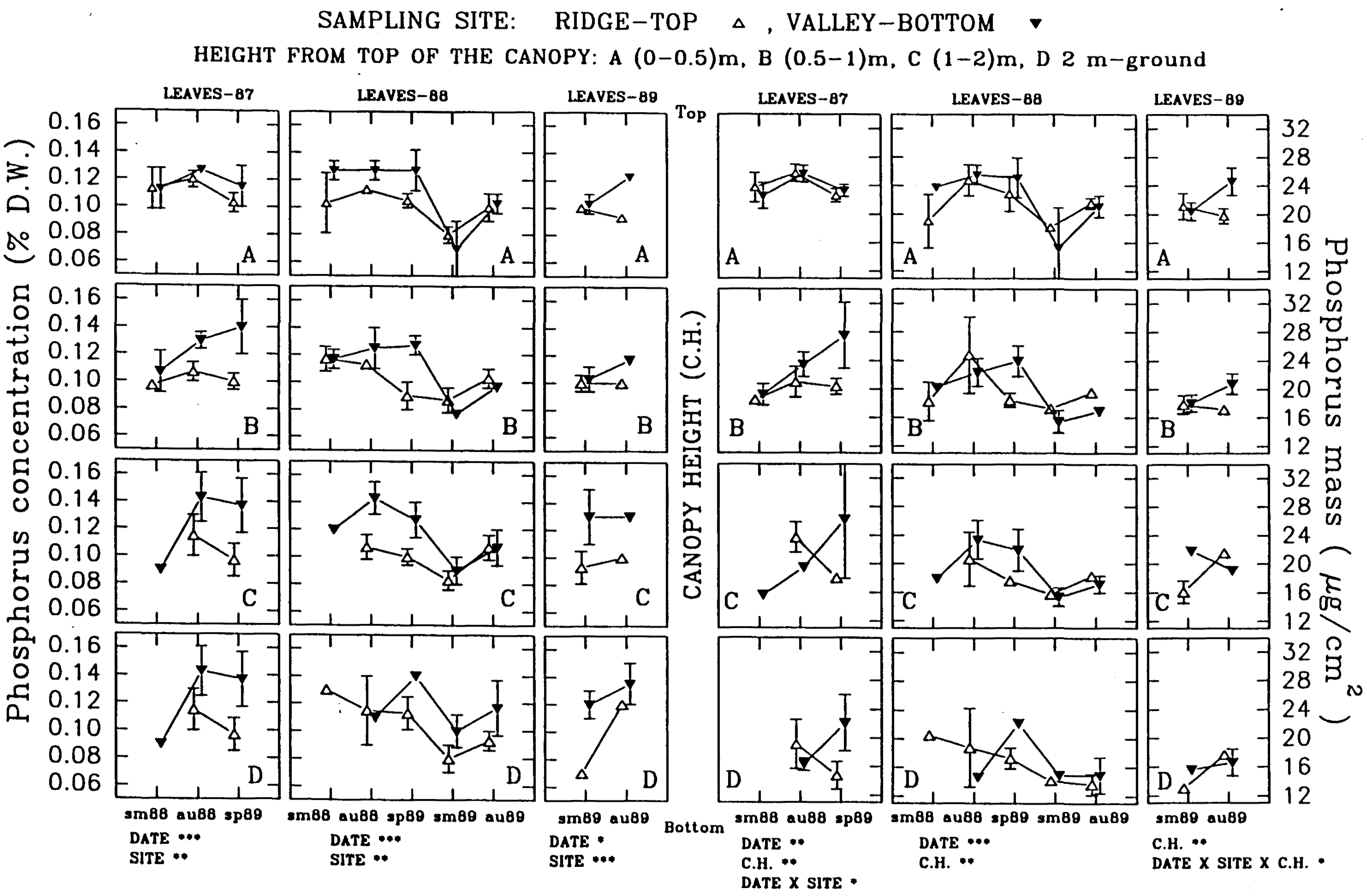

SAMPLING SITE: RIDGE-TOP △ , VALLEY-BOTTOM ▼
HEIGHT FROM TOP OF THE CANOPY: A (0-0.5)m, B (0.5-1)m, C (1-2)m, D 2 m-ground
LEAVES-87
LEAVES-88
LEAVES-89
Top
CANOPY HEIGHT (C.H.)
Bottom
Phosphorus concentration (% D.W.)
0.16
0.14
0.12
0.10
0.08
0.06
Phosphorus mass ($\mu g/cm^2$)
32
28
24
20
16
12
A
B
C
D
sm88 au88 sp89
sm88 au88 sp89 sm89 au89
sm89 au89
DATE ***
SITE **
DATE ***
SITE **
DATE *
SITE ***
DATE **
C.H. **
DATE X SITE *
DATE ***
C.H. **
C.H. **
DATE X SITE X C.H. *

FIGURE 3.1.3.

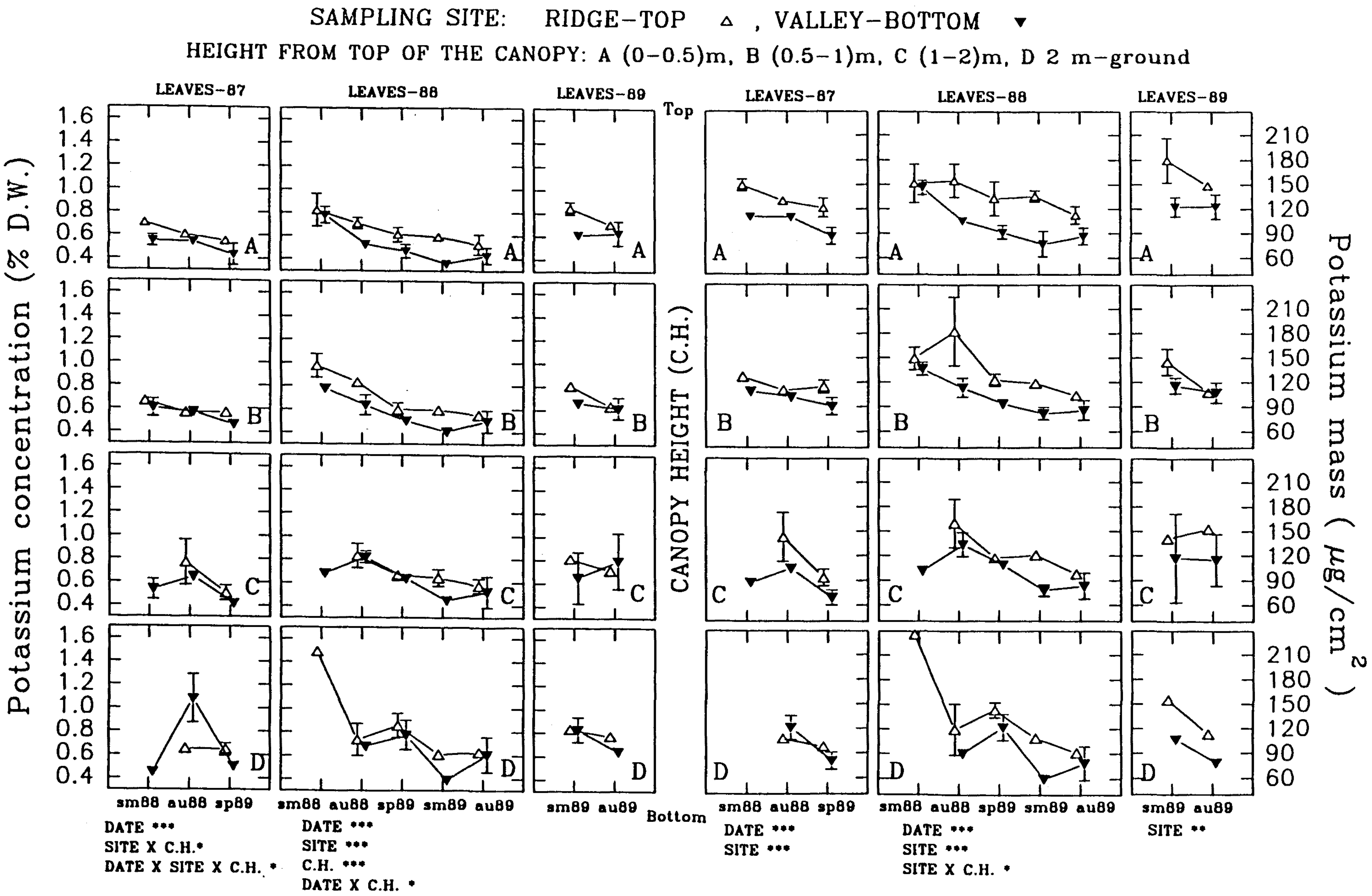

SAMPLING SITE: RIDGE-TOP △ , VALLEY-BOTTOM ▼
HEIGHT FROM TOP OF THE CANOPY: A (0-0.5)m, B (0.5-1)m, C (1-2)m, D 2 m-ground
LEAVES-87
LEAVES-88
LEAVES-89
Top
Bottom
CANOPY HEIGHT (C.H.)
Potassium concentration (% D.W.)
Potassium mass (µg/cm^2)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
210
180
150
120
90
60
A
B
C
D
sm88 au88 sp89
sm88 au88 sp89 sm89 au89
sm89 au89
DATE ***
SITE X C.H.*
DATE X SITE X C.H. *
DATE ***
SITE ***
C.H. ***
DATE X C.H. *
DATE ***
SITE ***
DATE ***
SITE ***
SITE X C.H. *
SITE **

FIGURE 3.1.4.

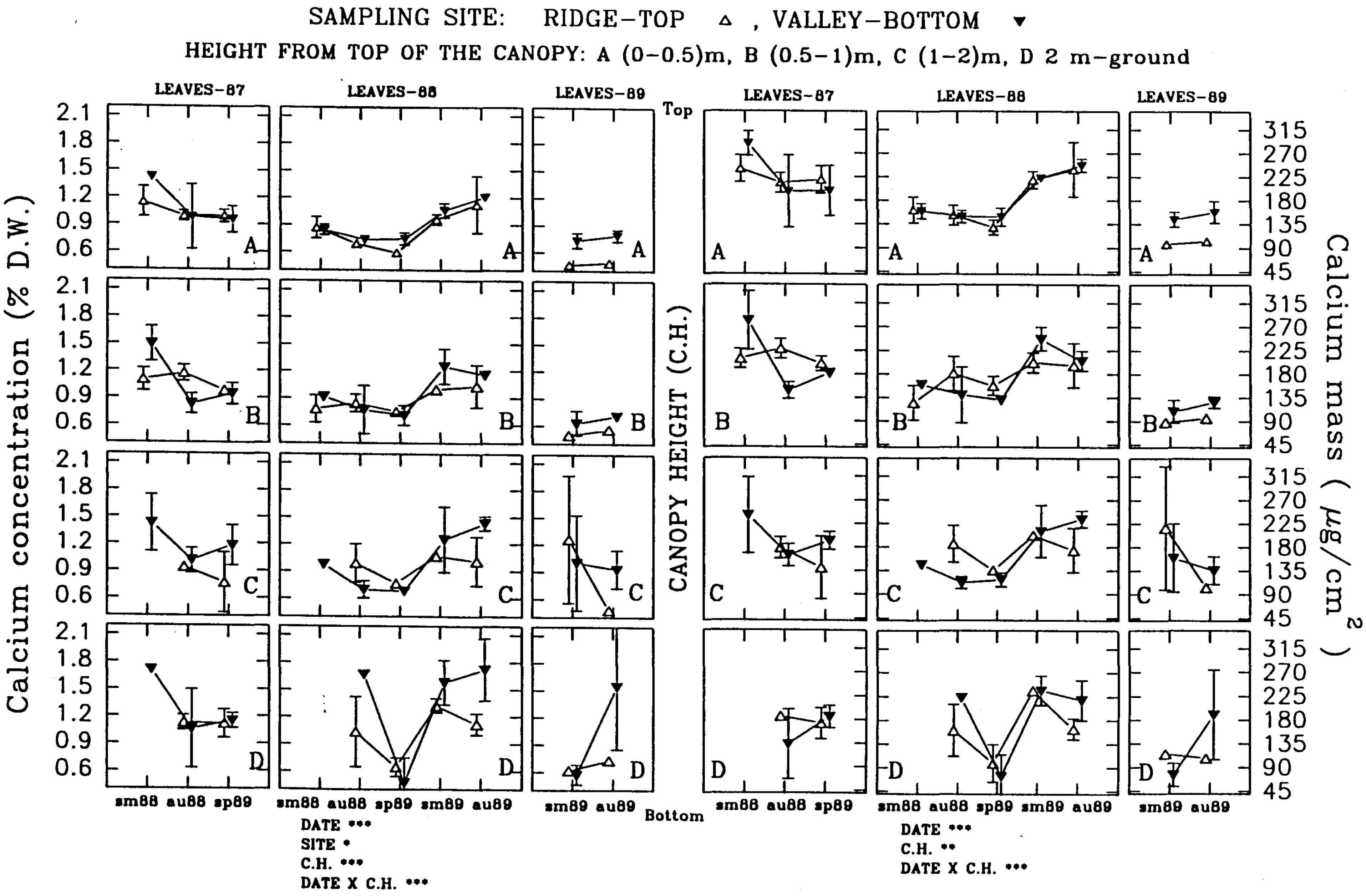

SAMPLING SITE: RIDGE-TOP △ , VALLEY-BOTTOM ▼
HEIGHT FROM TOP OF THE CANOPY: A (0-0.5)m, B (0.5-1)m, C (1-2)m, D 2 m-ground
LEAVES-87
LEAVES-88
LEAVES-89
LEAVES-87
LEAVES-88
LEAVES-89
Top
Bottom
CANOPY HEIGHT (C.H.)
Calcium concentration (% D.W.)
Calcium mass ($\mu g/cm^2$)
2.1
1.8
1.5
1.2
0.9
0.6
315
270
225
180
135
90
45
A
B
C
D
sm88 au88 sp89
sm88 au88 sp89 sm89 au89
sm89 au89
DATE ***
SITE *
C.H. ***
DATE X C.H. ***
DATE ***
C.H. **
DATE X C.H. ***

FIGURE 3.1.5.

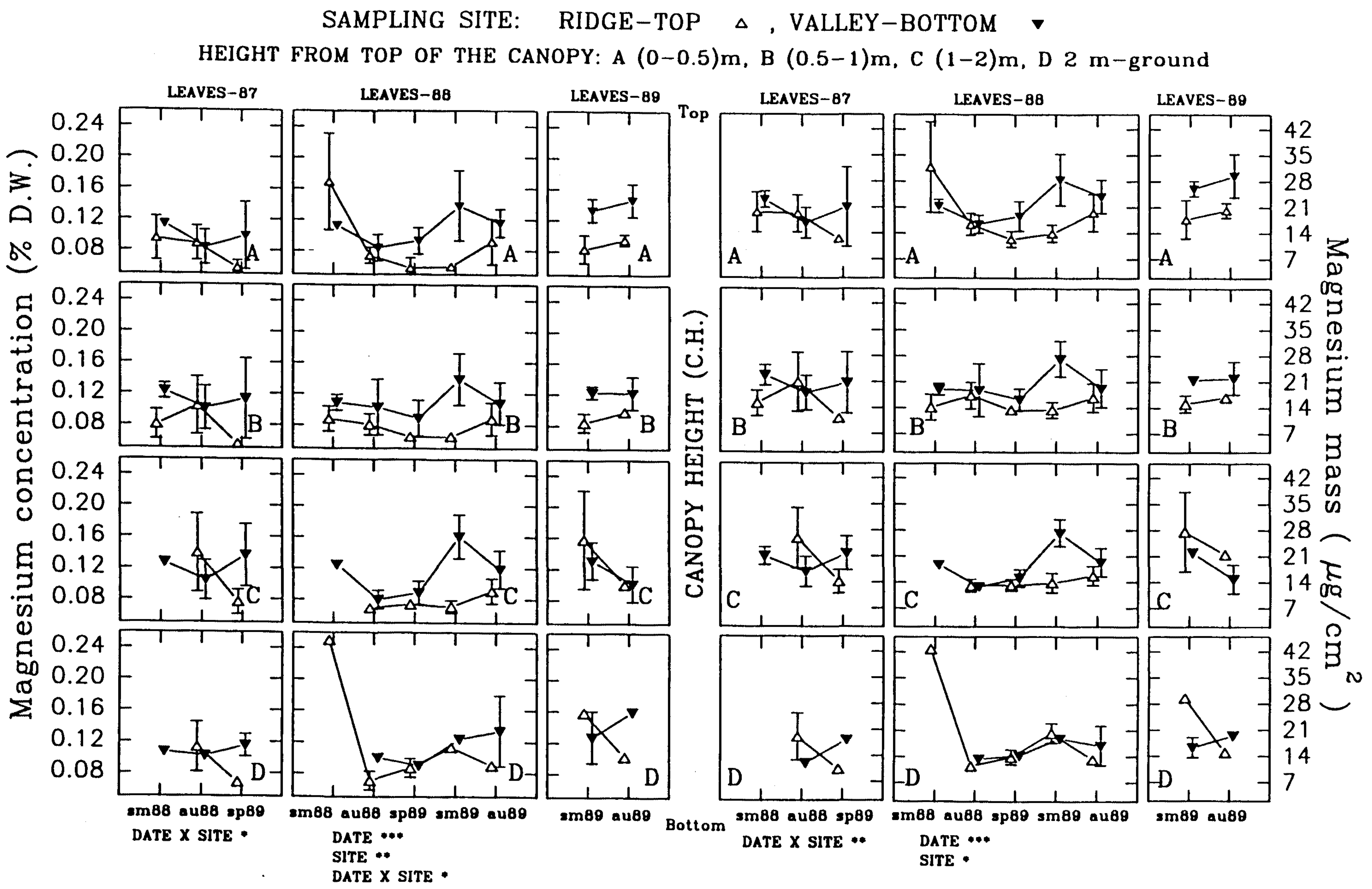

SAMPLING SITE: RIDGE-TOP △ , VALLEY-BOTTOM ▼
HEIGHT FROM TOP OF THE CANOPY: A (0–0.5)m, B (0.5–1)m, C (1–2)m, D 2 m–ground
LEAVES-87
LEAVES-88
LEAVES-89
Top
Bottom
CANOPY HEIGHT (C.H.)
Magnesium concentration (% D.W.)
0.24
0.20
0.16
0.12
0.08
Magnesium mass (μg/cm²)
42
35
28
21
14
7
A
B
C
D
sm88 au88 sp89
DATE X SITE *
sm88 au88 sp89 sm89 au89
DATE ***
SITE **
DATE X SITE *
sm89 au89
sm88 au88 sp89
DATE X SITE **
sm88 au88 sp89 sm89 au89
DATE ***
SITE *
sm89 au89

Table 3.1. Some characteristics of the two sampling sites.

SITE	RIDGE-TOP	VALLEY-BOTTOM
Elevation (m)	975	700
Soil depth (cm) $^{(a)}$	47	86
Tree height (m)	3-6	8-12
Tree density (stems ha^{-1})$^{(b)}$		
Quercus ilex	9314	3491
Quercus pyrenaica	43	0
Arbutus unedo	0	3273
Phillyrea media	29	1527
Viburnum tinus	0	473

Data not obtained in this study are from (a) Piñol (1990) and (b) Lledó (1990).

Table 3.2.1. Mean value ± standard error, for all canopy, of P and K concentrations in stems collected in 1988 and 1989 sampling period (sp=spring, sm=summer and au=autumn).

FRACTION	(% Dry Weight)	sm88	au88	sp89	sm89	au89	DATE effect (P value)
STEMS-89	P	-	-	-	0.13±0.01	0.11±0.01	0.0066
					n=21	n=20	
	K	-	-	-	0.86±0.05	0.70±0.07	0.0771
STEMS-88	P	0.14±0.00	0.12±0.00	0.11±0.01	0.13±0.00	0.11±0.00	0.0001
		n=21	n=21	n=23	n=24	n=24	
	K	1.08±0.03	0.70±0.05	0.64±0.03	0.59±0.03	0.52±0.03	0.0001
STEMS-87	P	0.15±0.01	0.14±0.01	0.12±0.01	-	-	0.0015
		n=20	n=23	n=23			
	K	0.68±0.04	0.63±0.04	0.57±0.04	-	-	0.0209

Table 3.2.2. Mean value ± standard error of nutrient concentrations for all canopy in stems collected in the ridge-top and the valley bottom sites at l'Avic watershed.

FRACTION	SITE	n	C (%)	N (%)	P (%)	K (%)	Ca (%)	Mg (%)
STEMS-89	RT	18	49.1±0.2	0.91±0.03	0.12±0.01	0.85±0.03	1.45±0.18	0.14±0.01
	VB	23	48.7±0.2	0.93±0.03	0.13±0.01	0.73±0.06	1.32±0.11	0.14±0.01
STEMS-88	RT	57	48.8±0.3	0.90±0.02	0.12±0.00	0.73±0.03	1.41±0.06	0.12±0.01
	VB	57	48.5±0.2	0.92±0.02	0.12±0.00	0.66±0.04	1.42±0.07	0.12±0.01
STEMS-87	RT	31	48.6±0.2	0.89±0.02	0.14±0.01	0.62±0.03	1.54±0.09	0.10±0.00
	VB	38	48.5±0.2	0.91±0.03	0.13±0.01	0.61±0.03	1.47±0.10	0.13±0.02
NO LEAVES BEARING STEMS <2cm	RT	56	48.5±0.1	0.73±0.02	0.12±0.01	0.44±0.03	1.48±0.06	0.09±0.02
	VB	60	48.5±0.2	0.76±0.01	0.12±0.00	0.46±0.03	1.50±0.08	0.09±0.01

Table 3.2.3. Mean value ± standard error of nutrient concentrations for all canopy in leaves collected in the ridge-top and the valley bottom sites at l'Avic watershed.

FRACTION	SITE	n	C (%)	N (%)	P (%)	K (%)	Ca (%)	Mg (%)
LEAVES-89	RT	20	50.2±0.3	1.08±0.02	0.10±0.00	0.77±0.02	0.67±0.14	0.11±0.01
	VB	23	50.4±0.2	1.35±0.06	0.12±0.00	0.67±0.04	0.83±0.09	0.13±0.01
LEAVES-88	RT	59	50.3±0.1	1.25±0.02	0.10±0.00	0.71±0.03	0.96±0.06	0.09±0.01
	VB	56	50.5±0.1	1.45±0.03	0.11±0.00	0.57±0.03	1.04±0.06	0.11±0.01
LEAVES-87	RT	34	50.4±0.1	1.31±0.02	0.11±0.00	0.61±0.02	1.03±0.05	0.09±0.01
	VB	38	50.5±0.2	1.48±0.03	0.12±0.01	0.57±0.04	1.15±0.07	0.11±0.01
SENESC. LEAVES	RT	14	48.7±0.2	1.13±0.09	0.08±0.01	0.39±0.05	1.21±0.09	0.07±0.01
	VB	60	49.3±0.2	1.08±0.05	0.07±0.01	0.35±0.02	1.31±0.08	0.13±0.02

Table 3.3.1. Nitrogen mass resorption on a leaf area basis (μg/cm^2) relative to the maximum nutrient mass in leaves produced in spring of 1987. Leaf litterfall from June of 1989. Values are means ± standard error, n=3.

NITROGEN MASS (μg/cm^2)	LEAF-LITTERFALL	HEIGHT FROM TOP OF THE CANOPY	LEAVES-87 (max. value)	RESORPTION MASS	(%)
RIDGE TOP	152 ± 4	0-0.5 m	316 ± 8	165	52
		0.5-1 m	275 ± 18	123	45
		1-2 m	259 ± 29	107	41
		2-ground	225 ± 14	73	33
VALLEY BOTTOM	165 ± 7	0-0.5 m	309 ± 7	145	47
		0.5-1 m	296 ± 13	132	44
		1-2 m	250 ± 4	85	34
		2-ground	194 ± 14	30	15

Table 3.3.2. Phosphorus mass resorption on a leaf area basis (μg/cm^2) relative to the maximum nutrient mass in leaves produced in spring of 1987. Leaf-litterfall from June of 1989. Values are means ± standard error, n=3.

PHOSPHORUS MASS (μg/cm^2)	LEAF-LITTERFALL	HEIGHT FROM TOP OF THE CANOPY	LEAVES-87 (max. value)	RESORPTION MASS	(%)
RIDGE TOP	11.1 ± 0.7	0-0.5 m	25.7 ± 1.2	14.7	57
		0.5-1 m	21.0 ± 2.1	9.9	47
		1-2 m	23.7 ± 2.1	12.6	53
		2-ground	19.1 ± 3.4	8.1	42
VALLEY BOTTOM	9.8 ± 0.6	0-0.5 m	25.6 ± 1.8	15.9	62
		0.5-1 m	27.5 ± 4.6	17.7	65
		1-2 m	26.2 ± 8.3	16.5	63
		2-ground	22.1 ± 3.9	12.3	56

Table 3.4.1. Nitrogen mass variation, on a leaf area basis (μg/cm^2), in leaves produced in spring of 1988 between larger values (in autumn of 1988 or spring of 1989) and lower values (in summer of 1989). Values are means ± standard error, n=3.

NITROGEN MASS (μg/cm^2)	HEIGHT FROM TOP OF THE CANOPY	LEAVES-88 (lower values)	LEAVES-88 (larger values)	DIFFERENCE (larger-lower)	(%)
RIDGE TOP	0-0.5 m	267 ± 18	316 ± 16	49	15
	0.5-1 m	245 ± 21	279 ± 56	34	12
	1-2 m	220 ± 25	222 ± 15	3	1
	2-ground	189 ± 33	200 ± 23	11	6
VALLEY BOTTOM	0-0.5 m	259 ± 19	328 ± 11	69	21
	0.5-1 m	247 ± 10	296 ± 13	49	17
	1-2 m	207 ± 9	250 ± 19	43	17
	2-ground	185 ± 5	220 ± 2	36	16

Table 3.4.2. Phosphorus mass variation, on a leaf area basis (μg/cm^2) in leaves produced in spring of 1988 between larger values (in autumn of 1988 or spring of 1989) and lower values (in summer of 1989). Values are means ± standard error, n=3.

PHOSPHORUS MASS (μg/cm^2)	HEIGHT FROM TOP OF THE CANOPY	LEAVES-88 (lower values)	LEAVES-88 (lager values)	DIFFERENCE (larger-lower)	(%)
RIDGE TOP	0-0.5 m	18.2 ± 0.0	24.8 ± 2.2	6.6	27
	0.5-1 m	17.3 ± 0.5	24.8 ± 5.3	7.5	30
	1-2 m	15.4 ± 1.5	20.7 ± 3.8	5.2	25
	2-ground	14.1 ± 0.4	18.8 ± 5.4	4.6	25
VALLEY BOTTOM	0-0.5 m	15.3 ± 5.6	25.5 ± 1.3	10.3	40
	0.5-1 m	15.5 ± 1.6	23.9 ± 2.2	8.5	35
	1-2 m	15.4 ± 1.3	23.4 ± 2.7	8.0	34
	2-ground	14.9 ± 0.7	22.1 ± 0.7	7.2	33

Table 3.5.1. Total canopy nutrient mass and biomass per unit of ground area in leaves and stems supporting these leaves at l'Avic, and in leaves from Le Rouquet and La Castanya. Leaf Area Index, Mean Specific Leaf Weight, Mean Annual Radiation, Mean Annual Temperature and Annual Rainfall (data from this study and bibliography). Values from l'Avic are means ± standard error, n=15 vertical profiles sampled. RT=Ridge-top , VB=Valley-bottom. (Significant differences between RT and VB are indicated by *:$P<0.05$, **:$P<0.01$). (1)Loissant and Rapp 1978,(2)Cole and Rapp 1981,(3)DeAngelis et al. 1981, (4)Escarré et al. 1987,(5)Gracia 1983,(6)Comin et al. 1987,(7)Sala 1992,(8)Riudabella Meteorological Station (1956-1990),(9)Bellot 1989).

		L'Avic (Prades)		(1,2,3)Le Rouquet	(4,5,6)La Castanya
	Site	Leaf Bearing Stems	Leaves	Leaves	Leaves
Carbon (g/m^2)	RT	100 ± 12	425 ± 34	-	-
	VB	174 ± 41	474 ± 32		
Nitrogen (g/m^2)	RT	1.8 ± 0.2*	10.7 ± 0.9*	9.3	8.3
	VB	3.0 ± 0.6	13.5 ± 0.8		
Phosphorus (g/m^2)	RT	0.25 ± 0.03	0.85 ± 0.07	1.0	0.7
	VB	0.43 ± 0.10	1.03 ± 0.08		
Potassium (g/m^2)	RT	1.3 ± 0.2	5.4 ± 0.4	4.3	2.9
	VB	2.0 ± 0.4	5.0 ± 0.4		
Calcium (g/m^2)	RT	3.1 ± 0.4	8.2 ± 0.7	7.0	4.1
	VB	4.5 ± 0.8	10.0 ± 0.8		
Magnesium (g/m^2)	RT	0.21 ± 0.02**	0.75 ± 0.07**	0.9	0.9
	VB	0.35 ± 0.06	1.08 ± 0.11		
Biomass (Mg/ha)	RT	2.0±0.2	8.4±0.7	7.0	6.1
	VB	3.6±0.8	9.3±0.6		
Leaf Area Index (m^2/m^2)	RT	4.6±0.4		4.5	5.7
	VB	5.3±0.3			
Mean Specific Leaf Weight (mg/cm^2)	RT	18.3		15.6	10.5
	VB	17.5			
Mean Annual Radiation (GJ/m^2/year^1)	RT	5.7		5.2	3.4
	VB	4.9			
Mean Annual T °C	RT	12.8(7)		12.4	9
	VB	13.8(7)			
Annual Rainfall (mm)	RT	647(8,9)		770	862
	VB				

Table 3.5.2. Mean nutrient concentration (computed as nutrient mass / biomass per unit of ground area, table 5.1). Units are % of dry weight.

		L'Avic (Prades)		Le Rouquet	La Castanya
	Site	Leaf Bearing Stems	Leaves	Leaves	Leaves
(%) Nitrogen	RT	0.90	1.27	1.32	1.36
	VB	0.83	1.45		
(%) Phosphorus	RT	0.13	0.10	0.14	0.11
	VB	0.12	0.11		
(%) Potassium	RT	0.65	0.64	0.61	0.48
	VB	0.55	0.53		
(%) Calcium	RT	1.55	0.97	1.00	0.67
	VB	1.25	1.07		
(%) Magnesium	RT	0.11	0.09	0.13	0.15
	VB	0.10	0.12		

Table 3.5.3. New leaves production at L'Avic (ridge top site = RT, valley bottom site = VB). Means ± standard error. Samples from summer of 1988 and summer of 1989 (n=3 at each site and sampling date). (ANOVA probabilities: DATE P=0.0110 and SITE P=0.0595).

	SITE	1988	1989	mean value (1988-1989)
Leaf Production current leaves in summer (Mg/ha/year)	RT	2.9±0.3	1.6±0.6	2.2±0.4
	VB	3.4±0.1	2.5±0.1	2.9±0.2
Pre-growth rainfall (September- June) (mm)	RIUDABELLA Meteorological Station	734	328	531

3.6. Discussion

Site differences of nutrient contents

Higher N, P and Mg concentration values in leaves and lower K concentration values in leaves and stems at the valley bottom site indicated a site effect on nutrient concentrations (% dry weight). A dilution effect was involved in a part of these site differences because leaves at the ridge top site tended to show a higher specific leaf weight (mg/cm^2) since they received higher annual radiation load (Sala 1992) and had lower soil water availability (Piñol 1990). Therefore, when nutrients in leaves were expressed on a leaf area basis, significant differences in N, K and Mg remained, although somewhat reduced. The sign of these differences only changed sometimes for some leaves (see results above, N in leaves-87). So, in general, a soil nutrient richness (Alcañiz unpublished data, 1993) or possibly also a higher microbial activity on decomposition influenced by higher temperature and soil moisture at the valley bottom site (see Carlyle 1986) was parallel to higher N and Mg richness on a leaf area basis. On the other hand, the increased values of K at the ridge top site agrees with Chapin (1988) who pointed out how species and varieties growing on infertile soils have a high capacity to absorb potassium (highly mobile in the soil). These higher K values at the ridge top site could be related to the increased stomatal control at this site as compared to the valley bottom site (Sala 1992).

Some implications of differences in N content in leaves may involve differences in photosynthetic capacity between sites (Field and Mooney 1986, Evans 1989, Reich et al. 1992). Reich et al. (1992) suggested that this relation is universal when expressed on a mass basis but not on a leaf area basis. Nevertheless, Evans (1989) found a strong causal correlation across many species between leaf nitrogen content expressed on a leaf area basis and photosynthesis. Other leaf characteristics of species, such as differences in specific leaf weight (leaf weight/leaf area) may mask this relationship if these characteristics are mixed. In addition, many evergreen sclerophyll species possess nitrogen-based antiherbivore compounds (Field and Mooney 1986) and possibly some deciduous species (Karlsson 1991), in this way storing more nitrogen than is required for photosynthesis and affecting negatively the potential photosynthetic N use efficiency, but increasing photosynthesis with increasing N content. Thus, accepting the positive N content-photosynthesis relationship in *Quercus ilex*, the valley bottom site had higher photosynthetic capacity than the ridge top site, due to higher N content expressed as concentration on dry weight and also N mass on leaf area basis. This higher photosynthetic capacity may explain some differences in stand structure (taller and less dense forest at the valley bottom site), besides other historical causes such as forest management (Lledó et al. 1992).

Vertical organization

The canopy structure was not constant with depth, the foliage tending to concentrate at the top of the canopy (Sala et al. submited manuscript). In addition specific leaf weight tended to decline from top to bottom of the canopy. This was extensive to the N and P mass on a leaf area basis on the vertical profile axis, and consistent with other studies on *Quercus ilex* (Ferrés 1984), or even on other species as *Nothofagus solandri* when analyzing N (Hollinger 1989). Considering the link between photosynthesis and N leaf content (see comments above, Field and Mooney 1986, Evans 1989, Reich et al. 1992) and according to Hollinger's results, concentrations and mass on a leaf area basis may affect leaf photosynthetic capacity at different canopy heights declining with depth inside the canopy. Sala (1992) simulated values of modeling carbon canopy gain on a leaf surface basis and found negative carbon balances at the bottom of the canopy at the valley bottom site. This was in accordance with lower photosynthetic capacity but did not explain how maintaining these leaves might be beneficial in terms of nutrient retention and retranslocation to new growth. The lower canopy layers did not show higher N or P resorptions than the upper ones. So if these leaves may represent an expense for the whole canopy in terms of net carbon, probably other explanations should be explored or probably stronger differentiation of sun-shade leaves when modeling on carbon balance should be considered.

Seasonal variability

Rainfall during the pre-growth period of 1987, 1988 and 1989 variet greatly. The pre-growth period of 1987 was drier than the pre-growth period of 1988, and 1989 was the driest (Sabaté et al. 1992). Although these differences affected structural characteristics of leaves such as mean weight and leaf area (Sala 1992, Sala et al. submited manuscript), some patterns of nutrient concentration on dry weight and mass on leaf area have been reproduced over time when comparing these leaves, produced in different springs, through their life span. The lower N and P values of leaf concentrations in summer and higher values in autumn or winter was also found on *Quercus ilex* by De Lillis and Fontanella (1992). Although Escudero et al. (1992a) interpreted concentration variations as a dilution effect, but not to N re-location movements from leaves, in our case nutrient mass variations over time supported the role of old leaves as storage organs (Chapin 1980, Chabot and Hicks 1982, Nambiar and Fife 1987). So N and P withdrawal possibly took place to supply new growth as reflected by the lower concentrations in summer after growth period. On the other hand, N and P replenishment took place during lower growth activity period and without water stress, possibly leading to a luxurious N and P consumption. In addition, these estimated resorption values may be higher if wider differences between sampling in this study occurred. The higher resorption values at the valley bottom site could be related to the higher water availability at this site and consequently, in mediterranean conditions, higher growth. This fact probably enhanced nutrient translocation processes (source-sink effect) and consequently, also nutrient resorption efficiency (Chapin and Moilanen 1991, Pugnaire and Chapin 1992, Sabaté and Gracia, unpublished manuscript). Probably then , when water availability declines, N and P resorption from green leaves, as translocated compounds, declines until more extreme situations, such as those studied by Escudero et al. (1992), where resorption from green leaves seems to vanish. The complementary variations of P concentrations in stems as compared to leaves may be related with the storage of P in stems during resorption from leaves, but this pattern was not evident with N mass comparing leaves and stems.

Lower values during summers suggested N withdrawal during spring new growth (source-sink effect) since increases of summer N concentrations in stems were not found; probably N leaf withdrawal and stems and leaf new growth were parallel. The increased P concentration in stems suggests its luxurious accumulation and its probable use later on, since it declined again in autumn and winter. Some studies reported how summer drought increases free aminoacids in shoots and roots, probably related to an osmotic adjustment (see Cyr et al. 1990). This coincides with Lajtha (1987) who found, in a desert shrub, that leaves that abscise during periods of drought are able to remobilize greater amounts of nutrients (in agreement with higher free aminoacids referred to above) than leaves that abscise during periods of greater water availability and new leaf growth. So in Lajtha's case the source-sink effect seemed less important. Free aminoacids are highly movables. The importance of osmotic control through free aminoacids, after hydrolysing proteins is unknown to *Quercus ilex*. However, results of Escudero et al. (1992) do not seem to support this hypothesis, since they found steady N mass in leaves in drier conditions. Nevertheless the role of drought increasing free aminoacids is an interesting point to explore.

Nutrient resorption from leaf litterfall

In general, green leaves (leaves-87) with higher leaf nutrient mass on leaf area basis they resorbed a larger proportion of the leaf nutrient mass before leaf abscission as compared to those with low nutrient mass. This suggests that the proportion of the total nutrient mass allocated to structural or non-hydrolysable compounds decreases and nutrients that serve in metabolic functions increases, when nutrient concentration increases (see Chapin and Kedrowski 1983, Chapin and Shaver 1986, Karlsson 1991). Thus, despite N resorption differences between sites were narrow the slightly higher values at the ridge top site were probably related to more hydrolysable N compounds at this site as suggested by the lower mass in leaf litterfall and the higher mass in leaves-87, when largest values were measured. Differences on the pattern of N resorption from green leaves (see above) as compared to the pattern of N resorption from leaf litterfall were due mainly to differences in N mass content in leaf litterfall. The largest values of N and P mass measured in leaves-87 and leaves-88 were very similar across each canopy height. The pattern for P was the reverse contrary, higher resorption at the valley bottom site from leaf litterfall as occurred for green leaves (see above). So then higher water availability on a site may be reflected in higher P resorption. More detailed studies of the role of free aminoacids for example, may reveal the reason for these different patterns for N.

N resorption efficiency was always lower than P resorption. This was in agreement with other studies on holm oak forests conducted by Mayor and Roda (1992) who found 33% of N and 43% of P resorption efficiency. The N resorption value found by Mayor and Rodà (1992) was slightly higher than the one (29.7%) reported by Escudero et al.(1992a), but both studies showed lower values than those estimated in this study. The coincidence of higher site nutrient availability with higher resorption efficiency (from leaf litterfall) agreed with the group of studies that found greater resorption in more fertile soils (for instance, Chapin and Kedrowski 1983, Lajtha 1987, Nambiar and Fife 1987). This coincidence at l'Avic catchment was in accordance with the higher biomass ratio (new leaves/old leaves) at the valley bottom site than at the ridge top site (Sala et al. submited manuscript) and so, the largest nutrient sink was to be found at the valley bottom site. Differences between sites may be larger if the pre-growth period is wetter, as happened in 1988; the pre-growth period of 1989 was very dry (Sala et al. submited manuscript).

Canopy biomass, nutrient mineralomass and environmental characteristics

In general, except K at L'Avic, nutrient mass differences between sites followed biomass differences. Thus environmental conditions determine leaf biomass, and may also determine the amount of nutrient mass in the canopy. The leaf canopy biomass may be distributed on different dimensional ways: leaf area index that increases light interception and water losses, and specific leaf weight that is related to leaf thickness (Specht and Rundel 1990) and leaf resistance to water losses (Specht 1988, Specht and Specht 1989). Thus, it is not surprising that plants respond to increased rainfall and decreased radiation and temperatures by increasing leaf area index and decreasing specific leaf weight.

Higher N, P and Mg concentrations at the valley bottom site are in part due to a dilution effect, because of the accumulation of carbon compounds when specific leaf weight increases, but the increased mass on leaf area basis suggests a site effect on nutrient amount. These higher N, P and Mg concentrations in leaves from the valley bottom site agreed with its higher photosynthetic potential as compared to those concentrations from the ridge to site. If N and P concentrations in leaves are related to their differential availabilities, probably these availabilities depend in part on microbial activity. This activity presumably increases when high temperature and high water availability coincide, but increased temperature also increases biomass respiration costs. When leaf biomass increases this may be due to increased specific leaf weight and/or increased leaf area. Higher values of specific leaf weight are followed by increases of energy maintenance costs since no photosynthetic/photosynthetic leaf biomass ratio increases (Gracia 1988). In this way maintenance costs are probably higher at L'Avic than at Le Rouquet and La Castanya. So, despite its higher leaf biomass, L'Avic leaf biomass production is somewhat lower or similar to the others (see comments of Table 3.5.3). Nevertheless, as biomass allocation patterns are modified by water availability (see Canadell and Rodà 1991) it is difficult to extrapolate this lower or similar leaf biomass production to the total net primary production. Assuming this extrapolation problem, La Castanya showed higher total aboveground production (Escarré et al. 1987, 9.4 Mg/ha/year) than Le Rouquet (Lossaint and Rapp 1978, 6.0 Mg/ha/year) and L'Avic (Lledó et al. 1992, 6.1 Mg/ha/year). This agreed with higher leaf area index and somewhat high N concentration at La Castanya. Le Rouquet mean leaf N concentration and its leaf area index are between values found at the ridge top site and the valley bottom site at l'Avic, thus in agreement with their relative total aboveground net primary production.

The opposite pattern of mean Mg concentrations to specific leaf weight is probably explained because it is in part linked to chlorophyll (limited in leaf depth because of light extinction) which also follows an opposite relationship to specific leaf weight (Gracia 1988, Stewart et al. 1990). K plays an important role in the cell, being involved in the maintenance of enzyme structure, in protein synthesis and the maintenance of electrostatic balance and turgor (Lüttge and Clarkson 1989). The increased K concentration as radiation increased agreed with the role of potassium of stomatal control of transpiration since radiation could increase the possibility of water stress episodes if rainfall shows the reverse pattern than radiation.

Nutrient use efficiency

Some authors expressed nutrient use efficiency as the amount of dry matter produced per unit nutrient, which is the inverse of nutrient concentration (see Chapin 1980, Vitousek 1982, Shaver and Melillo 1984, Lajtha and Klein 1988, Schlesinger et al. 1989). Chapin (1988) pointed out that in all species, nutrient use efficiency increases under low nutrient availability or under conditions that promote growth and thereby distribute the nutrient pool over a larger biomass (equivalent to a dilution effect). The lower stem nutrient concentration at the valley bottom site when average the whole canopy basis (total canopy nutrient mass/canopy biomass), indicates in part a higher nutrient productivity of fine stems (equivalent to nutrient dilution) at this site, and thus a higher nutrient use efficiency. However, when considering leaves, the reverse is true because leaves at the ridge top site accumulated more carbon compounds as indicated by its higher specific leaf weight. Thus different canopy compartments showed different efficiency patterns following the above definitions.

Other authors suggested nutrient use efficiency as the ratio of litterfall mass to litterfall nutrient, or the ratio of aboveground productivity to nutrient loss in litterfall (Vitousek 1982, Gray 1983, Birk and Vitousek 1986). Leaf litterfall nutrient mass, as shown in Tables 3.3, was opposite to nutrient resorption, which increases residence times. The higher nutrient mass in leaf litterfall, the lower nutrient resorption when sites were compared. Thus N resorption efficiency was higher for N and lower for P at the ridge top site, but adding to resorption before leaf fall, resorption from withdrawal and replenishment in green leaves, N mass resorption was compensated, and thus similar at both sites, but P reinforced resorption efficiency, which was higher at the valley bottom site. Leaf productivity (as the ratio between leaf production to leaf biomass) was higher at the valley bottom site, and resorption similar for N but higher for P, thus N and P use efficiency were higher at the valley bottom site, in agreement with this point of view. However, Berendse and Aerts (1987) and Aerts (1990) suggested that these definitions are inappropriate for an assessment of the efficiency of using nutrient taken up for dry matter production. The main opposition is that those indexes are focused on the aboveground nutrient use efficiency and that they may differ when the entire plant is considered. In fact, this appeared yet when considering parts of the canopy system, where fine stems showed pattern that was opposite to leaves. The problem of the plasticity on allocation patterns is consistent with this idea. Canadell and Rodà (1991) found different root biomass allocation patterns of holm oak depending on mesic or xeric conditions. The balance between total production and nutrient in plant is difficult to measure and to conside, especially in those species growing on dry areas with lager and depth root biomass systems. This is important, but we also think that knowledge about patterns at different compartments levels is also important, although it needs to be integrated on a global plant view.

3.7. Conclusions

Differences of site nutrient availabilities affect leaf nutrient mass on leaf area basis of holm oak canopy structures, but other environmental conditions such as rainfall, annual radiation load, and temperature are also important governing structural characteristics such as specific leaf weight that also influence leaf nutrient concentration on dry weight basis, as well as leaf area index, total leaf biomass and total nutrient mass in canopy.

Higher N and Mg mass on leaf area basis at the valley bottom site could be associated with higher photosynthetic capacity at the valley bottom site which stimulates a taller and less dense forest, besides other historical causes such as forest management. On the other hand, higher K mass and concentration at the ridge top site were found. This is in accordance with increased effectiveness in stomatal control of transpiration at the ridge tope site as compared to the valley bottom site (Sala 1992).

Leaf nutrient content along holm oak canopy height and nutrient resorption and resorption efficiency decreased from top to bottom of the canopy. So these leaves are of minor importance as nutrient storage components.

N and P mass variations on leaf area basis suggest withdrawal and replenishment processes during slowed growth periods, which could supply nutrients to new growth. These variations were higher at the valley bottom site, where water and nutrients were more available. In addition, resorption before leaf litterfall was slightly higher for N and lower for P at the ridge top site. Thus lower N resorption from green leaves variations was compensated by higher resorption before leaf fall, but P resorption was always higher at the valley bottom site. The higher new growth at the valley bottom site, which acts as nutrient sink, probably stimulated resorption.

N and P use efficiencies at canopy level tended to be higher at the valley bottom site since it had higher stems and leaf productivity than the ridge top site. Nevertheless, using only the inverse of leaves nutrient concentration as efficiency index, leaves at the ridge showed lower values, except for K. Although it is valuable to obtain nutrient use efficiency on partial plant elements, an integrated view is needed.

3.8. References

Berendse F, Aerts R (1987) Nitrogen-use-efficiency: a biologically meaningful definition? Func Ecol 1:293-296

Aerts R (1990) Nutrient use efficiency in evergreen and deciduous species from heathlands. Oecologia (Berlin) 84:391-397

Bellot J, Sánchez JR, Lledó MJ, Martínez P and Escarré A (1992) Litterfall as a measure of primary production in Mediterranean holm-oak forest. Vegetatio 99-100:69-76

Bellot J (1989) Análisis de los fluidos de deposición global, trascolación, escorrentía cortical y deposición seca en el encinar mediterráneo de l'Avic (Serra de Prades, Tarragona). Ph D Thesis. Univ. Alacant

Birk EM, Vitousek PM (1986) Nitrogen availability and nitrogen use efficiency in loblolly pine stands. Ecology 67:69-79

Canadell J and Vilà M (1992) Variation in tissue element concentrations in *Quercus ilex* L. over a range of different soils. Vegetatio 99-100:273-282

Carlyle JC (1986) Nitrogen cycling in forested ecosystems. Forestry Abstracts 47(5):307-336

Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. Ann. Rev. Ecol. Syst. 13:229-259

Chapin III FS (1980) The mineral nutrition of wild plants. Ann Rev Ecol Syst 11:233-259

Chapin III FS (1988) Ecological aspects of plant mineral nutrition. Adv. Mineral Nutri. 3:161-191

Chapin III FS, Kedrowski RA (1983) Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. Ecology 64(2):376-391

Chapin III FS, Shaver GR (1986) Differences in carbon and nutrient fractions among arctic growth forms. Oecologia 77:506-514

Chapin III FS and Moilanen L (1991) Nutritional controls over nitrogen and phosphorus resorption from Alaskan birch leaves. Ecology 72(2):709-715

Clemente A (1983) Componentes específico y estacional en la variación de contenidos en elementos químicos de las especies y formas biológicas del encinar mediterráneo. Master Thesis. Univ. Alacant

Cole DW, Rapp MR (1981) Elemental cycling in forest ecosystems. In Reichle D (ed) Dynamic properties of forest ecosystems. International Biological Program Synthesis Volume 23. Cambridge University Press. pp 341-409

Comin MP, Escarré A, Gracia CA, Lledó MJ, Rabella R, Savé R, Terradas J (1987) Water use by *Quercus ilex* L. forests near Barcelona, Spain. In: Tenhunen et al. (eds) Plant Responses to stress. Functional Analysis in Mediterranean Ecosystems. Nato ASI Ser. Vol. G15. Springer Verlag. Berlin. pp 259-266

Cyr DR, Buxton GF, Webb DP, Dumbroff EB (1990) Accumulation of free amino acids in the shoots and roots of three northern conifers during drought. Tree Physiology 6:293-303

DeAngelis DL, Gardner RH, Shugart HH (1981) Productivity of forest ecosystems studied during the IBP: the woodlands data set. In Reichle D (ed) Dynamic properties of forest ecosystems. International Biological Program Synthesis Volume 23. Cambridge University Press. pp 567-672

Del Arco JM, Escudero A, Vega Garrido M (1991) Effects of site characteristics on nitrogen retranslocation from senescing leaves. Ecology 72:701-708

De Lillis M and Fontanella A (1992) Comparative phenology and growth in different species of Mediterranean maquis of central Italy. Vegetatio 99-100:83-96

Escarré A, Ferrés Ll, López R, Martín J, Rodà F, Terradas J (1987) Nutrient use strategy by evergreen-oak (*Quercus ilex* ssp *ilex*) in NE Spain. In: Tenhunen et al. (eds) Plant Responses to stress. Functional Analysis in Mediterranean Ecosystems. Nato ASI Ser. Vol. G15. Springer Verlag. Berlin. pp:429-435

Escudero A, del Arco JM, Garrido MV (1992) The efficiency of nitrogen retranslocation from leaf biomass in *Quercus ilex* ecosystems. Vegetatio 99-100:225-237

Escudero A, del Arco JM, Sanz IC, Ayala J (1992) Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. Oecologia 90:80-87

Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78:9-19

Ferrés L (1984) Biomasa, producción y mineralomasas del encinar montano de La Castanya (Montseny). Ph D Thesis, Autonomous University of Barcelona

Field C, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In T Givnish (ed). On economy of plant form and function. Cambridge University Press. London, pp 25-55

Gracia CA (1983) La Clorofila en los Encinares del Montseny. Ph. D. Thesis, University of Barcelona

Gracia CA (1988) Chlorophyll content and leaf energetics of plant communities in south eastern Queensland (Australia) in relation to water availability. In: F di Castri, C Floret, S Rambal, J Roy (eds) Time Scales and Water Stress. Proceedings of the Fifth International Conference on Mediterranean Ecosystems. International Union of Biological Sciences (IUBS). Paris, pp 87-93

Gray JT (1983) Nutrient use by evergreen and deciduous shrubs in Southern California. I. Community nutrient cycling and nutrient-use-efficiency. J Ecol 71:21-41

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111:1169-1194

Hollinger DY (1989) Canopy organization and foliage photosynthetic capacity in broad-leaved evergreen montane forest. Functional Ecology 3:53-62

Karlsson PS (1991) Intra-specific variation in photosynthetic light response and photosynthetic nitrogen utilization in the mountain birch, *Betula pubescens* ssp. *tortuosa*. Oikos 60:49-54

Lajtha K (1987) Nutrient reabsorption efficiency and the response to phosphorus fertilization in the desert shrub *Larrea tridentata* (DC) Cov. Biogeochemistry 4:265-276

Lajhta K, Klein M (1988) The effect of varying nitrogen and phosphorus availability on nutrient use by *Larrea tridentata*, a desert evergreen shrub. Oecologia (Berlin) 75:348-353

Lledó MJ (1990) Compartimentos y flujos biogeoquímicos en una cuenca de encinar del Monte Poblet. Ph D Thesis. Univ. Alacant

Lledó MJ, Sánchez JR, Bellot J, Boronat J, Ibañez JJ and Escarré A (1992) Structure, biomass and production of a resprouted holm-oak (*Quercus ilex* L.) forest in NE Spain. Vegetatio 99-100:51-59

Lossaint P, Rapp M (1978) La forêt méditerranéenne de chênes verts (*Quercus ilex* L.). In: M Lamotte, F Bourlière (eds) Problèmes d'écologie, structure et fonctionnement des ecosystèmes terrestres. Masson, Paris pp 129-185

Mateo MA, Sabaté S (1993) Vegetal Tissue Wet Digestion Using a Domestic Microwave Oven. Analitica Chimica Acta 00:00-00 (in press, see chapter 2)

May JD, Killingbeck K (1992) Effects of preventing nutrient resorption on plant fitness and foliar nutrient dynamics. Ecology 73(5):1868-1878

Mayor X (1990) Paper dels nutrients com a factors limitants de la producció primaria de l'alzinar de la conca del Torrent de la Mina (Montseny). Master Science thesis. Autonomous University of Barcelona.

Mayor X and Rodà F (1992) Is primary production in holm oak forest nutrient limited? A correlational approach. Vegetatio 99-100:209-217

Piñol J (1990) Hidrologia i biogeoquímica de conques forestades de les Montanyes de Prades. Ph D Thesis. Univ. of Barcelona

Nambiar EKS and Fife DN (1987) Growth and nutrient retranslocation in needles of rediata pine in relation tonitrogen supply. Annals of Botany 60:147-156

Pugnaire FI, Chapin III FS (1992) Environmental and physiological factors governing nutrient resorption efficiency in barley. Oecologia 90:120-126

Pugnaire FI, Chapin III FS (1993) Controls over nutrient resorption from leaves of evergreen mediterranean species. Ecology 74(1):124-129

Reich PB, Walters MB, Ellsworth DS (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecological Monographs 63(2):365-392

Sabaté S, Gracia CA (1993) Effects of clearcutting and fire on *Quercus ilex*. II. Nutrient content and resorption in the regenerating canopy. (manuscript see chapter 4)

Sabaté S, Calvet S and Gracia CA (1992) Preliminary results of a fertilization-irrigation experiment in a *Quercus ilex* L. forest in relation to leaves and twigs characteristics. Vegetatio 99-100:283-287

Sala A (1992) Water relations, Canopy structure and Canopy gas exchange in a *Quercus ilex* forest: Variation in time and space. Ph D Thesis. Univ. Barcelona. Spain

Sala A, Sabaté S, Gracia C, Tenhunen JD (1993) Canopy structure of a *Quercus ilex* forest: site and seasonal variability in relation to water availability. (manuscript, see appendix)

SAS (1988) User's guide. SAS Institute Inc. Cary, NC, USA

Schlesinger WH, DeLucia EH, Billings WD (1989) Nutrient-use-efficiency of woody plants on contrasting soils in the western Great Basin, Nevada. Ecology 70(1):105-113

Shaver GR, Melillo JM (1984) Nutrient budgets of marsh plants: efficiency concepts and relation to availability. Ecology 65:1491-1510

Specht RL (1988) Vegetation, nutrition and climate - examples of integration. (2) Climatic control of ecomorphological characters and species richness in mediterranean ecosystems of Australia. In: RL Specht (ed) Mediterranean-type Ecosystems. A data source book. Kluwer Academic Publishers. pp 149-155

Specht RL, Specht A (1989) Canopy structure in *Eucaliptus* - dominated communities in Australia along climatic gradients. Oecol Plant 10:191-213

Specht RL, Rundel PW (1990) Sclerophylly and foliar nutrient status of mediterranean-climate plant communities in southern Australia. Aust J Bot 38:459-474

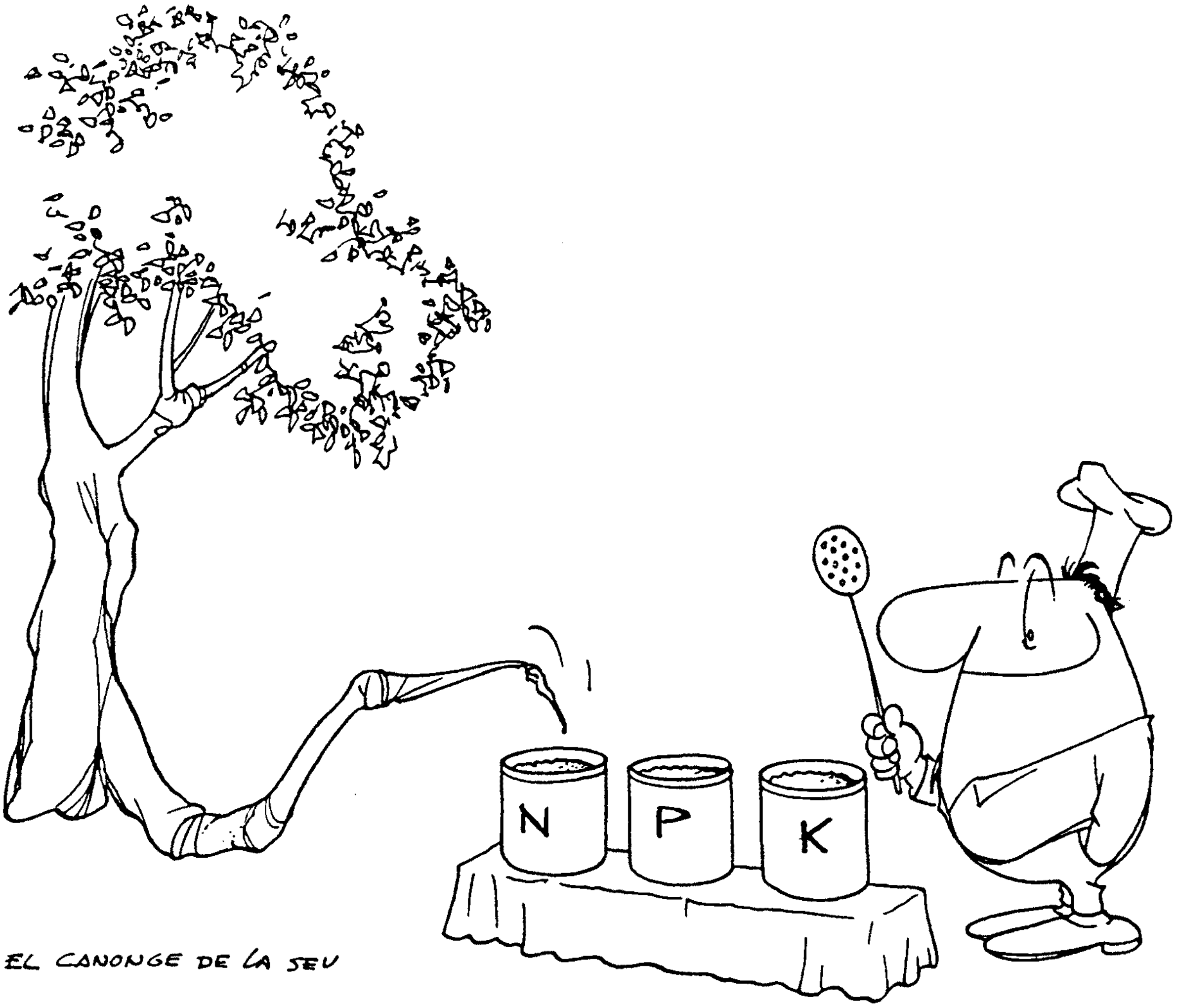
Stewart GR, Gracia CA, Hegarty EE, Specht RL (1990) Nitrate reductase activity and chlorophyll content in sun leaves of subtropical Australian closed-forest (rainforest) and open-forest communities. Oecologia 82:544-551

Vitousek PM (1982) Nutrient cycling and nutrient use efficiency. Am Nat 119:553-572

Woodwell GM (1974) Variation in the nutrient content of leaves of *Quercus alba*, *Quercus coccinea* and *Pinus rigida* in the Brookhaven Forest from bud-break to abscission. American Journal of Botany 61:749-753

4. Efectes de la irrigació i la fertilització - amb nitrogen i fòsfor - de l'alzinar sobre l'estructura de les capçades i el seu contingut de nutrients:

Canopy structure and nutrient content of a Quercus ilex forest: fertilization and irrigation effects



EL CANONGE DE LA SEU

4.1. Summary

A multifactorial ANOVA experiment was designed for a *Quercus ilex* L. forest at the Prades Experimental Complex of Catchments in Tarragona (NE Spain). The purpose of this study was to clarify the relative importance of water, nitrogen and phosphorus as factors controlling primary production. Eight plots comprising all possible combinations of the three factors (including a control) were laid out in three replicate blocks. Fertilizers were applied in March 1989 with a dose of 125 kg of P/ha and 250 kg of N/ha. Irrigation was applied at a rate of 20 mm per week during the warm season. To evaluate the effects on canopy structure, specific leaf weight (mg/cm^2), average leaf weight (mg), average stem weight and average stem length were measured. In addition, N, P, K, Ca, Mg and S content and their distribution in leaves and stems were analyzed. These variables as well as the structural characteristics were selected because they are among the most dynamic and should present changes over short time periods following changes in environmental conditions. Sampling dates included the period between autumn of 1988 (before treatments) and summer of 1990. Results showed that water and nitrogen treatments have a positive effect on the growth of canopy structures, increased mean weight of leaves and stems, stem length, leaf turnover and leaf area index were general trends of water and nitrogen effects. Nitrogen produced the increase in mean leaf area. Phosporus effect seems to be negative on canopy growth. Mean leaf area and stem length of current leaves after treatments were smaller in phosphorus treatments. Water treatments affect the nutrient content, showing lower concentrations in water treatments since a dilution effect after an increase of production took place. The nitrogen treatments significantly increased the nitrogen concentration in young leaves while phosphorus treatments did not have a significant effect on the phosphorus concentration. Nevertheless, phosphorus treatments lower the potassium concentration. This decreased potassium concentration in phosphorus treatments, could explain the negative effect of phosphorus treatments since the calcium added to the superphosphate, probably decreased potassium uptake. This in turn affected leaf expansion and stem elongation and the plant water economy. The increased nitrogen and phosphorus resorptions in nitrogen treatments was probably stimulated by increased new leaf growth, so nutrient demand (source-sink effect).

4.2. Introduction

Water and nutrient availability can be influenced by management practices, atmospheric deposition and climate change. Forest exploitation removes nutrients from a site, and may thereby affect later production by decreasing soil fertility. Thus, nutrient availability can play a key role in many forest ecosystems. In this context, nitrogen has probably received the most attention because it is one of the most limiting elements (Miller 1981 1984, Bowen & Nambiar 1984, Field & Mooney 1986,). The availability of water is another limiting factor (Gholz *et al.* 1990), but in spite of its great importance in mediterranean forests, has received scarce experimental manipulation. Such studies have only been attempted in intensive forest plantations, as is the case of *Populus* sp., *Eucalyptus* sp. and *Pinus radiata* (Hopmans *et al.* 1990; McMurtie 1990, Benson *et al.* 1992).

Some years ago, studies on a *Quercus ilex* L. forest began at the Prades Experimental Complex of Catchments (NE Spain). This holm-oak forest was managed, until the 1950's, as a source of charcoal, and the result was a multistemmed structure in the aboveground biomass and an older root system corresponding to the initial trees. Studies at the watershed level (Piñol 1990) as well as throughfall and stemflow (Bellot 1989) show some interesting results in relation to water and nutrient balances. On an annual basis 93% of the water input is lost by evapotranspiration and the vegetation acts as a sink of nitrogen. The main sources of phosphorus are the recycling of organic matter in soil and bedrock weathering. Water is probably the main limiting factor controlling photosynthesis since summer drought is a characteristic trait of Mediterranean-type climates. The canopy is an integrator of water and nutrient availability and productivity. Changes in these factors could dramatically modify the canopy structure (Gholz *et al.* 1990) and nutrient dynamics. It is important to understand how water and nutrients interact in affecting tree growth.

To clarify the relative importance of water, nitrogen, and phosphorus as factors controlling primary production of holm-oak, a multifactorial ANOVA experiment (fertilization and irrigation) was designed. The aim of this study was to evaluate the changes of structure and nutrient content in the canopy of *Quercus ilex* L. as a response to the treatments. Other aspects of this experiment were conducted in other complementary studies by other researchers.

4.3. Methods

Study area and experimental design

The study was carried out in a holm-oak forest at the Prades Experimental Complex of Catchments (NE Spain, 41° 13' N, 0° 55' E). Slope within the study plots ranges from 11° to 30° with a mean of 24°, oriented SSE and at about 950 m altitude. The climatic conditions are typically mediterranean, with hot and dry summers, fresh and wet springs and autumns, and mild as well as fairly dry winters. Poblet Monastery Meteorological Station is close to the study site where the mean annual temperature was 13.5°C and the average annual precipitation was 528 mm in the 1975-1990 period. Rainfall at Poblet Monastery Meterorological Station during 1986-1990 period is shown on Figure 4.1. The main rock type in the area is schist and the soils are Lithic and typic Xerochrepts (USDA Soil Taxonomy, 1975). The tree layer is 6 m high and it is dominated by holm oak with occasional individuals of other evergreen (*Phyllirea angustifolia*, *Arbutus unedo*) or deciduous (*Quercus x cerrioides*, *Acer monspessulanum*, *Sorbus torminalis*) tree species.

On this site, eight plots (8mx8m) were delimited within each of three replicate blocks. The relatively small size of the plots reflects the low stature and high density of trees. Larger plots would have included small clearings and screes, thus producing an unacceptable degree of within - and between- plot heterogeneity. Plots were separated from each other by an untreated corridor at least 4 m wide. Treatments were assigned to plots to minimize the possibility of cross-contamination. Treatments were Control, Water, Nitrogen, Phosphorus, Water+Nitrogen, Water+Phosphorus, Nitrogen+Phosphorus and Water+Nitrogen+Phosphorus. Thus, each factor (Water, Nitrogen, Phosphorus) included four treatments. So, for instance, when we refer to N treatments (or N factor) we include Nitrogen, Nitrogen+Phosphorus, Nitrogen+Water, Nitrogen+Phosphorus+Water treatment plots. Fertilizers were applied in March 1989, in phosphorus treatments by the addition of 125 Kg of P/ha (as calcium superphosphate) and in nitrogen treatments, 250 Kg of N/ha (as ammonium nitrate). Water from a nearby stream was impounded in a small reservoir, pumped to the plots and delivered by drip irrigation through a system of pipes. Each irrigated plot was crossed by eight parallel pipes separated by 1 m from each other and perforated from one end to another by drip holes spaced at 40 cm intervals. Irrigation was supplied between July and October 1989 and from April to August 1990 with a dose of about 20 mm per week to satisfy the evapotranspiration demand of water by the plants. All plots received ambiental rainfall. Spring fertilization seems to be more effective than in other periods of the year, due to the reduction of potential losses, as pointed out by McGrath and McArthur (1990).

Sampling procedure and analysis

In the autumn of 1988, before treatments, three branches were taken from the upper part of the canopy in each of the 24 plots. Each branch came from a separate multistemmed crown. The separated fractions were: (1) current leaves and leaf bearing stems produced in spring '88, (2) old leaves and leaf bearing stems produced in spring '87 and (3) branches < 1.5 cm in diameter, without leaves (rest of the branch). In the summer of 1990, after treatments, sampling was repeated and, on this occasion, the following fractions were separated: (1) current leaves and leaf bearing stems produced in spring '90, (2) 1-year old leaves and leaf bearing stems produced in spring '89, (3) 2-year old leaves and leaf bearing stems produced in spring '88, (4) branches, <1.5 cm in diameter, without leaves, (5) fruits. Additional samples were obtained, as the ones mentioned above, in autumn of 1989 and spring of 1990. Nevertheless, only leaves produced in spring '88 and spring '87, to compute leaf nutrient variation or resorption, are considered in this work. The following variables were quantified and average values in each plot were computed from the three branches collected: *mean leaf weight* (mg) and *area* (cm^2), *specific leaf weight* (mg/cm^2), *mean stem weight* (mg) and *mean stem length* (cm). In the case of holm oak, once the current shoots have developed, length does not increase over time but thickness does. New shoots may, however, be added. For every fraction carbon and nitrogen content were analyzed using a Carlo-Erba D-700 elemental analyzer. Phosphorus and cations were analyzed using wet digestion and ICP-AES determination (Mateo and Sabaté, in press, see chapter 2). Mean values of nutrient concentration of each considered fraction were computed. Nutrient resorption from leaves was computed as the difference between the largest and the lowest nutrient mass on leaf area basis, or the difference between the largest nutrient mass and remainig nutrient mass in leaf litterfall on leaf area basis, collected between May and July of 1990 (when mainly leaf litterfall occurred). These leaf litterfall nutrient analyses were taken from MV.Diego working on complementary studies (in prep.). Statistical analyses were performed using the SAS package (SAS Institute Inc.).

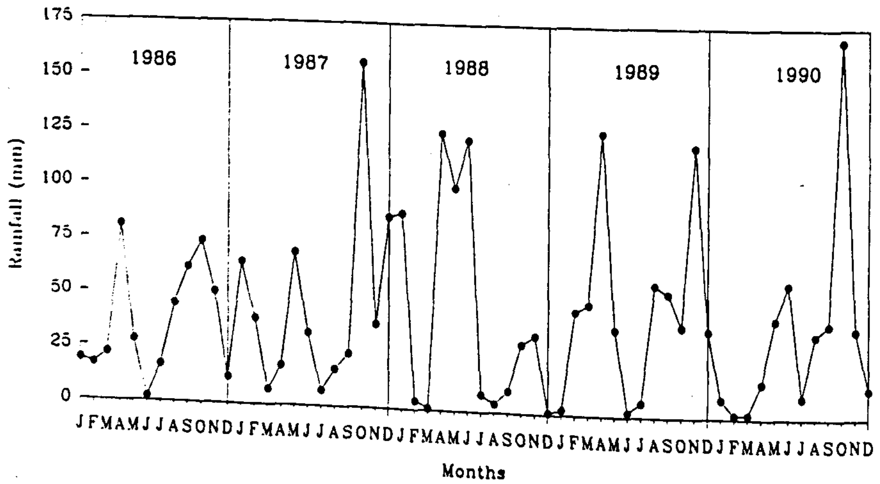


Figure 4.1. Monthly rainfall during 1986-1990. Data from the meteorological station at Poblet.

4.4 Results

Variability of structural leaf and stem characteristics before treatments

Figure 4.1 shows the monthly rainfall during 1986-1990 at the meteorological station at Poblet Monastery, close to experimental site. These data allow us to compare the structural characteristics of leaves and stems with the availability of water at the moment of their formation. The period that preceded the growth of shoots in the spring of 1988 was very wet (750 mm, September 87-June 88) as compared to the corresponding period in 1987 (431 mm, September 86-June 87). The differences in water availability for plants during these periods should therefore be considered when trying to explain the results obtained in autumn 1988 (before treatments). During the initial phases of the experiment, the weather was relatively dry. Rainfall during September 88-June 89 was 343 mm, while during September 89-June 90 it was 390 mm.

Mean values of structural variables chosen for the characterization of leaves and stems are shown in Table 4.1. These values correspond to samples collected before treatments in autumn 1988 (no significant differences were obtained among experimental treatments to the ANOVA), and refer to fractions produced in spring 1988 and spring 1987. The mean weight and mean area of the leaves produced in 1988 were greater than those of the older leaves. The specific leaf weight of leaves produced in 1988 was smaller than that of the older leaves.

The mean weight of stems elongated in 1988 was lower that one of the stems elongated in 1987 (Figure 4.1). The weight per unit of length (mg/cm) was 15.5 for those formed in 1988, compared to 26.4 for those formed in 1987. The higher values of mean weight and weight per unit of length for stems formed in 1987 can be explained by the fact that they combined the growth of two years (1987 and 1988). Length, which is not modified once stem is formed, is very different for those stems formed in 1987 and for those formed in 1988. This presumably results from differences in rainfall, and therefore differences of water availability in both years.

Structural canopy characteristics after treatments

Table 4.2 shows the effect of *water, phosphorus* and *nitrogen* treatments on light extinction as a result of changes in canopy structure (measures from spring '92). PAR (photosynthetically active radiation) measured below the canopy and light extinction were significantly lower in *water* and *nitrogen* treatments ($P<0.01$).

Table 4.1. Structural properties of leaves and stems produced in spring 1987 an 1988. Sampling date: autumn 1988 (before treatment). Values are the mean (±S.E.), n=24.

	1987	1988
LEAVES:		
Mean weight (mg)	45.3±2.2	53.6±1.9
Specific leaf weight (mg/cm^2)	19.3±0.2	18.2±0.2
Mean area (cm^2)	2.3±0.1	3.0±0.1
STEMS:		
Mean weight (mg)	50.2±4.5	43.4±3.5
Mean lenght (cm)	1.9±0.1	2.8±0.1

Table 4.2. Water, Phoshorus and Nitrogen main effects on PAR (photosynthetically active radiation, µE/m^2/s) measured bellow the canopy and % of light extinction. Measures obtained in spring of 1992. Values are mean ± SE, n=12.

	PAR µE/m^2/s	Light extinction (%)
Water	64.9±5.2	95.3±0.5
No Water	90.9±7.6**	93.6±0.5**
Phosphorus	76.2±8.5	94.4±0.6
No Phosphorus	79.2±8.5	94.4±0.6
Nitrogen	65.2±6.0	95.4±0.4
No Nitrogen	90.8±7.0**	93.6±0.5**

Table 4.3 presents the mean weight of leaves, stems and fruits collected in summer of 1990 after treatments. Weight of 1988 leaves was not significantly different among treatments, as we would expect because these leaves were formed before treatments. Nevertheless, *nitrogen* and *water* treatments tended to increase mean stem weight of stems elongated in 1988 due to the accumulation of stem production during 1989 and 1990. Leaves and stems formed during 1989 tended to show higher mean weight in *water* treatments ($P<0.05$ in stems '89). *Phosphorus* decreased the mean weight of both leaves and stems but not significantly. The presence of *phosphorus* seems to counter-balance the positive effect of *water* on leaf and stem growth. Since 1989 was a dry year and leaf production was very low, not enough leaf samples from this year were obtained to test the factorial model. Differences in leaves '89 were not tested. Nevertheless, leaves formed during spring of 1990, showed the same pattern of variation (higher weight in *water* and *nitrogen* treatments ($P<0.05$) and lower in *phosphorus* treatments ($P<0.01$). Despite water treatments began in 1989, water was supplied from mid-July. Thus, differences between 1989 and 1990 are due, in part, to the differences in water experimental supply, as well as to differences in water availability during the 1990 pre-productive period. This was slighly wetter than the same period in 1989 (see Figure 4.1 and comments above). Weight of fruits was clearly affected by *water* treatments ($P<0.001$).

Table 4.4 presents the mean stem length. Irrigation and fertilization did not affect the length of stems that were formed before treatments (Stems '88). Stems formed under the effect of the treatments (1989 and 1990) show a very clear pattern of response, with higher values in *water* treatments, and, to a lesser extent, *nitrogen* (only in stems elongated in 1990). Once again, *phosphorus* treatments seem to have a negative effect on growth.

Specific leaf weight and mean area were not significantly affected by *water* treatments contrary to our expectation. Nevertheless, they were significantly affected by *nitrogen* treatments ($P<0.05$), which were lower and higher respectively, in *nitrogen* treatments (17.0 ± 0.2 mg cm^{-2} and 2.9 ± 0.2 cm^{-2}, ±SE) as compared to *no nitrogen* treatments (18.2 ± 0.4 mg cm^{-2} and 2.4 ± 0.1 cm^{-2}, ±SE) of leaves '90. *Phosphorus* treatments did not significantly affect specific leaf weight of leaves '90 (17.5 ± 0.4 mg cm^{-2} against 17.7 ± 0.3 mg cm^{-2} in *no phosphorus* treatments, ±SE). Nevertheless, it significantly affects mean leaf area, lower in *phosphorus* treatments ($P<0.05$, 2.4 ± 0.2 cm^{-2} in *phosphorus* against 2.9 ± 0.2 cm^{-2} in *no phosphorus* treatments, ±SE). Thus, differences in mean weight of leaves '90 pointed out above are in agreement with differences in leaf area.

Table 4.3. Mean weight ± S.E. (mg) of leaves, stems and fruits. Sampling date: Summer 1990. ANOVA after logarithmic transformation of individual variables. P=Phosphorus, N=Nitrogen and W=Water. Results for grouped treatments are obtained comparing treated against no treated plots (n=3 for individual treatments, and n=12 for grouped treatments; *: P=0.05, **:P=0.01, ***:P=0.001)

	1988		1989		1990		
TREATMENT	Leaves	Stems	Leaves	Stems	Leaves	Stems	Fruits
Control	63.5 ± 2.3	67.1 ± 7.3	16.2 ± 0.4	28.5 ± 3.0	46.6 ± 3.1	26.2 ± 1.0	18.0 ± 6.1
P	62.3 ± 14.0	90.6 ± 44.5	13.6 ± 0.9	44.8 ± .	36.7 ± 3.2	27.6 ± 5.9	37.7 ± 28.3
N	64.7 ± 3.4	75.1 ± 18.3	12.9 ± 5.4	35.5 ± 11.2	47.7 ± 9.5	35.5 ± 4.3	23.1 ± 12.5
W	64.3 ± 7.1	93.7 ± 33.4	22.6 ± 3.1	62.2 ± 24.3	50.1 ± 7.9	50.0 ± 20.9	194.4 ± 38.0
NP	56.4 ± 6.1	65.6 ± 4.8	17.9 ± .	24.9 ± 4.3	41.4 ± 4.6	29.2 ± 0.6	62.6 ± 50.0
PW	53.2 ± 2.8	66.6 ± 7.5	19.7 ± .	43.6 ± .	38.2 ± 4.9	39.1 ± 6.5	112.4 ± 31.7
NW	64.0 ± 7.1	131.4 ± 2.4	33.8 ± 7.2	74.3 ± 14.1	59.8 ± 2.3	60.3 ± 11.9	132.4 ± 14.0
PNW	61.7 ± 9.2	107.6 ± 24.5	19.1 ± 4.3	53.2 ± 7.9	49.0 ± 4.3	58.4 ± 4.6	112.6 ± 32.8
GROUPED TREATMENTS:							
Without P	64.1 ± 2.3	91.8 ± 11.1	21.5 ± 3.2	53.7 ± 9.7	51.0 ± 3.2	43.0 ± 6.5	92.0 ± 24.3
With P	58.4 ± 4.0	82.6 ± 12.2	17.1 ± 1.6	42.5 ± 5.7	41.3 ± 2.3**	38.6 ± 4.3	81.3 ± 18.4
Without N	60.8 ± 3.7	79.5 ± 12.7	18.4 ± 1.7	47.4 ± 10.8	42.9 ± 2.7	35.7 ± 5.6	90.6 ± 24.3
With N	61.7 ± 3.1	94.9 ± 10.3	21.4 ± 4.0	50.3 ± 7.7	49.5 ± 3.2*	45.8 ± 5.0	82.7 ± 18.6
Without W	61.7 ± 3.5	74.6 ± 10.8	14.8 ± 1.4	31.8 ± 3.8	43.1 ± 2.8	29.6 ± 1.9	35.3 ± 13.6
With W	60.1 ± 3.3	99.8 ± 11.4	24.2 ± 2.9	61.3 ± 8.2*	49.3 ± 3.2*	51.9 ± 6.0**	138.0 ± 16.5***

Table 4.4. Mean lenght (±S.E.) (cm) of stems in summer 1990. ANOVA after logarithmic transformation of individual variables. P = Phosphorus, N = Nitrogen and W = Water. Results for grouped treatment are obtained comparing treated against non treated plots. (n=3 for individual treatments and n=12 for grouped treatments; *: P = 0.05, **: P = 0.01, ***: P = 0.001).

TREATMENT	Stems 1988	Stems 1989	Stems 1990
Control	3.4 ± 0.3	1.6 ± 0.4	1.6 ± 0.1
P	3.3 ± 0.6	1.3 ± 0.3	1.4 ± 0.2
N	3.5 ± 0.4	1.3 ± 0.3	2.1 ± 0.2
W	3.7 ± 0.7	2.2 ± 0.3	2.4 ± 0.6
NP	3.1 ± 0.2	1.2 ± 0.3	2.0 ± 0.0
PW	3.1 ± 0.4	1.6 ± .	2.5 ± 0.4
NW	3.2 ± 0.3	2.9 ± 0.3	3.5 ± 0.3
PNW	3.3 ± 0.0	1.5 ± 0.1	3.5 ± 0.2
GROUPED TREATMENTS:			
With P	3.2 ± 0.2	1.4 ± 0.1	2.3 ± 0.2
Without P	3.5 ± 0.2	2.1 ± 0.2**	2.4 ± 0.3
With N	3.3 ± 0.1	1.7 ± 0.2	2.8 ± 0.2
Without N	3.4 ± 0.2	1.8 ± 0.2	2.0 ± 0.2**
With W	3.5 ± 0.2	2.2 ± 0.2	3.0 ± 0.2
Without W	3.4 ± 0.2	1.3 ± 0.1**	1.8 ± 0.1***

Table 4.5. Mean ***Leaf area /branches basal area*** (±S.E.) ($cm^2\ cm^{-2}$) of different treatments of branches collected in summer 1990. P = Phosphorus, N = Nitrogen and W = Water. Results for grouped treatments are obtained comparing treated against no treated plots. The mean ratios in different age classes of leaves were obtained from the average of the mean ratios obtained in each plot, so n=3 for individual treatments and n=12 for grouped treatments; *: P = 0.05, **: P = 0.01, ***: P = 0.001)). The column Total is the summation of mean ratios from different age classes.

TREATMENT	Total ($cm^2\ cm^{-2}$)	To Leaves 1988 ($cm^2\ cm^{-2}$)	To Leaves 1989 ($cm^2\ cm^{-2}$)	To Leaves 1990 ($cm^2\ cm^{-2}$)
Control	43.8	22.1 ± 1.7	0.2 ± 0.1	21.5 ± 2.6
P	42.1	27.4 ± 2.5	0.6 ± 0.2	14.1 ± 2.8
N	53.9	26.0 ± 11.7	0.1 ± 0.1	27.8 ± 4.0
W	48.5	23.5 ± 5.6	1.1 ± 0.3	23.9 ± 1.9
NP	44.8	15.2 ± 7.1	1.0 ± .	28.6 ± 6.5
PW	30.4	12.7 ± 4.2	0.8 ± .	16.9 ± 4.3
NW	38.7	12.5 ± 3.1	1.7 ± 1.1	24.5 ± 5.3
PNW	54.4	13.1 ± 2.3	0.6 ± 0.4	40.8 ± 9.6
GROUPED TREATMENTS:				
With P	42.9	17.1 ± 2.6	0.7 ± 0.2	25.1 ± 4.2
Without P	48.8	21.0 ± 3.3	0.9 ± 0.4	26.9 ± 2.2
With N	50.5	16.7 ± 3.4	0.9 ± 0.5	32.9 ± 3.3
Without N	40.2	21.4 ± 2.3	0.7 ± 0.2	18.1 ± 1.7***
With W	45.6	15.4 ± 2.1	1.2 ± 0.4	29.0 ± 3.8
Without W	48.1	22.7 ± 3.3*	2.4 ± 0.1	23.0 ± 2.5*

The ratios *leaf area /branches basal area* shown on Table 4.5, to different age classes, indicate a higher new leaf area production in *water* and *nitrogen* treatments (in spring of 1990). Since leaves produced in spring '88 had less area as compared to *no water* or *no nitrogen* treatment plots, an increase in leaf turnover is also evident (significant differences shown on table 4.5). *Phosphorus* treatments did not show an increase in new leaf area production, but did tend to show less leaf area in leaves produced in spring '88.

The Total summation of ratios of different age classes tended to be higher in *nitrogen* as compare to *no nitrogen*. Differences in *water* and *phosphorus* treatments tended to be lower.

Nutrient content

Table 4.6 shows the mean nutrient concentration in leaves and stems collected in autumn of 1988. Before treatments, no differences between plots testing the same experimental design that the one applied after treatments were found. Thus, we assume that differences obtained in summer of 1990 were due to the treatment effects. The same was true for structural characteristics as shown above in Table 4.1. The general pattern of nutrient concentrations in this experimental area is similar to those shown in other studies from the same forest (see chapter 3) and other holm oak forests (see Ferrés 1984, Mayor 1990); higher carbon and nitrogen concentrations and lower phosphous, potassium and calcium concentrations in leaves than stems.

The nitrogen and phosphorus concentration in stems and leaves of *Quercus ilex* are shown in Figure 4.2. The values presented, as an example, are for the leaves and the stems produced in the spring of 1988 and collected in the autumn of 1988 (before treatments) and the summer of 1990 (after treatments). As we pointed out above, higher nitrogen concentration in leaves and a higher phosphorus concentration in stems were observed. Nitrogen and phosphorus concentration increased in stems and decreased in leaves in summer 1990 as compared to autumn 1988. In older stems (no bearing leaf stems and <1.5 cm in diameter) the concentrations were 0.121 % ±0.004 of P and 0.66 % ±0.03 of N in those collected in autumn of 1988 and 0.125 % ±0.002 of P and 0.80 % ±0.02 of N in those collected in summer of 1990 (mean ± SE). This is in agreement with the same temporal pattern that stems show in Figure 4.2, but in lower concentrations.

Table 4.6. Nutrient content in leaves and stems produced in spring 1987 and 1988. Sampling date: autumn 1988 (before treatment). Values are the mean (±S.E.), n=24.

% Dry Weight	No leaf bearing stems <1.5 cm	Leaf bearing Stems		Leaves	
		1987	1988	1987	1988
% C	47.2±0.1	48.3±0.1	48.2±0.1	49.7±0.1	49.1±0.2
% N	0.66±0.03	0.81±0.02	0.80±0.02	1.30±0.02	1.50±0.02
% P	0.121±0.004	0.136±0.004	0.115±0.002	0.099±0.003	0.111±0.002
% K	0.45±0.01	0.53±0.02	0.67±0.01	0.46±0.02	0.51±0.01
% Ca	1.22±0.05	1.21±0.04	1.15±0.04	1.06±0.04	0.80±0.03
% Mg	0.076±0.002	0.100±0.005	0.139±0.005	0.086±0.004	0.103±0.004
µg N/cm^2	-	-	-	242.6±7.2	272.1±4.9
µg P/cm^2	-	-	-	18.4±0.6	20.2±0.3

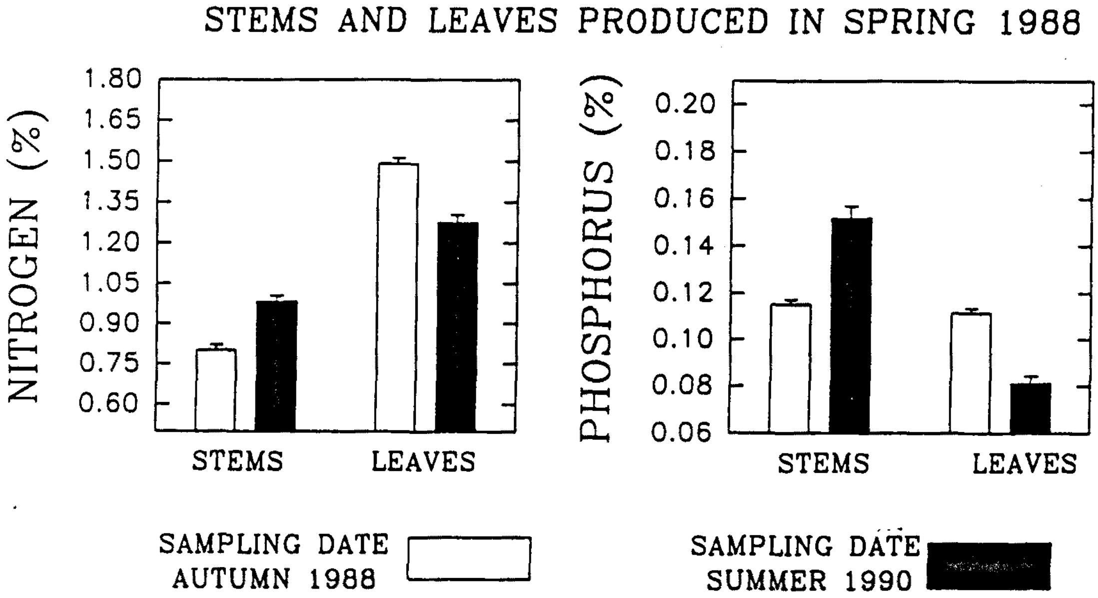


Figure 4.2. Nitrogen and phosphorus concentration in stems and leaves produced in the spring of 1988. Samples from 72 branches collected in the autumn of 1988 (before treatments) and the summer of 1990 (after treatments). Values are *mean ± SE.*

Figure 4.3 shows *water* against *no water* effects on nitrogen and phosphorus concentration (samples collected in summer of 1990). A lower concentration of nitrogen and phosphorus in *water* treatments was a common result. Significant differences were found in stems produced in the spring of 1988 and 1990 ($p<0.001$), and in stems produced in the spring of 1989 ($p<0.05$) for nitrogen concentration. Moreover, significant differences were found in leaves produced in the spring of 1990 ($P<0.05$) for phosphorus concentrations.

The effects of *nitrogen* treatments on nitrogen concentrations are presented in Figure 4.4. A general increase in nitrogen concentration was observed with *nitrogen* treatments, but a significant increment was noted only for leaves produced in the spring of 1990 ($p<0.01$) and stems produced in spring of 1988 ($p<0.05$). *Phosphorus* treatments did not significantly affect phosphorus concentration. Nevertheless, there seemed to be a general pattern of variation in potassium concentration, which decreased in *phosphorus* treatments. These decreased values were significanly different in leaves produced in spring of 1988 and 1990 and stems produced in spring of 1989 ($p<0.05$) (see Figure 4.5).

The effect of *water* treatments on potassium and sulphur concentrations show a similar pattern to the one produced on nitrogen and phosphorus (decreasing concentration in its presence, see Table 4.7). On the other hand, calcium concentration was significantly higher in *water* treatments in leaves produced in spring 1990 (0.38 % ±0.03 against 0.57 % ±0.03 of Ca, $p<0.01$, mean ±SE).

Table 4.8 shows the effect of *water, phosphorus* and *nitrogen* treatments on nutrient concentration in fruits collected in summer '90. Significant differences were only found in *water* treatments where nutrient concentrations were lower as compared to *no water* treatments. This is in agreement with the higher mean weight in these treatments (see Table 4.3). The pattern observed is in accordance with the one produced in leaves and stems (see Figure 4.3 and Table 4.7).

Nutrient resorption

Nutrient resorption was computed for the period between autumn '89 and summer '90. The resorption values presented on the Table 4.9 were calculated, taking into account three possibilities. (1) Nutrient variation in those leaves produced in the spring of 1988, which were still retained in the canopy in summer of 1990. (2) Nutrient resorption prior to leaf abscission, assuming the origin of leaf litterfall from leaves produced in spring of 1988. (3) Nutrient resorption prior to leaf abscission, assuming the origin of leaf litterfall from leaves produced in spring of 1987. The largest values of nutrient mass on leaf area basis were found in autumn of 1989 or spring of 1990, prior to leaf abscission which occurred in late spring and early and mid-summer of 1990.

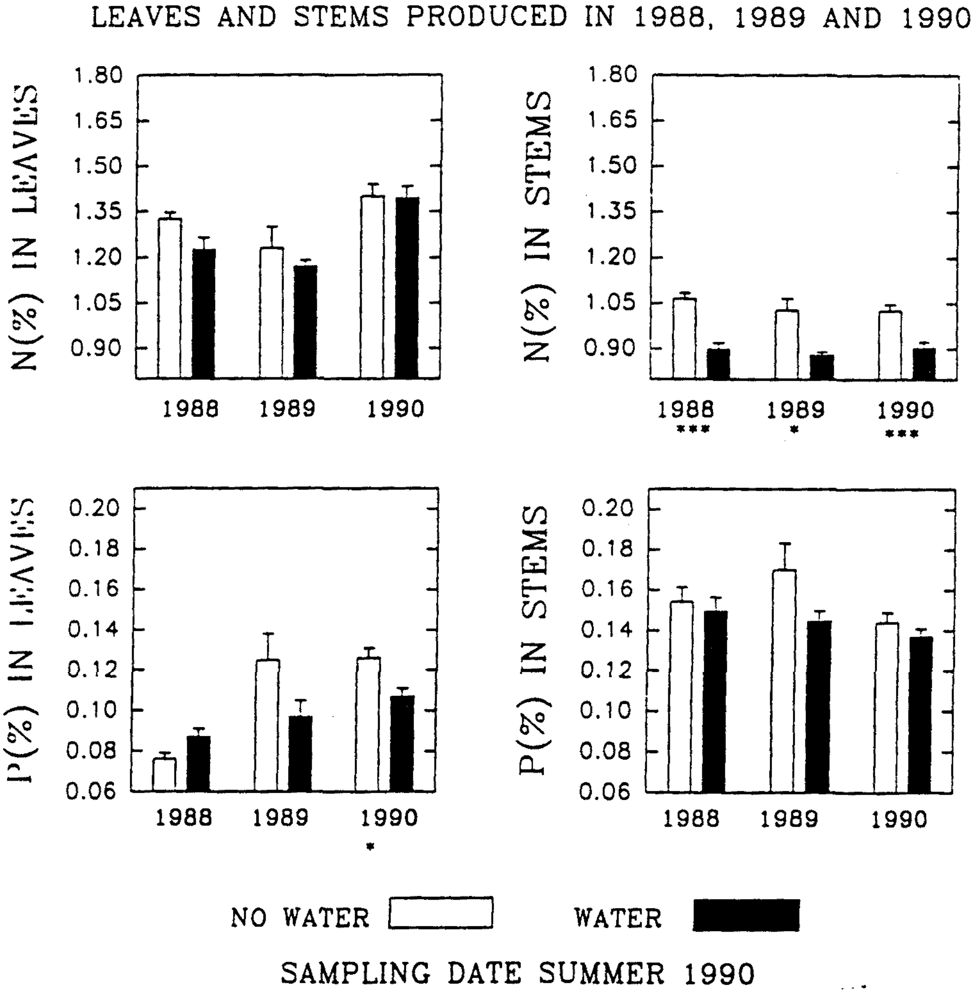


Figure 4.3. *Water* against *no water* effects on nitrogen and phosphorus concentration (samples collected in the summer of 1990). The significant difference is indicated by asterisks below the fraction compared (*:P=0.05; **:P=0.01; ***:P=0.001). Values are *mean* ± *SE*, n=12.

Table 4.7. Effect of water on potassium and sulphur concentrations. Values of leaves and stems than shown significant differences. (No B. L. Stems = no bearing leaves stems). Values are *mean* ± *SE*, n=12.

		No Water	Water	(P value)
K % Dry Weight	Stems 1989	1.03±0.07	0.86±0.04	(0.0368)
	Leaves 1990	0.91±0.02	0.77±0.03	(0.0007)
S % Dry Weight	Stems 1990	0.094±0.003	0.080±0.003	(0.0025)
	No B.L. Stems	0.056±0.002	0.048±0.001	(0.0077)

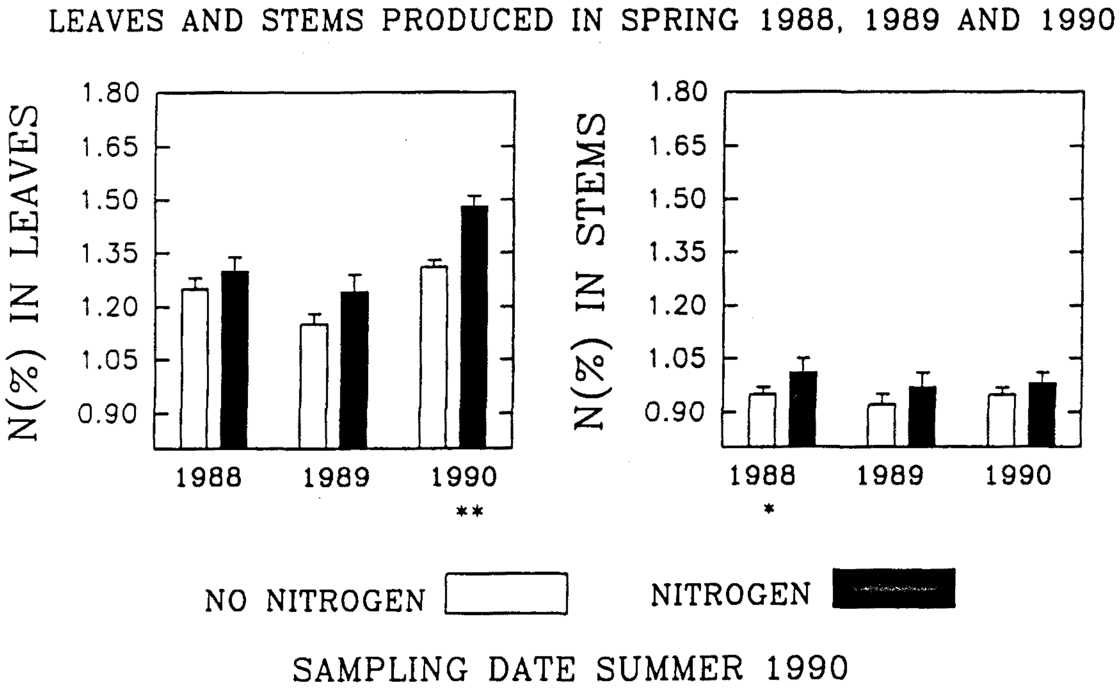


Figure 4.4. *Nitrogen* against *no nitrogen* effects on nitrogen concentrations. The significant difference is indicated by asterisks below the fraction compared (*:P=0.05; **:P=0,01; ***:P=0.001). Values are *mean* ± *SE*, n=12.

Table 4.8. Water, Phosphorus and Nitrogen effects on nutrient content in fruits collected in summer of 1990. Values are Mean ± SE, n=12. (Significant differences are indicated by *: P = 0.05, **: P = 0.01, ***: P = 0.001).

GROUPED TREATMENTS	N (% D.W.)	P (% D.W.)	K (% D.W.)	Ca (% D.W.)	Mg (% D.W.)	S (% D.W.)
Water	1.01±0.03	0.110±0.002	0.89±0.01	0.53±0.02	0.174±0.008	0.096±0.003
No Water	1.37±0.03***	0.161±0.012***	1.14±0.06***	0.75±0.07***	0.211±0.016*	0.159±0.019
Phosphorus	1.27±0.05	0.139±0.014	1.01±0.07	0.64±0.05	0.198±0.012	0.141±0.021
No Phosphorus	1.21±0.05	0.131±0.009	1.01±0.04	0.65±0.07	0.187±0.016	0.114±0.010
Nitrogen	1.01±0.04	0.151±0.006	0.69±0.02	1.17±0.05	0.163±0.038	0.079±0.002
No Nitrogen	0.95±0.02	0.154±0.008	0.71±0.02	1.11±0.07	0.122±0.006	0.083±0.002

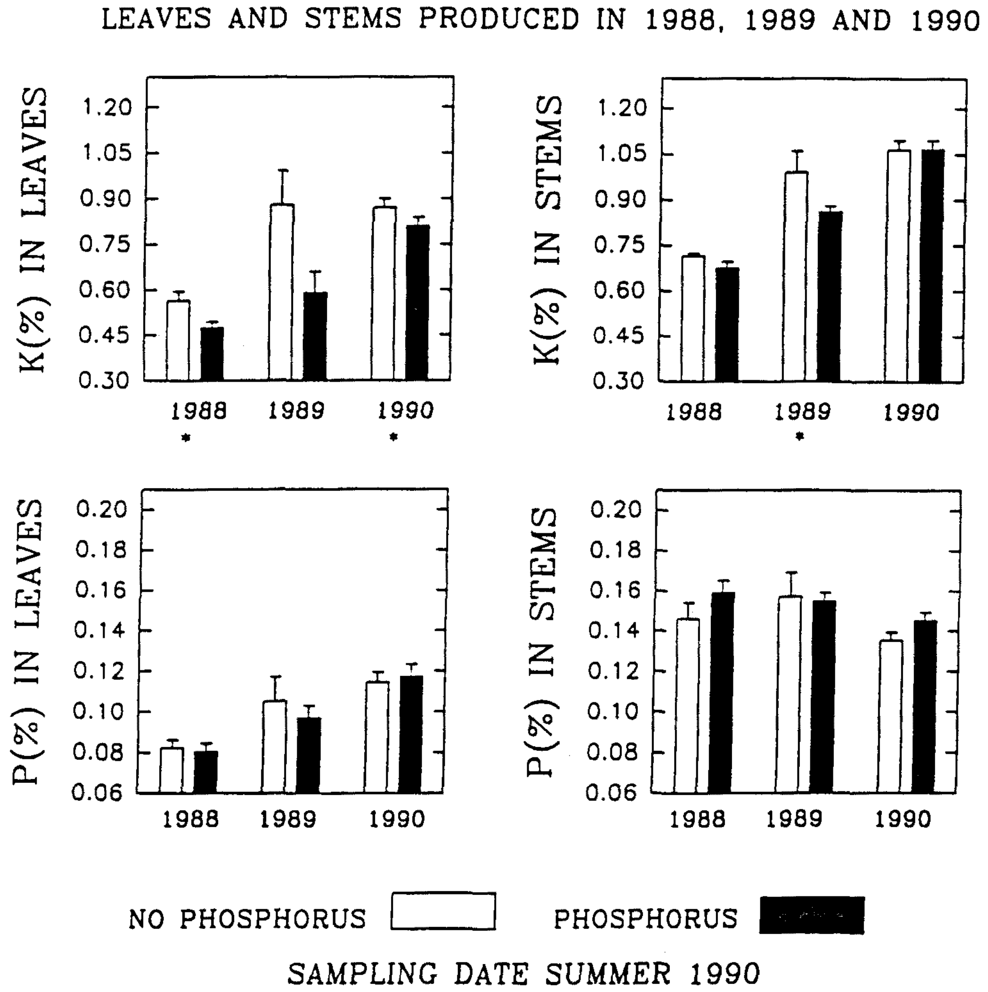


Figure 4.5. *Phosphorus* against *no Phosphorus* effects on potassium and phosphorus concentration. The significant difference is indicated by asterisks below the fraction compared (*:P=0.05; **:P=0.01; ***:P:0.001). Values are *mean* ± *SE*, n=12.

The percentage of nitrogen variation (20.7%) was lower than phosphorus variation (31.8%). Nevertheless, resorption prior to leaf abscission was higher to nitrogen (45.6% in leaves '88 and 39.2% in leaves '87) as compared to phosphorus (14.4% in leaves '88 and 31.2% in leaves '87) in agreement with the results shown in other studies of holm oak from the same area (see chapter 3).

Some differences in nitrogen and phosphorus resorptions were found after treatments. *Nitrogen* treatments increased nitrogen mass reabsorbed prior to leaf abscission from leaves '87 ($P<0.001$, 120.9±5.9 μg/cm^2 against 88.9±5.0 μg/cm^2 in *nitrogen* and *no nitrogen* treatments respectively, ±SE). The percentages were also significantly different ($P<0.01$, 47.1%±1.4 against 44.2%±1.5 in *nitrogen* and *no nitrogen* treatments respectively, ±SE). No differences in nitrogen resorption from leaves '88 were found.

Water treatments tended to increase phosphorus mass resorption prior to leaf abscission in leaves '87 ($P=0.0857$, 7.1±1.1 μg/cm^2 against 4.4±0.5 μg/cm^2 in *water* and *no water* treatments respectively, ±SE) and in leaves '88 ($P=0.0854$, 2.9±0.6 μg/cm^2 against 2.2±0.5 μg/cm^2 in *water* and *no water* treatments respectively, ±SE). No significant differences in percentage were found as compared *water* to *no water* treatments. *Nitrogen* treatments significantly increased the percentage of phosphorus resorption prior to leaf abscission in leaves '88 ($P<0.05$, 33.8%±1.8 against 29.8%±2.3 in *nitrogen* and *no nitrogen* treatments respectively, ±SE). In addition, significant differences in phosphorus mass variation in leaves '88 were found ($P<0.05$, 3.3±0.7 μg/cm^2 against 1.8±0.4 μg/cm^2 in *nitrogen* and *no nitrogen* treatments respectively, ±SE)

Table 4.9. Nitrogen and Phosphorus resorption from leaves computed in summer '90. Values are mean (±SE), n=24 treatment plots. (%) are of the largest nutrient mass values measured in green leaves (collected in autumn 1989 or spring 1990).

		Units	Nitrogen resorption	Phosphorus resorption
Variation in green leaves	Leaves 88	μg cm^{-2}	62.4 ± 6.2 20.7% ± 1.9	2.6 ± 0.3 31.8% ± 1.9
Differences between largest nutrient mass in green leaves and nutrient mass in leaf litterfall	Leaves 88	μg cm^{-2}	135.8 ± 5.4 45.6% ± 1.0	5.6 ± 0.4 14.4% ± 1.7
	Leaves 87	μg cm^{-2}	104.9 ± 3.1 39.2% ± 0.9	5.7 ± 0.7 31.2% ± 2.9

4.5 Discussion

According to Miller (1981, 1984) and Van den Driesche (1984) the maximum response of trees to fertilization is obtained before canopy closure. After that, internal cycling becomes more important, buffering the effects of fertilization. Scarce information is available about the old *Quercus ilex* root crown system and how much it contributes to the stocks of nutrients and water availability. Canadell and Rodà (1991) found that the underground biomass in this kind of multistemmed crown structure could be greater than the aboveground biomass. However, despite the old root system and stabilised leaf area index of this holm-oak forest, responses after the treatments were evident. *Quercus ilex* canopy showed different structural characteristics and nutrient concentrations in response to the treatments.

Effects on nutrient content and structure

Inter-annual differences in rainfall between years were followed by differences in leaf and stems structural characteristics. Before treatments, leaves and stems formed during a dry year (1987), were smaller than those formed during a wet one (1988). This shows the importance of water availability and the plasticity of canopy elements. Thus, as should be expected, irrigation increased stem elongation, stem mean weight, mean leaf weight and mean weight of fruits. Nevertheless, in contrast to our expectation, specific leaf weight did not decrease in irrigated plots. This is probably due to the importance of radiation determining the annual evaporative power which determines leaf area and specific leaf weight (Specht and Specht 1989). Raison *et al.* (1992a) also found that specific leaf weight was lower for *Pinus radiata* needles formed under lower light (see also chapter 7). Radiation was not modified during the experiment because the addition of water to the soil does not affect cloudiness as it is affected by rainfall.

Water also affected nutrient content in leaves and stems. The increased production in *water* treatments could explain the lower nutrient concentrations since a dilution effect took place. According to the *water* effect on canopy growth, Mayor and Rodà (in press) found that only *water* treatments gave a higher increase in stem diameter three years after nutrient application. Diego and Rodà (1992) found different effects on leaf litterfall dynamics comparing 1989 and 1990 experimental years. In 1989 *water* increased leaf retention (irrigation was applied from mid summer) since it decreased drought stress and so leaf shedding. On the other hand, in 1990 *water* increased leaf turnover (irrigation was applied from early spring). The 1990 Diego and Rodà's results are in agreement with the increased new leaf area produced and decreased old leaf area in *water* treatments measured in this study in summer '90.

Nitrogen treatments also had effects on growth. Stems showed a higher mean weight and length. Leaves showed a lower specific leaf weight and higher mean weight and leaf area. *Nitrogen* also increased new leaf area production and leaf turnover. In addition, *nitrogen* treatments affected the nitrogen concentration in young leaves. Therefore, the increased leaf area and nutrient concentration probably increased its photosynthetic capacity (Field and Mooney 1986, Evans, 1986). Miller (1986) found a positive correlation between the weight of current year foliage (i.e. foliage production) and annual above-ground biomass increment, with deciduous and evergreen trees sharing a similar line. It therefore seems clear that *water* and *nitrogen* could act as limiting factors in holm oak production.

Snowdon and Benson (1992) examined the allocation of annual above ground biomass production to foliage, branches and stem wood in *Pinus radiata* after a fertilisation and irrigation experiment. They suggested that fertilisation stimulated allocation to branches rather than stems, whereas irrigation alone stimulated stem rather than branch growth. The results obtained in our experiment suggest this is true for *Quercus ilex*. We found positive effects on canopy growth with *water* and *nitrogen* treatments, but Mayor and Rodà (in press) only found positive *water* effects during the same period on stem diameter growth. The light interception by the canopy in our experiment (three years later) support the role of *nitrogen* and *water* on canopy production. The significant increase of light interception under *nitrogen* and *water* treatments could be related to an increase of canopy production and also probably to an increase in leaf area index (LAI).

The relationship between the increment in light extinction and shoot production has been shown in other species, such as *Pinus contorta* by Schoettle and Smith (1991). The stimation of LAI from measurements of light extinction has been analyzed by Lang and Xiang-Yueqin (1986) and Lang (1991). Raison *et al.* (1992b) found that indirect estimates of LAI from light extinction, and direct estimates of LAI from biomass measurements were well correlated in *Pinus radiata* ($r^2>0.9$). Fertilisation and irrigation could change the allometric relationships after treatments. The new allometric relationships, after treatments, to estimate leaf biomass were not available. However the observed trend to increase in foliar area per unit of branch basal area after *nitrogen* fertilisation (see *Total* ratio summation in Table 4.5) shows that such allometric shift did take place in holm oak, and that it resulted in an increased LAI in *nitrogen* treatments. Irrigation apparently had not produced such effect on total LAI in summer '90, though it increased the foliar area of leaves produced in 1990 per unit of branch basal area. Taking into account that irrigation in 1989 was only moderate, and that irrigation increased light extinction by the canopy in spring '92, it seems that irrigation also increased LAI in this forest, though perhaps later and to a lesser extent than *nitrogen* did.

Phosphorus treatments had no significant effect on phosphorus concentration in leaves and stems, but they decreased potassium concentrations. Potassium uptake and allocation may be modified by fertilization with calcium superphosphate. Therefore, the negative effects of *phosphorus* treatments on canopy growth could be related to a calcium antagonism with potassium rather than a *phosphorus* negative effect. This antagonism is well described in Agricultural Sciences (i.e. Gros 1986, Urbano 1989). Thus changes in potassium availability could affect growth of canopy components since potassium is important in processes of leaf expansion, stem elongation and hidric economy of plants (Domingez 1984, Marschner 1986).

Nutrient resorption trends

Quercus ilex seems to have lower nitrogen and phosphorus concentration in leaves during summer and higher ones during autumn or early spring (see chapter 3). In addition, these variations were opposite to those shown by stems, higher concentration values in summer, therefore in supporting the role of nutrient resorption processes. The patterns of nutrient variation observed were in accordance with higher nitrogen and phosphorus concentrations in leaves, and lower nitrogen and phosphorus concentrations in stems, in autumn of 1988 as compared to values obtained in summer of 1990 in this study.

The high concentration of phosphorus in stems of fine branches of *Quercus ilex* has been previously pointed out (Escarré et al., 1987). In *Pinus radiata* McGrath and McArthur (1990) found fluctuations in nutrient concentrations in leaves and woody tissues, which was interpreted as the effect of internal resorption processes. These fluctuations in leaf nutrient concentrations have been previously described by Fife and Nambiar (1984) and Nambiar and Fife (1987).

In this study, phosphorus resorption from retained foliage in the canopy was rather similar to phosphorus resorption prior to leaf abscission. Nitrogen showed a different pattern. Nitrogen resorption from retained foliage in the canopy was lower than nitrogen resorption prior to leaf abscission. This is in accordance with values obtained in chapter 3. Beets and Pollock (1987) also measured higher nitrogen resorption from foliage prior to leaf abscission. These differences could be due to a more general nitrogenous-compounds hydrolysis during senescence.

Nitrogen resorption prior to leaf abscission was higher than that found by Mayor and Roda (1992) - 33% of N resorption- and Escudero et al. (1992) - 29.7% of N resorption- in other holm oak forests, and slightly lower or similar to the values obtained in chapter 3. Nevertheless, phosphorus resorption values were lower than those found by Mayor and Rodà (1992) - 43% of P resorption - and those found in chapter 3. Our fertilization and irrigation experiment was on a south facing as compared to l'Avic (north-facing). Thus water availability is likely to be involved in these differences. This is in accordance with the effect of *water* enhancing phosphorus mass resorption, despite the fact that percentage differences were not significant.

The effect of *nitrogen* treatments enhancing phosphorus and nitrogen resorptions could be related to the higher new leaf area production in these treatments and thus a higher nutrient demand (source-sink effect). In addition, the increased nitrogen resorption in *nitrogen* treatments could be related to an increased nitrogen availability and mobility as found by Nambiar and Fife (1987) in *Pinus radiata* after N-fertilisation.

4.6 Conclusions

Water and Nitrogen are the main limiting factors of holm oak growth. Nevertheless, the effect of phosphorus (calcium superphosphate) is not clear. Possible indirect effects of calcium on decreasing potassium uptake could explain the negative effects of *Phosphorus* treatments on canopy growth.

Water treatments increased mean weight of canopy components and decreased its nutrient concentration since nutrients were diluted with higher growth.

Nitrogen treatments also increased mean weight of canopy components. Nitrogen increased nitrogen concentration. Mean leaf area of new leaves was larger in *nitrogen* treatments and specific leaf weight was lower.

Water and *Nitrogen* treatments increased new leaf area production and LAI. Nevertheless, *nitrogen* acted on canopy components earlier than water, which also increased stem diameter (Mayor and Roda in press)

Phosphorus treatments decreased mean leaf area and stem length. The decreased potassium concentration in these treatments could explain the lower growth of canopy components.

Nitrogen treatments increased nitrogen and phosphorus resorption since it increased new leaf production (source-sink effect). *Water* treatments increased phosphorus mass resorption but not in percentage.

4.7. References

Benson ML, Landsberg JJ, Borough CJ (1992) The Biology of Forest Growth experiment: an introduction. For Ecol Manage 52:1-16

Beets PN, Pollock DS (1987) Uptake and accumulation of N in *Pinus radiata* stands as related to age and thining. NZ J For Sci 17:353-371

Bellot J (1989) Análisis de los fluidos de deposición global, translocación, escorrentía cortical y deposición seca en el encinar mediterráneo de L'Avic (Serra de Prades, Tarragona). Ph D. Thesis. Univ. Alacant

Bowen GD, Nambiar EKS (eds) (1984) Nutrition of Plantation Forests. Academic Press, London. 516 p

Canadell J, Rodà F (1991) Root biomass of *Quercus ilex* in a montane Mediterranean forest. Can J For Res 21:1771-1778

Diego MV, Rodà (1992) Litterfall responses to increased availability of water, nitrogen and phosphorus in a holm oak forest. In: Teller A, Mathy P, Jeffers JNR (eds). Responses of Forests Ecosystems to Environmental Changes. Elservier. London. pp 673-674

Domíngez A (1984) Tratado de fertilización. Mundi Prensa. Madrid 585 p

Escarré A, Ferrés Ll, López R, Martin J, Rodà F, Terradas J (1987) Nutrient use strategy by evergreen-oak (*Quercus ilex* ssp *ilex*) in NE Spain. In Tenhunen *et al.* (eds) Plant Responses to stress. Functional Analysis in Mediterranean Ecosystems. Nato ASI Ser. Vol. G15. Springer Verlag. Berlin

Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78: 9-19

Ferrés L (1984) Biomasa, producción y mineralomasas del encinar montano de La Castanya (Montseny). Tesis doctoral. Universidad Autònoma de Barcelona

Field Ch, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In ThJ Givnish (Ed). On the economy of plant form and function. Cambridge University Press. pp: 25-55

Fife DN, Nambiar EKS (1984) Movement of nutrients in radiata pine needles in relation to the growth of shoots. Ann Bot (London), 54: 303-314

Gros A (1986) Abonos -Guía práctica de la fertilización. 7ª Ed. Mundi Prensa Madrid. 560 p

Gholz HL, Ewel KC, Teskey RO (1990) Water and forest productivity. For Ecol and Manage 30: 1-18

Hopmans P, Stewart HTL, Flinn DW, Hillman TJ (1990) Growth, biomass production and nutrient accumulation by seven tree species irrigated with municipal effluent and Wodonga, Australia. For Ecol Manage 30: 203-211

Lang ARG (1991) Application of some of Cauchy's theorems to stimation of surface areas of leaves, needles and branches of plants, and light transmittance. Agric For Meteorol 55:191-212

Lang ARG, Xiang-Yueqin (1986) Estimation of leaf area index from transmission of direct sunlight in discontinuous canopies. Agric For Meteorol 37:229-243

Lledó MJ (1990) Compartimentos y flujos biogeoquímicos en una cuenca de encinar del Monte Poblet. Ph D. Thesis. Univ. Alacant. Alacant

Marschner H (1986) Mineral Nutrition of Higher Plants. Academic Press. London. 674 pp

Mateo MA, Sabaté S, (in press) Vegetal tissue wet digestion using a domestic microwave oven. Analytica Chimica Acta 00:000-000

Mayor X (1990) El paper dels nutrients com a factors limitants de la producció primària de l'alzinar de la conca del Torrent de la Mina (Montseny). Master dissertation. Autonomous University of Barcelona

Mayor X, Rodà F (1992) Is primary production in holm oak forests nutrient limited?: A correlational approach. Vegetatio 99-100:209-217

Mayor X, Rodà F (in press) Effects of irrigation and fertilization on stem diameter growth in mediterranean holm oak forest. For Ecol and Manage 00:000-000

McGrath JF, McArthur SL, (1990) Influence of Fertilizer Timing on Seasonal Nutrient Uptake and Dry-Matter Production by Young *Pinus radiata* in Southern Western Australia. For Ecol and Manage 30:259-269

McMurtrie RE, Benson ML, Linder S, Running SW, Talsma T, Crane WJB, Myers BJ (1990). Water/nutrient interactions affecting the productivity of stands of *Pinus radiata*. For Ecol Manage 30: 415-423

Miller HG (1981) Forest fertilization: some guiding concepts. Forestry 54: 157-167

Miller HG (1984) Dynamics of nutrient cycling in plantation ecosystems. In: GD Bowen, EKS Nambiar (eds). Nutrition of forest trees in plantations. Academic press. London, pp 53-78

Miller HG (1986) Carbon X nutrient interactions -the limits to productivity. Tree Physiol 2:373-385

Nambiar EKS, Fife DN (1987) Growth and nutrient retranslocation in needles of radiata pine in relation to nitrogen supply. Ann Bot. (London) 60:147-156

Piñol J (1990) Hidrologia i biogeoquímica de conques forestades de les Muntanyes de Prades. PhD Thesis. Univ. Barcelona

Raison RJ, Myers BJ (1992) The Biology of Forest Growth experiment: linking water and nitrogen availability to the growth of *Pinus radiata*. For Ecol and Manage 52:279-308

Raison RJ, Myers BJ, Benson ML (1992a) Dynamics of *Pinus radiata* foliage in relation to water and nitrogen stress: I. Needle production and properties. For Ecol and Manage 52: 139-158

Raison RJ, Khanna PK, Benson ML, Myers BJ, McMurtrie RE, Lang ARG (1992b) Dynamics of

Pinus radiata foliage in relation to water and nitrogen stress: II Needle loss and temporal changes in total foliage mass. For Ecol and Manage 52:159-178

SAS (1988) SAS/STAT User's Guide. SAS Institute Inc. Cary, NC. USA

Sabaté S (unpublished manuscript, 1993) Nutrient content in *Quercus ilex* canopies: Seasonal and Spatial variation within a cachtment. (see chapter 3)

Schoettle AW, Smith WK (1991) Interrelation between shoot characteristics and solar irradiance in the crown of *Pinus contorta* ssp. *latifolia*. Tree Physiology 9: 245-254

Snowdon P, Benson ML (1992) Effects of combinations of irrigation and fertilisation on the growth and above-ground biomass production of *Pinus radiata*. For Ecol and Manage 52:87-116

Specht RL, Specht A (1989) Canopy structure in *Eucaliptus*-dominated communities in Australia along climatic gradients. Acta Oecologica. Oecol Plant 10(2):191-213

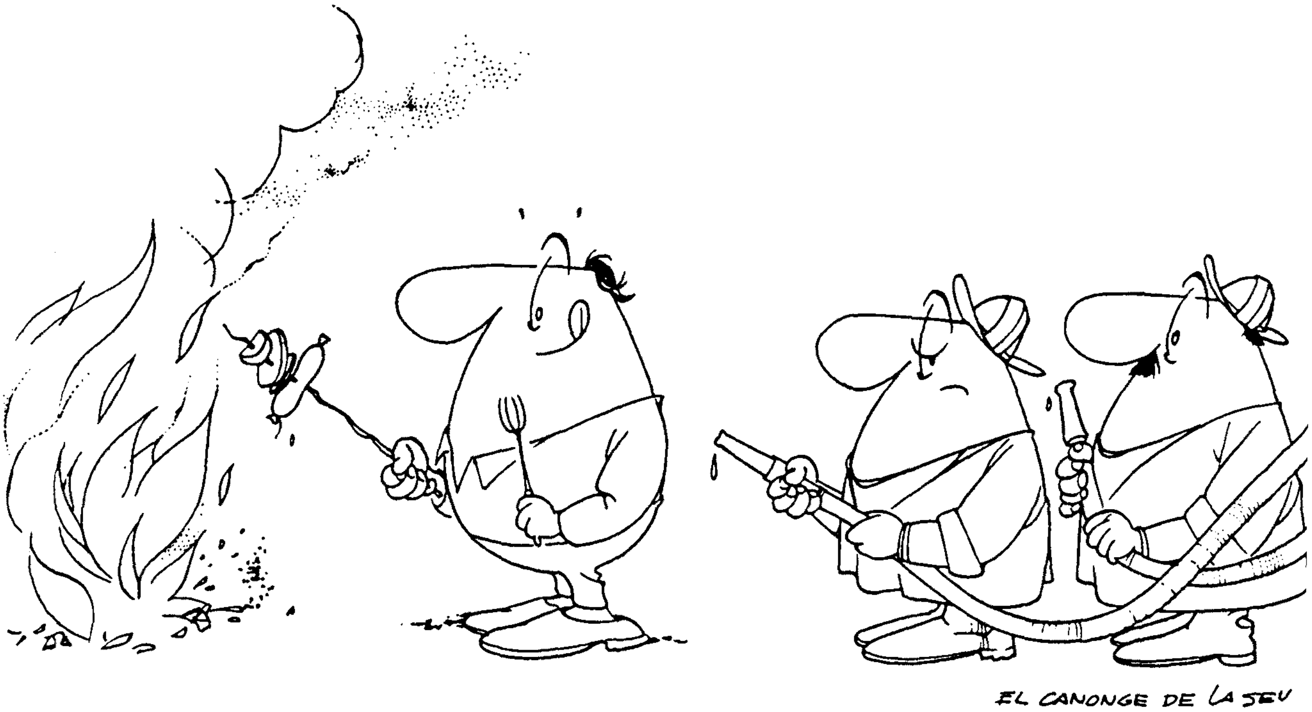
Urbano P (1989) Tratado de fitotecnia general. Mundi Prensa. Madrid 836 p

Van den Driesche R (1984) Nutrient storage, retranslocation and relationship of stress of nutrition. In: GD Bowen and EKS Nambiar (eds). Nutrition of forest trees in plantations. Academic Press. London, pp. 181-209

5. Resposta de l'alzina al foc i a la tallada arreu

5.1. Estructura de les capçades dels rebrots d'alzina:

Effects of clearcutting and fire on Quercus ilex L. I. Canopy structural characteristics of coppice regrowth


EL CANONGE DE LA SEU

5.1.1. Summary

Holm oak (*Quercus ilex*) possesses adaptative traits to survive or easily regenerate after disturbance. In order to compare the short-term effects of forest fire and clearcutting on a holm-oak forest, a disturbance experiment was designed. The study was carried out at the Prades Experimental Complex of Catchments. This holm-oak forest was managed until 1950's as a source of charcoal resulting in a multistemmed structure in the above ground biomass. In August 1988 two 40mx20m contiguous plots were clearcut. The logs and branches greater than 2 cm in diameter were removed but the slash was homogeneously distributed on the plots. In order to burn the slash a firebreak was established around one plot where all the aboveground biomass was removed. The plot was burned in October 1988. This study analyses how *Quercus ilex* responds by reconstructing its canopy structure after (1) burning, (2) clearcutting and leaving the slash and (3) clearcutting removing the slash (firebreak area). The structural characteristics of the coppice regrowth were compared with the undisturbed forest. Leaves and stems from different axis position were separated quantifying stem basal diameter, leaf and stem biomass (g), mean leaf and stem weight (mg), specific leaf weight (mg/cm^2), mean leaf area (cm^2), stem weight per unit length (mg/cm) and mean stem length (cm). *Quercus ilex* had a vigorous coppice regrowth in each treatment. Large leaves (mean weight and area) on the main axis resprouts were produced, followed by the second, and the third axis. The largest stem elongation took place during the first year. The fourth and fifth axis growth appeared mainly during the second year and they tended to show similar leaf and stem structural characteristics than those showed by leaves and stems from the undisturbed forest. The slash presence affected the initial pattern of canopy development, lowering lateral biomass expansion and the initial *specific leaf weight*. The firebreak area (without slash) affected holm oak regrowth taken place a lower production, as indicated the lower *leaf area/basal area* and the lower *weight/length* of the main axis growth, on this plot.

5.1.2. Introduction

Most species growing in ecosystems where disturbances are common, such as Mediterranean-type ecosystems, possess adaptative traits that allow them to survive or easily regenerate after disturbance (Dell et al. 1986, Terradas 1987). Fire, as a disturbance, has been received considerable attention (see, e.g. Hanes 1971, Kozlowski and Ahlgren 1974, Naveh 1975, Keeley and Zedler 1978, Gill et al. 1981, Wright and Bailey 1982, Trabaud 1987). This is understandable because forest fires are among the most important desertification factors in the mediterranean area (Klein & Perkins, 1990). But in addition, coppicing for firewood or charcoal production has been practised in the woodlands of the Mediterranean basin for a long time. Both disturbances kill the aboveground parts of trees and shrubs which can then develop massive root crowns (lignotubers or burls). Holm-oak forests are a good example (Canadell and Rodà 1991). In the California chaparral Rundel et al. (1987) suggest that a large root system reduces root crown mortality because it can buffer the disturbance effects by having more carbohydrate storage and therefore resprout capacity.

The importance of resprouting capacity is a general characteristic of *Quercus* species and several studies have been carried out specially about fire responses of *Quercus coccifera* in the mediterranean basin (Trabaud and Lepart 1980, Trabaud and Lepart 1981, Malanson and Trabaud 1987, Malanson and Trabaud 1988, Sala et al. 1987). Rundel et al. (1987) compared cutting and different burning intensities on the root crown mortality of *Adenostoma fasciculatum* in the California chaparral. They also compared the seasonal effect of fire and found a lower mortality following autumn disturbances.

In spite of the fact that *Q. ilex* (holm oak) has been managed for firewood and charcoal production and is sometimes subjected to forest fires, there is little information available on short-term disturbances effects on soil characteristics and its resprouting capacity where fire and clearcut disturbances are compared.

Rapp et al. (1992) found a quick recovery after the clearcut of a *Q. ilex* L. coppice. They concluded that the clearcut produced a reactivation of the stand potential and that leaves produced on a clearcut site and on a mature site tended to be similar in weight and structure during the second year after disturbance. Nevertheless, wood production was greater in the young stand because, based on the same quantity of foliage, less proportion of photosynthetic potential is required for the maintenance of the system (see also Leonardi et al. 1992). Ferran and Vallejo (1992) studied the reconstitution of soil litter dynamics after fire in *Q. ilex* forests. The high initial holm oak productivity after fire explained that after 4 years the litterfall per unit of canopy area was similar to that of mature trees. Those studies indicated a quick recovery of holm oak canopy structure after fire and clearcut.

In order to study the short-term effects of forest fire and clearcutting a disturbance experiment was designed on a holm-oak forest. The aim of this study was to analyze how *Quercus ilex* individuals (root crowns) responded by reconstructing their canopy structures after (1) burning, (2) clearcutting leaving the slash and (3) clearcutting removing the slash (firebreak area) and to compare the structure of the coppice regrowth to that of the undisturbed forest.

How canopy regrowth is established is important to understand the relative quick recovery of resprouters after different disturbances. The unbalanced above:underground biomass ratio affects the propierties of the new canopy components and growth patterns. In addition, these three different situations could act differently since the amount and characteristics of nutrients and organic matter remaining on site are different. There are also practical questions about these three situations. Forest managers usually leave the slash on site after clearcutting, but this increases the fire risk during the dry mediterranean summers. The alternative is to remove all material but with increasing costs, nutrient site impoverishment and erosion danger. Finally, fire can cause nutrient losses and soil erosion, but also a thermal impact on individuals. In addition to our study, other researchers were studying effects on soil properties, soil erosion, photosynthesis and transpiration (Serrasolsas et al. 1991, Fleck et al. 1993).

5.1.3. Study area and methods

Study site

The study was carried out in a holm-oak forest at the Prades Experimental Complex of Catchments (NE Spain). The experimental plots are located on a steep slope (28°) oriented SSE (41° 21' N, 1° 01' E, 920 m elevation). Riudabella is a meteorological station close to the study site (600 m altitude and about 3 km distant) where the mean annual temperature was 13.8°C and the average annual precipitation was 647 mm in the 1957-1990 period. The climatic conditions are typically mesomediterranean, with hot and dry summers, fresh and wet springs and autumns, and mild as well as fairly dry winters. The main rock type in the area is schist and the soils are Lithic and Typic Xerochrepts (USDA Soil Taxonomy, 1975) (Serrasolsas et al. 1991).

The forest is a holm-oak coppice that was managed until the 1950's as a source of charcoal, resulting in a multistemmed structure in the aboveground biomass (now about 40 years old and 6 m height) and an older root system of unknown age. The stand density measured on a plot at the site was 18000 stems/ha or 2571 multistemmed crowns/ha (these measurements considered all stems wider than 2 cm in diameter at 50 cm from the ground). The aboveground biomass was 101.1 Mg/ha (79.8 Mg of trunk > 5cm in diameter, 14.5 Mg/ha of branches < 5 cm in diameter and 6.8 Mg/ha of leaves). These values were estimated by the allometric relationships obtained for holm oak at Prades and the stem diameter (unpublished data and Lledó 1990).

The disturbance experiment

In August 1988 two 40mx20m contiguous plots were clearcut. The logs and branches greater than 2 cm in diameter were removed but the slash was homogeneously distributed on the plots giving a slash depth of about 0.5 m height. In order to burn the slash a firebreak area (about 7 m wide) was established around one plot. This plot was burned in October 1988. The meteorological conditions during the fire were recorded by Serrasolsas et al. (1991). Serrasolsas et al. (1991) estimated that the burnt dry matter was at about 10.4 Mg/ha of leaves and 76.8 Mg/ha of branches while on the remaining clearcut plot there were 7.2 Mg/ha of leaves and 52.7 Mg/ha of branches. The difference was due to dry matter being removed to form the firebreak, and being added to the burnt plot. Temperatures measured in L and F horizons were homogeneously greater than 400°C during burning. The maximum temperatures reached were 750°C on the forest floor, 370°C under the forest floor, 240°C at 2.5 cm soil depth and 60°C at 7.5 cm depth. Fire speed was irregular with about 2.3 cm/s and a front advance power of 9350 cal/cm/s (Serrasolsas et al. 1991,1992). To compare the resprouts structural characteristics with the undisturbed *Q. ilex* trees, three replicate control plots (8mx8m) were available in a contiguous area. After disturbance we studied three different initial environments for *Q. ilex* regrowth: (1) burned plot, (2) clearcut plot and (3) firebreak plot.

Sampling procedure and measurements

Experimental plots could not be replicated due to massive labour needed for the treatments nad the large impact of the applied disturbances in a protected natural area. However, the initial characteristics of the adjacent plots were homogeneous enough to provide suitable conditions for comparing the effect of the different disturbance treatments on canopy regrowth at the individual level. In each of the three experimental plots, three different root crowns were randomly selected at each collection date and several dominant coppice shoots were collected from each root crown. Samples were collected in late spring 1989 (sp89), summer 1989 (sm89), late autumn 1989 (au89), spring 1990 (sp90) and summer 1990 (sm90). Dominant coppice shoots were selected as representative of the possible future dominant stems. Three dominant branches were also collected from different root crowns of the three control plots.

The samples were taken to the laboratory and separated into leaves and stems for different axis growth positions. Leaves-1 and Stems-1 for the main axis, Leaves-2 and Stems-2 for second order axis, Leaves-3 and Stems-3 for third order axis, etc. Since on each axis was too difficult to separate fractions (leaves and stems) produced in different growth flushes, only immature shoots, where leaves had not been clearly expanded, were considered separadly. These shoots were only taken account to the whole resprouts relations (total leaf area or biomass). Control samples were separated into leaves and stems of different ages.

The following variables were quantified: stem basal diameter, leaf and stem biomass (g), mean leaf and stem weight (mg), specific leaf weight (SLW) (mg/cm^2), mean leaf area (cm^2), stem weight per unit length (mg/cm) and mean stem length (cm). To obtain measurements of dry mass the samples were oven-dried at 70°C for 48 h. Specific leaf weight was estimated from more than 60 discs (0.60 cm in diameter) obtained from each leaf class samples. Leaf areas were stimated for each sample dividing its leaf weights by its specific leaf weights.

Statistical analysis

Data were analysed using the SAS GLM procedure (SAS 1988) for a complete two-factor factorial model with disturbance treatment (PLOT) and sampling date (DATE) as the main effects. Comparisons of dependent variables among control and disturbed plots were made for each disturbed plot in summer of 1990 with leaves or stem origin as the main factor. Multiple comparisons among means were made using Least Significant Difference if the ANOVA F test revealed significant differences. Where dependent variables were log-transformed prior to statistical analysis this is indicated in the text.

5.1.4. Results and discussion

Whole resprout relations

Figure 5.1.1 shows the different relationships between measurements on the coppice regrowth: leaf area/basal area, leaf/stem biomass, Leaves-1/other leaves biomass and Stems-1/other stems biomass. In each case the statistical analysis was performed on log-transformed variables. These variables changed significantly over time ($P<0.001$). The leaf area/basal area ratio tended to be higher with time. This is in agreement with a faster expansion of the leaf area than stem basal area after disturbance. The firebreak plot did not increase this parameter as quickly as burned and clearcut plots ($P<0.001$), probably reflecting worse regeneration conditions.

The leaf/stem biomass ratio was initially higher than 1.5 on the burned and firebreak plot. This declined to between 0.5-0.7 when the canopy structural support (mainly Stems-1) had developed. A steady decline of Leaves-1/other leaves for all treatments took place as lateral canopy increased. The proportion of Leaves-1/other leaves, as well as Stems-1/other stems was initially higher for the clearcut plot, reflecting a lower lateral growth ($P<0.05$, and $P<0.01$ respectively). This then decreased to give similar values to the other plots. These results suggest that the slash changed the light extinction pattern and so modified the initial canopy development pattern in relation to burned and firebreak treatments.

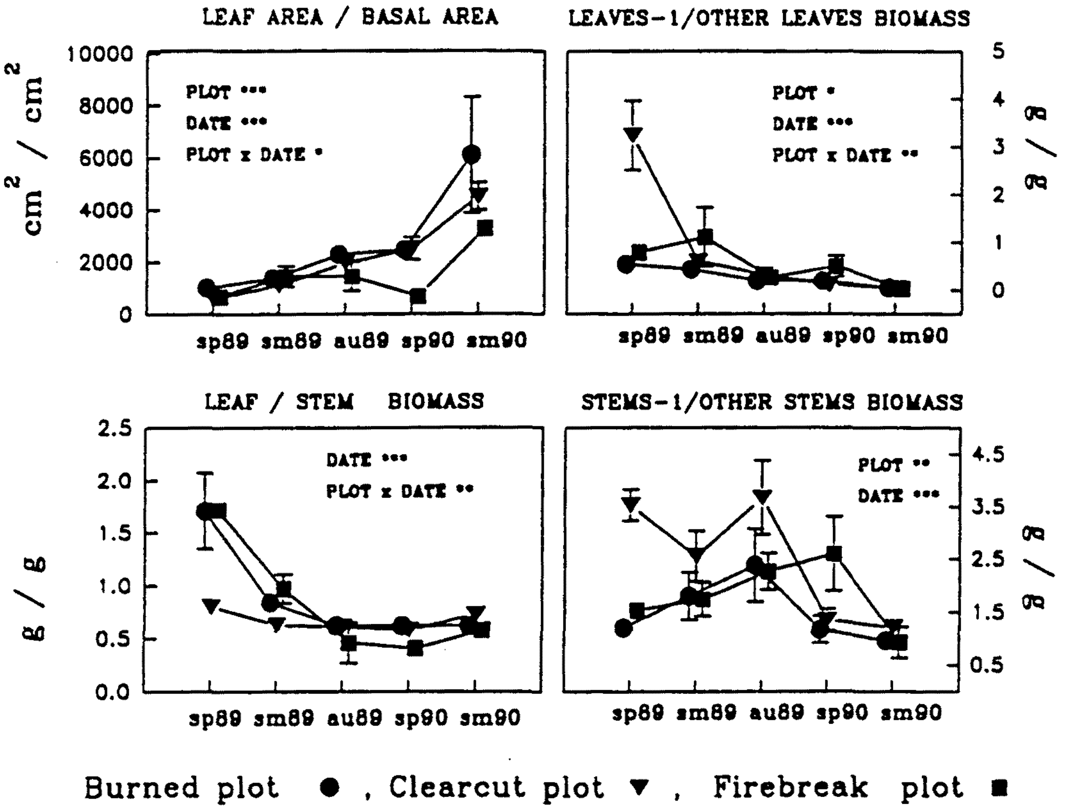


Figure 5.1.1. Seasonal pattern of different structural ratios on the whole resprout canopy basis (Leaf Area/Basal Area, *Leaf/Stems Biomass*, *Leaves-1/other leaves Biomass* and *Stems-1/other stems Biomass*). ANOVA after logarithmic transformation of variables. Significant differences between plots, samplig dates or interaction indicated by *, ** and *** at $P<0.05$, $P<0.01$ and $P<0.001$ respectively. Values are means ± SE, n=3 root crowns. SE is not shown if smaller than symbol. (sp=spring, sm=summer, au=autumn, Leaves and Stems -1 are from the main axis).

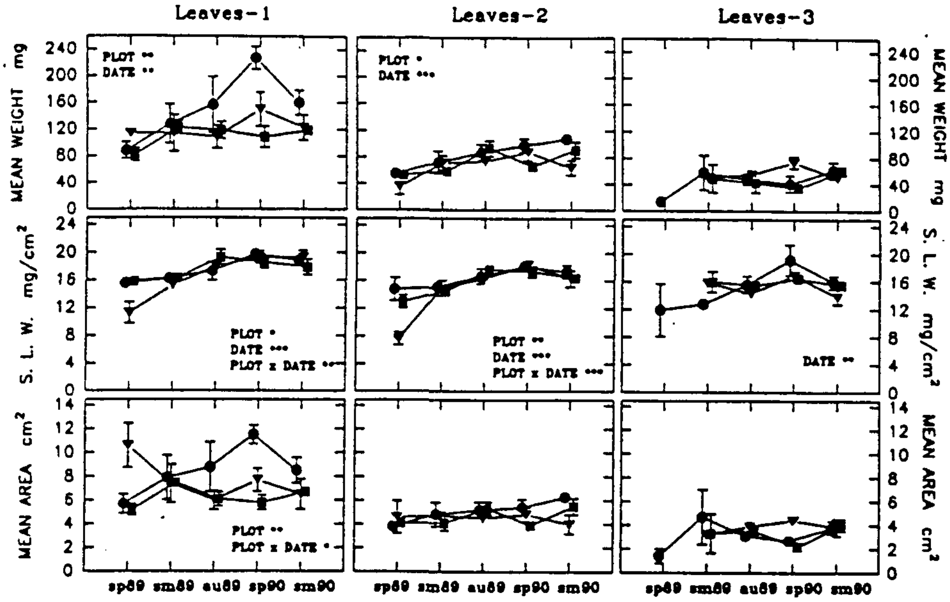


Figure 5.1.2. Seasonal pattern of *mean weight, specific leaf weight* and *mean area* for Leaves-1, -2 and -3. Significant differences between plots, sampling dates or interaction indicated as in Figure 5.1.1. Values are means ± SE, n=3 (root crowns). For Leaves-3 n=2 in sp89 and sm89 on the burned plot, n=1 in sm89 and au89 in the clearcut plot, and n=2 in sp89 and sm90. SE is not shown if smaller than symbol. (symbols as Figure 5.1.1).

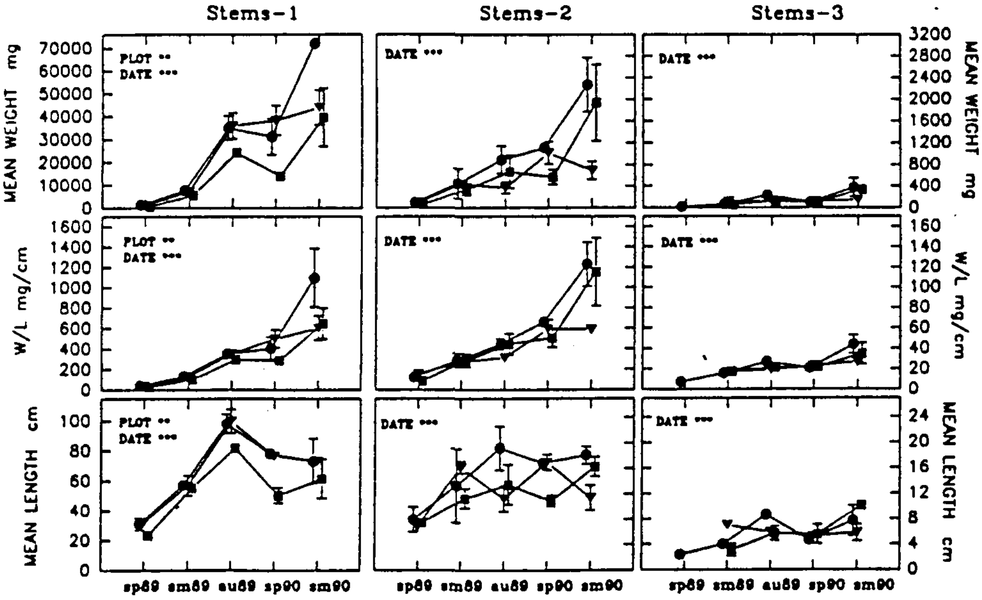


Figure 5.1.3. Seasonal pattern of *mean weight, weight/length* and *mean length* for Stems-1, -2 and -3. ANOVA after logarithmic transformation of variables. Significant differences between plots, sampling dates or interaction indicated as in Figure 5.1.1. Data are means ± SE, n=3 (three root crowns). For Stems-3 n=2 in sp89 and sm89 in the burned plot, n=1 in sm89 and au89 on the clearcut plot, and n=2 in sp89 and sm90 on firebreak plot. SE is not shown if smaller than symbol. Stems-1 represented on a larger scale than Stems-2 and -3. (Symbols as Figure 5.1.1).

Leaves and stems structural characteristics

The structural characteristics of leaves are shown in Figure 5.1.2 (Leaves-1,-2, and -3) and Table 5.1 (Leaves-4 and -5). The mean weight and area were larger in leaves-1 than the others. When new axes appeared, the leaf size on these new axes were smaller. These results are in agreement with Rapp et al. (1992) after clearcutting *Q. ilex* forest, as well as with results for *Q. coccifera* after fire (Sala et al. 1987). Both studies showed larger leaves during the initial regeneration. On the other hand Malanson and Trabaud (1987) found that the average size of *Q. coccifera* leaves in the lower canopy was larger than those of the upper canopy on 9 and 33 years-old burned plots. This should be compatible with our results as the new axis appeared mainly on the upper canopy layers.

The mean weight of Leaves-1 and -2 tended to increase with time ($P<0.01$ and $P<0.001$ respectively) and Leaves-1 from burned plot were significantly larger (higher mean weight and larger leaf area) than Leaves-1 in clearcut and firebreak plots ($P<0.01$) except for the two initial sampling dates (sp89 and sm89). In sp89 Leaves-1 from clearcut plot were larger (higher mean weight and larger leaf area) than the others (Figure 5.1.2). This may be explained by the same reason considered above with an initial inhibition of lateral growth on the clearcut plot and increased carbon allocation in leaves of the first axis. The lower specific leaf weight in the clearcut plot for Leaves-1 and -2 could be due to the slash presence which reduced radiation. In addition, this explain the initial larger leaf area for Leaves-1. The values then increased to reach the same as the other treatments and then stabilised from (au89) ($P<0.001$).

Figure 5.1.3 shows the structural characteristics of Stems-1, -2 and 3, and Table 5.1.2 for Stems-4 and -5. The statistical analysis for stems structural characteristics were performed on log-transformed variables. All of these variables showed differences with time ($P<0.001$). A general increase of mean weight as well as weight/length reflecting growth was a common trait for all the stems measured. Growth was mainly allocated to Stems-1, followed by Stems-2, -3, -4 and -5 according to their structural position. Leaves and stems on the fourth and fifth axes were developed mainly in summer 1990 (Table 5.1.1 and 5.2.2). However on the clearcut plot one stump at each sampling date had already developed a fourth axis. This seems paradoxical given the lower initial lateral canopy development argued for the clearcut plot above.

Although the fourth axis appeared in summer 1989 in the clearcut plot, the lateral development was not quantitatively important (Figure 5.1.1) (higher initial relation Stems-1/other stems biomass). If a general lateral development was initially inhibited, probably the same reason stimulated axis differentiation on a few stems, where more carbon allocation took place from the available reserves in the root system. That agrees with Borchert (1975) who pointed out that the maximum initial growth reflects the available reserves of carbohydrates stored in the root system (see also Rundel et al. 1987).

Some differences were found for Stems-1 between plots (Figure 5.1.3). The firebreak plot had a significantly lower growth than burned and clearcut plots. This is compatible with the lower leaf area/basal area (Figure 5.1.1). Nevertheless, at the last sampling (sm90), the firebreak plot approached similar values to that of the clearcut plot. The pattern of mean stem length (Figure 5.1.3) shows a different trend from the other variables. Stems-1 reached a maximun of about 1 m in au89, significantly different to the values measured in sm89, sp90 and sm90 of about 60 to 80 cm. This could be probably explained by the fact that new, but shorter, dominant resprouts were collected from each stump after au89 so reducing the mean length values. Another explanation could be low winter temperatures, that would reduce length on the main axis although we have no evidence for this. Cold winters can kill a large fraction of *Q. ilex* leaves (Rapp et al. 1992), but in this study we found no damage to the top resprout segments collected in spring and summer 1990. The length growth of stems was greatest in the first year then decreased in the second year which is analogous to the trend in height growth shown by Giovannini et al. (1992).

Table 5.1.1. Mean weight, specific leaf weight and mean area for Leaves-4 and -5. Data are means ± SE, n=3 (three root crowns). SE=. when n=1. For Leaves-5 n=2 on the clearcut and firebreak plots. Differences were not significant. (sp=spring, sm=summer, au=autumn; first, second and third axes represented by -1, -2, and -3 respectively).

		Leaves-4				Leaves-5
	PLOT	sm89	au89	sp90	sm90	sm90
Mean Weight mg	Burned	-	23.0± .	-	63.0±14.3	33.7±5.2
	Clearcut	35.0± .	28.0± .	69.0± .	60.7±23.3	47.5±16.5
	Firebreak	-	-	-	48.3±13.4	41.5±1.5
S.L.W. mg/cm^2	Burned	-	-	-	17.8±2.4	16.7±1.9
	Clearcut	14.4± .	-	15.3± .	14.5±0.5	13.6±0.2
	Firebreak	-	-	-	16.6±1.0	16.0±0.6
Mean Area cm^2	Burned	-	-	-	3.5±0.6	2.2±0.6
	Clearcut	2.4± .	-	4.5± .	4.1±1.5	3.5±1.3
	Firebreak	-	-	-	3.0±1.0	2.6±0.0

Table 5.1.2. Mean weight, weight/length and mean length for Stems-4 and -5. Data are means ± SE, n=3 (root crowns). SE=. when n=1. For Leaves-5 n=2 on the clearcut and firebreak plots. Differences were not significant. (sp=spring, sm=summer, au=autumn; fourth and fifth axes represented by -4 and -5 respectively).

		Stems-4				Stems-5
	PLOT	sm89	au89	sp90	sm90	sm90
Mean Weight mg	Burned	-	58.0± .	-	149.7±46.2	70.7±17.6
	Clearcut	53.0± .	28.0± .	118.0± .	142.3±56.6	95.0±62.0
	Firebreak	-	-	-	116.0±44.3	72.0±1.0
W/L mg/cm	Burned	-	12.1± .	-	29.0±6.9	17.4±1.4
	Clearcut	13.5± .	13.6± .	26.6± .	15.8±1.7	13.8±4.5
	Firebreak	-	-	-	18.5±4.2	15.1±1.0
Mean Length cm	Burned	-	4.7± .	-	5.2±1.1	4.0±1.0
	Clearcut	3.9± .	2.0± .	4.4± .	8.4±2.9	6.1±2.5
	Firebreak	-	-	-	5.8±1.8	4.8±0.3

Strucrure of coppice regrowth compared to that of the undisturbed forest

Table 5.1.3 shows the structural characteristics of leaves and stems measured in the undisturbed forest in summer 1990. The comparisons between the mean weight and mean area of leaves collected in summer 1990 from different axes on the treated plots and from the undisturbed forest are summarized for each plot in Table 5.1.4. Analogous comparisons between the mean stem length and weight (performed on log-transformed variables) are shown in Table 5.1.5.

The mean weight and area, of leaves produced in spring 1989 were lower than for those produced in spring 1988 and 1990 (Table 5.1.3). This was probably because of the relatively dry period between summer 1988 and autumn 1989 (Sabaté et al. 1992). In spite of this dry period, the disturbed area regenerated vigorously particularly the first and the second axis. The third, fourth and fifth axes were more similar to the control plots (Table 5.1.4). The stems on the control plots showed a similar pattern to the leaves, with a lower production in 1989. The stem differences were stronger as compare stems from different axes and control plots than those showed as compare leaves (Table 5.1.4 and 5.1.5).

The structural differentiation patterns as compare the different axes and the control plots is different for each disturbance treatment. For example, the mean weight and area of leaves in the burned plot showed the greatest differences between different axes and from control plots (Table 5.1.4). The firebreak plot followed a similar pattern, but there were few significant differences between the control and clearcut plot. The main differences observed with the clearcut plot were in relation to the main axis. This was probably because on the clearcut plot production was concentrated on the main axis in the initial stages of regeneration , with lateral canopy expansion ocurring later. After these initial steps the imbalance between root/shoot biomass (higher water availability for leaves) probably diminished. This imbalance during the first year was found in *Adenostoma fasciculatum* from the California chaparral by Rundel et al. (1987) and is in agreement with the results obtained by Rapp et al. (1992) on *Q. ilex*, as well as for our results. Fleck et al. (1989) found higher transpiration and photosynthesis during the first year after fire on *Arbutus unedo* and *Coriaria myrtifolia* resprouts than on undisturbed individuals, as also obtained by Castell (1992) on *Q. ilex* and *A. unedo* after cutting. Fleck et al. (1993) found, at our experiment during the second year (1990), higher values of photosynthesis, transpiration and leaf conductance on burned and clearcut plots than on undisturbed plots. A root/shoot equilibrium had still probably not been reached by the second year, although differences in structural characteristics between disturbed and control plots were narrowing.

There were greater differences between stems for control and disturbed plots (Table 5.1.5). On the other hand, there were fewer differences between disturbances. The plant biomass measured by Serrasolsas et al. (1991) in July of

1989, on the clearcut and the burned plots, showed a similar total biomass (1.32, 0.72 and 0.84 Mg/ha of *Q.ilex*, shrubs and herbs respectively on the burned plot against 1.74, 0.86 and 0.52 Mg/ha on the clearcut plot). We do not have the same measurements for summer 1990; however the plots appeared similar. Studies in macchia after coppicing (Giovannini et al. 1992), dominated by *Q. ilex*, *Phyllirea latifolia* and *Fraxinus ornus*, showed that during the first three years after cutting, the stool mortality was very low and the horizontal reoccupation by shoots was very rapid, reaching 95% of the available space.

Rundel et al. (1987) suggest that differential carbohydrate storage is the key factor in limiting postfire resprout growth (see also Borchert 1975). In spite of some differences between treatments our holm oak forest (about 40 years old) regenerated vigorously. We did not find any dead root crowns. Thus, the space re-occupation was mainly due to vegetative re-coverage. However, between resprouted root crowns in the burned plot *Cistus albidus* seedlings were also observed.

The autumn fire probably favoured the availability of carbohydrate reserves (Rundel et al. 1987) and a dry period after treatments in 1989 meant there was no substantial soil erosion, when soil remained uncovered by plants during the first regeneration steps. So factors which might have given large treatment differences were not present in this study. Even during the 1989 dry period, the large functional root crown system, which is relatively important in this kind of forest (Canadell and Rodà 1991), probably permited the vigorous resprouts growth for all treatments.

In spite of the structural convergence between treatments during the study, it is important to note that two years is a short time to predict future differences. Other aspects such as nutrient use have to be considered. Christensen (1987) compared burned and clipped shrub bog communities for four years. Initially he found no differences between treatments, but during the second year growth was higher in the burned plot. However during the fourth and fifth years growth of the clipped plot increased resulting in higher values of leaf area index and aboveground biomass. Christensen pointed out that the decreased growth in the burned plot could reflect the loss of nutrient capital with burning. So initial structural similarities or differences could change over time, and the initial conditions of nutrient use could influence future canopy developments. These aspects are considered in a second part of this study (Sabaté and Gracia unpublished manuscript, see chapter 5.2).

Table 5.1.3. Leaves and stems structural characteristics measured on the control plot. Leaves and stems produced in spring 88,89 and 90. Samples collected in summer 1990. Data are means ± SE, n=9. (S.L.W.= specific leaf weight, W/L = stem weight/length).

	CONTROL SAMPLED IN SUMMER 1990 (sm90)		
	Leaves-88	Leaves-89	Leaves-90
Mean Weight mg	63.0±6.7	16.1±1.9	46.6±4.7
S.L.W. mg/cm^2	18.2±0.2	17.0±1.0	17.3±0.6
Mean Area cm^2	3.4±0.2	1.2±0.1	2.7±0.3
	Stems-88	Stems-89	Stems-90
Mean Weight mg	66.1±21.2	29.5±3.0	26.2±2.3
W/L mg/cm	19.8±1.5	17.8±1.6	17.0±2.0
Mean Length cm	3.3±0.1	1.7±0.1	1.6±0.2

Captions of Tables 5.1.4 and 5.1.5

Table 5.1.4. Multiple comparisons of mean leaf area (above diagonal matrix) and weight (below diagonal matrix) for leaves from different axes and control plots (produced in spring 88, 89 and 90) to each disturbance treatment. Values from summer 1990. ANOVA probability in parenthesis. Significant differences between mean values indicated by n.s. (no significant), *, ** and *** at $P<0.05$, $P<0.01$ and $P<0.001$ respectively (LSD test).

Table 5.1.5. Multiple comparisons of mean stem length (above diagonal matrix) and weight (below diagonal matrix) for stems from different axes and control plots (produced in spring 88, 89 and 90) to each disturbance treatment. Values from summer 1990. ANOVA probability in parenthesis. Significant differences as in Table 5.1.4.

Table 5.1.4.

MEAN AREA (P<0.0001)

	BURNED PLOT					CONTROL PLOT		
SAMPLING DATE sm90	Leaves-1	Leaves-2	Leaves-3	Leaves-4	Leaves-5	Leaves-88	Leaves-89	Leaves-90
Leaves-1	——	*	***	***	***	***	***	***
Leaves-2	**	——	**	**	***	***	***	***
Leaves-3	***	**	——	n.s.	n.s.	n.s.	**	n.s.
Leaves-4	***	**	n.s.	——	n.s.	n.s.	*	n.s.
Leaves-5	***	***	n.s.	n.s.	——	n.s.	n.s.	n.s.
Leaves-88	***	**	n.s.	n.s.	*	——	**	n.s.
Leaves-89	***	***	**	**	*	***	——	n.s.
Leaves-90	***	***	n.s.	n.s.	*	n.s.	*	——

MEAN WEIGHT (P<0.0001)

MEAN AREA (P<0.0083)

	CLEARCUT PLOT					CONTROL PLOT		
SAMPLING DATE sm90	Leaves-1	Leaves-2	Leaves-3	Leaves-4	Leaves-5	Leaves-88	Leaves-89	Leaves-90
Leaves-1	——	*	*	*	*	**	***	***
Leaves-2	**	——	n.s.	n.s.	n.s.	n.s.	*	n.s.
Leaves-3	***	n.s.	——	n.s.	n.s.	n.s.	*	n.s.
Leaves-4	**	n.s.	n.s.	——	n.s.	n.s.	*	n.s.
Leaves-5	***	n.s.	n.s.	n.s.	——	n.s.	n.s.	n.s.
Leaves-88	***	n.s.	n.s.	n.s.	n.s.	——	*	n.s.
Leaves-89	***	**	n.s.	*	n.s.	**	——	n.s.
Leaves-90	***	n.s.	n.s.	n.s.	n.s.	n.s.	*	——

MEAN WEIGHT (P<0.0002)

MEAN AREA (P<0.0001)

	FIREBREAK PLOT					CONTROL PLOT		
SAMPLING DATE sm90	Leaves-1	Leaves-2	Leaves-3	Leaves-4	Leaves-5	Leaves-88	Leaves-89	Leaves-90
Leaves-1	——	n.s.	**	**	**	**	**	**
Leaves-2	n.s.	——	n.s.	**	**	**	**	**
Leaves-3	***	*	——	n.s.	n.s.	n.s.	**	n.s.
Leaves-4	***	**	n.s.	——	n.s.	n.s.	*	n.s.
Leaves-5	***	**	n.s.	n.s.	——	n.s.	n.s.	n.s.
Leaves-88	***	*	n.s.	n.s.	n.s.	——	**	n.s.
Leaves-89	***	***	**	*	n.s.	***	——	n.s.
Leaves-90	***	***	n.s.	n.s.	n.s.	n.s.	*	——

MEAN WEIGHT (P<0.0001)

Table 5.1.5.

MEAN LENGTH (P<0.0001)

SAMPLING DATE sm90	BURNED PLOT					CONTROL PLOT		
	Stems-1	Stems-2	Stems-3	Stems-4	Stems-5	Stems-88	Stems-89	Stems-90
Stems-1	——	***	***	***	***	***	***	***
Stems-2	***	——	***	***	***	***	***	***
Stems-3	***	***	——	n.s.	*	***	***	***
Stems-4	***	***	*	——	n.s.	*	***	***
Stems-5	***	***	***	*	——	n.s.	*	**
Stems-88	***	***	***	*	n.s.	——	**	***
Stems-89	***	***	***	***	*	**	——	n.s.
Stems-90	***	***	***	***	*	***	n.s.	——

MEAN WEIGHT (P<0.0001)

MEAN LENGTH (P<0.0001)

SAMPLING DATE sm90	CLEARCUT PLOT					CONTROL PLOT		
	Stems-1	Stems-2	Stems-3	Stems-4	Stems-5	Stems-88	Stems-89	Stems-90
Stems-1	——	***	***	***	***	***	***	***
Stems-2	***	——	*	n.s.	*	***	***	***
Stems-3	***	***	——	n.s.	n.s.	*	***	***
Stems-4	***	***	n.s.	——	n.s.	**	***	***
Stems-5	***	***	n.s.	n.s.	——	n.s.	***	***
Stems-88	***	***	*	n.s.	n.s.	——	**	***
Stems-89	***	***	***	*	*	*	——	n.s.
Stems-90	***	***	***	*	*	***	n.s.	——

MEAN WEIGHT (P<0.0001)

MEAN LENGTH (P<0.0001)

SAMPLING DATE sm90	FIREBREAK PLOT					CONTROL PLOT		
	Stems-1	Stems-2	Stems-3	Stems-4	Stems-5	Stems-88	Stems-89	Stems-90
Stems-1	——	***	***	***	***	***	***	***
Stems-2	***	——	n.s.	***	***	***	***	***
Stems-3	***	***	——	**	**	***	***	***
Stems-4	***	***	**	——	n.s.	*	***	***
Stems-5	***	***	**	n.s.	——	n.s.	**	***
Stems-88	***	***	***	n.s.	n.s.	——	**	***
Stems-89	***	***	***	**	*	*	——	n.s.
Stems-90	***	***	***	***	**	***	n.s.	——

MEAN WEIGHT (P<0.0001)

5.1.5. Conclusions

Regeneration of *Q. ilex* occurred after each disturbance treatment but there were some differences.

The common traits were the development of big leaves and stem growth concentrated on the first axis. The new axes approached the characteristics of the undisturbed forest reaching it during the second year.

The presence of slash on the clearcut plot modified some initial canopy coppice characteristics compared with burned and firebreak plots. These differences basically involved less lateral canopy development as well as lower initial specific leaf weight. The firebreak plot development was slower as shown by a lower leaf area/basal area and a lower Stems-1 mean weight. Treatment differences lessened over the study period, however research over a longer time span may show further treatment differences.

In relation to structural characteristics, it seems that an auto-succession process took place for each treatment (see Hanes 1971, Floret et al. 1992), where resprouters played the main role (see Dell et al. 1986, Keeley and Zedler 1978). In our study, the disturbance characteristics and the structure of our forest before disturbance (multistemmed root crown systems) provided good conditions for regrowth.

5.1.6. References

Borchert R (1975) Endogenous shoot growth rhythms and intermediate shoot growth in oak. Physiol Plant 35:152-157

Canadell J, Rodà F (1991) Root biomass of *Quercus ilex* in a montane Mediterranean forest. Can J For Res 21:1771-1778

Castell C (1992) Ecofisiologia d'individus adults i rebrots de dues espècies esclerofil.les mediterrànies: *Arbutus unedo* i *Quercus ilex*. Ph D Thesis. Autonomous University of Barcelona.

Christensen NL (1987) The biogeochemical consequences of fire and their effects on the vegetation of coastal plain of Southeastern United States. In: The role of fire in Ecological Systems. SPB Academic Publishing. The Hague. The Netherlands. 1-21

Dell B, Hopkins AJM, Lamont BB (eds) (1986) Resilience in Mediterranean-Type Ecosystems. Dr Junk Publishers, Dordrecht

Ferran A, Vallejo R (1992). Litter dynamics in post-fire successional forests of *Quercus ilex* L. Vegetatio 99-100:239-246

Fleck I, Iñiguez FJ, Diaz C, Pascual M (1989) Effects of fire on photosynthesis and transpiration in a mediterranean ecosystem. In: Baltscheffsky M (ed) Current Research in Photosynthesis. Kluwer Academic Publishers. Stockholm. Vol IV.19:695-698

Fleck I, Sanjosé M, Grau D, Vidal D (1993) The effects of fire and tree-fell on photosynthesis in *Quercus ilex* resprouts. In: Murata N (ed) Research in Photosynthesis. Kluwer Ac Publi. Dordrecht

Floret C, Galan MJ, Le Floc'h E, Romane F (1992) Dynamics of holm oak (*Quercus ilex* L.) coppices after clearcutting in southern France. Flora and life cycles changes. Vegetatio 99-100:97-105

Gill AM, Groves RH, Noble IR (eds) (1981) Fire and Australian Biota. Aust Acad Sci, Canberra

Giovannini G, Perulli D, Piussi P, Salbitano F (1992) Ecology of vegetative regeneration after coppicing in *macchia* stands in central Italy. Vegetatio 99-100: 331-343

Hanes TL (1971) Succession after fire in the chaparral of southern California. Ecol Monogr 41:27-52

James S (1984) Lignotubers and burls-their structure, function and ecological significance in Mediterranean ecosystems. Bot Rev 50:225-266

Kozlowski TT, Ahlgren CE (eds) (1974) Fire and Ecosystems. Academic Press, New York

Keeley JE, Zedler PH (1978) Reproduction of chaparral shrubs after fire: a comparison of the sprouting and seeding strategies. Amer Midland Natur 99:142-161

Klein RM, Perkins TD (1988) Primary and secondary causes of contemporary forest declive. Botanical Review 54(1):1-43

LLedó MJ (1990) Compartimentos y flujos biogeoquímicos en una cuenca de encinar del Monte de Poblet. PhD Thesis University of Alicante

Leonardi S, Rapp M, Denes A (1992) Organic matter distribution and fluxes within a holm oak (*Quercus ilex* L.) stand in the Etna volcano. A synthesis. Vegetatio 99-100:219-224

Malanson GP, Trabaud L (1987) Post-fire development of canopy structure in mediterranean shrub, *Quercus coccifera* L. Physical Geography, 8 (3):266-274

Malanson GP, Trabaud L (1988) Vigour of post-fire resprouting by *Quercus coccifera* L. Journal of Ecology 76:351-365

Naveh Z (1975) The evolutionary significance of fire in the Mediterranean region. Vegetatio 29:199-208

Rapp M, Ed Derfoufi F, Blanchard A (1992) Productivity and nutrient uptake in a holm oak (*Quercus ilex* L.) stand during regeneration after clearcut. Vegetatio 99-100:263-272

Rundel PW, Baker GA, Parsons DJ, Stohlgren TJ (1987) Postfire demography of resprouting and seedling establishment by *Adenostoma fasciculatum* in the California chaparral. In: Tenhunen JD, Catarino FM, Lange OL, Oechel WC (eds) Plant Response to Stress. Functional Analysis in Mediterranean Ecosystems. NATO ASI series, Ecological Sciences, 15. Springer-Verlag, Berlin, pp 575-596

Sabaté S, Gracia CA (1993) Effects of clearcutting and fire on *Quercus ilex* L. of Prades Mountains (NE Spain): II. Nutrient Content and Resportion in the Regenerating Canopy. (unpublished manuscript, see chapter 5.2)

Sabaté S, Calvet S, Gracia CA (1992) Preliminary results of a fertilization-irrigation experiment in a *Quercus ilex* L. forest in relation to leaves and twigs characteristics. Vegetatio 99-100:238-287

Sala A, Sabaté S, Gracia CA (1987) Structure and organization of a *Quercus coccifera* garrigue after fire. Ecologia Mediterranea 13(4):99-110.

SAS (1988) SAS/STAT User's Guide. SAS Institute Inc. Cary, NC. USA

Serrasolsas I, Arias JJ, Vallejo VR, Alcañiz JM, Josa R, Solé A (1991) The effects of clearcutting and fire on the forest soils of Prades Mountains. E.E.C. Repport

Serrasolsas I, Alcañiz JM, Arias X, Josa R, Solé A, Vallejo VR (1992) The effects of burning and clearcutting in forest floor layers of holm oak forest. In: Teller A, Mathy P, Jeffers JNR (eds) Responses of Forest ecosystems to Environmental changes. Elsevier Applied Science. London

Terradas J (ed) (1987) Ecosistemes terretres. La resposta als incendis i a d'altres pertorbacions. Quaderns d'Ecologia Aplicada 10. Diputació de Barcelona. 201 p.

Trabaud L, Lepart J (1980) Diversity and stability in garrigue ecosystems after fire. Vegetatio 43:49-57

Trabaud L, Lepart J (1981) Changes in floristic composition of a *Quercus coccifera* L. garrigue in relation to different fire regimes. Vegetatio 46:105-116

Trabaud L (1987) Natural and prescribed fire: survival strategies of plants and equilibrium in mediterranean ecosystems. In: Tenhunen JD, Catarino FM, Lange OL, Oechel WC (eds) Plant Response to Stress. Functional Analysis in Mediterranean Ecosystems. NATO ASI series, Ecological Sciences, 15. Springer-Verlag, Berlin, pp 607-621

Wright HA, Bailey AW (1982) Fire Ecology. United States and Southern Canada. Wiley, New York