## 9. CONCLUSIONES Y DISCUSIÓN GENERALES

A continuación se exponen las principales conclusiones obtenidas en este estudio sobre los efectos del $SO_2$ y del $O_3$, independientemente y en mezcla, en plantones de *Pinus halepensis* cultivados en cámaras abiertas.

### 1.- Cámaras abiertas (OTC)

Se obtuvieron buenos resultados del mantenimiento de las concentraciones deseadas de contaminantes, cercanas a 20 ppb de $SO_2$ (promedio de 20 meses de tratamiento) y 1.3 veces la concentración ambiente de $O_3$ (promedio de 10 meses de tratamiento durante 8 horas diurnas). Las cámaras variaron el microclima respecto a las condiciones al aire libre, con una atenuación media de la radiación fotosintéticamente activa de un 26 % y una disminución media de la humedad relativa del aire del 11 %, siendo su principal problema un incremento de la temperatura media de 2.4 ºC. Esos factores determinaron efectos en la fisiología de la planta, con cambios en la alteración de la emisión de fluorescencia y en las tasas fotosintéticas cuando las plantas eran expuestas a plena luz, modificaciones de la concentración foliar de pigmentos, y una distribución preferente de biomasa hacia la parte aérea de las plantas. No se observaron efectos importantes en la concentración foliar de nutrientes. El conjunto de alteraciones sobre la fisiología impide una extrapolación directa a condiciones naturales, sin embargo el nivel de aproximación a éstas es superior que el de estudios de laboratorio, invernadero o cámaras de cultivo. Este hecho, junto con unos costes de instalación y mantenimiento mucho menores que los de los dispositivos de fumigación a cielo abierto (ZAPS, *Zonal-air Pollution Systems*) hacen de las cámaras OTC un sistema adecuado para el estudio de los efectos de contaminantes atmosféricos en vegetales.

### 2. Efectos del $SO_2$

Los resultados obtenidos pusieron de manifiesto que el $SO_2$, incluso a las concentraciones relativamente bajas empleadas en nuestra experimentación, causaron efectos en las plantas de *Pinus halepensis*. En efecto, el $SO_2$ produjo alteraciones en todos los aspectos estudiados.

Junto con el aumento de $S_{total}$, las acículas mostraron una acumulación de cationes por efecto del $SO_2$, indicando hipotéticamente la existencia de mecanismos de neutralización de las cargas negativas que acompañan a la acumulación de

sulfatos en la vacuola de las células del mesófilo. Los cationes que contribuyeron más notablemente al incremento de cationes fueron el $K^+$ y el $Ca^{2+}$, mientras que el $Mg^{2+}$ solamente estuvo significativamente implicado en el proceso de manera puntual. Las acículas más maduras (originadas en 1995) y las más jóvenes (originadas en 1997) pudieron sufrir más desequilibrios en el balance anio-catiónico que las de 1996. Este mecanismo de destoxificación del $SO_2$ puede tener repercusiones ecológicas en condiciones de agotamiento de la reserva de cationes intercambiables en el suelo, conduciendo a largo plazo a deficiencias en las plantas. Además, el proceso de acumulación de cationes en la vacuola puede considerarse como una pérdida neta de cationes en la planta para otras funciones como el crecimiento.

El tratamiento con $SO_2$ disminuyó la concentración de $N_{total}$ en las acículas más maduras (de 1995) mientras que en las de 1996 prácticamente no se observó ese efecto e, incluso, el $SO_2$ mostró una tendencia a aumentar su concentración sobre la base del área foliar. La diferente naturaleza de los efectos en función de la edad de las hojas sugiere una respuesta compensatoria al estrés provocado por el contaminante, mediante la redistribución de los recursos en la planta. La retranslocación del N pudo explicar al menos en parte la disminución de su concentración en las acículas más maduras, aunque el efecto pudo también indicar una influencia directa del $SO_2$ en el metabolismo del nitrógeno.

Los efectos del $SO_2$ sobre el contenido de pigmentos fotosintéticos no fueron patentes hasta el segundo año de experimentación y, en cualquier caso, resultaron cuantitativamente poco importantes. Se observó una disminución de la concentración de clorofila en las acículas más maduras y un aumento en las más jóvenes por efecto del $SO_2$, sugiriendo de nuevo mecanismos compensatorios de estimulación de la actividad de las hojas más jóvenes frente a las más maduras a través de la alteración de los patrones normales de distribución de recursos. La disminución de clorofila en las acículas más maduras del tratamiento con $SO_2$ no estuvo asociada a una disminución de la concentración de Mg, pero sí pudo estar relacionado con los fenómenos de retranslocación de N desde las acículas más viejas a las de menor edad aludidos anteriormente.

Los resultados de las medidas de emisión de fluorescencia indicaron un sorprendente aumento de la eficiencia fotoquímica del PSII en el tratamiento con $SO_2$, que no obstante no estuvo asociado a un incremento de la asimilación de $CO_2$

conjunto, los resultados apoyaron la hipótesis de un posible papel de productos intermediarios del metabolismo de destoxificación del $SO_2$ como protectores contra el daño producido por un exceso de energía luminosa, quizá conjuntamente con un sistema antioxidante de la hoja estimulado por el contaminante. Sin embargo, esta vía consumiría energía y poder reductor sin incremento de la fijación de $CO_2$.

Se produjeron reducciones de la tasa de asimilación diaria de $CO_2$ de hasta un 34 % ($p<0.05$) respecto al control por efecto del $SO_2$. Tal efecto estuvo asociado principalmente a limitaciones de la conductancia estomática, sin descartar disminuciones de la concentración o actividad de la Rubisco (o bien otros enzimas del ciclo de Calvin) y alteraciones de la fotofosforilación u otra fase del transporte electrónico. Como se ha señalado, en ningún caso estuvo relacionado con la disminución de la eficiencia fotoquímica del PSII. Los efectos fueron más importantes durante la primera mitad del experimento que a lo largo de la segunda, lo que interpretamos como un efecto de aclimatación de la planta al estrés, mediado por los cambios promovidos por el $SO_2$ en la redistribución del N mencionados con anterioridad y las alteraciones en el área específica de las acículas, diferentes para cada clase de edad.

Los resultados de este estudio indicaron que la exposición crónica a $SO_2$ indujo alteraciones en el crecimiento y la acumulación de biomasa en *Pinus halepensis*. La biomasa de raíces disminuyó por efecto del $SO_2$ en un 10 % ($p<0.05$) y, como consecuencia de que la biomasa aérea apenas varió, la relación biomasa aérea/subterránea (S:R) aumentó en ese tratamiento ($p<0.10$). La altura de las plantas aumentó y se registró también una tendencia a presentar menor biomasa total por efecto del $SO_2$. El aumento del índice S:R indica una redistribución de los recursos de la planta con un aumento en la asignación de carbono a la parte aérea a expensas de la parte subterránea. Esos efectos pueden relacionarse con mecanismos encaminados a compensar la disminución de la capacidad fotosintética de las hojas, pero a su vez limitan la absorción de agua y de nutrientes. Los efectos mencionados se producirían como consecuencia de un conjunto de procesos, entre ellos los detectados en otros aspectos estudiados: disminución de la capacidad fotosintética de las acículas; derivación de la energía procedente de la fotosíntesis hacia otros procesos diferentes del crecimiento como la acumulación de cationes en las vacuolas; sustracción de esos cationes al crecimiento. Otros procesos posiblemente implicados serían: activación de sistemas antioxidantes y reparación /reemplazamiento de tejidos aéreos dañados (ambos consumen también energía procedente de la fotosíntesis), interferencia en el metabolismo de los carbohidratos

en las hojas y su transporte a las raíces, y disminución de la micorrización de las raíces.

### 3.- Efectos del $O_3$

A pesar de que se emplearon concentraciones potencialmente fitotóxicas y en contraste con los numerosos efectos debidos al $SO_2$, los efectos del $O_3$ fueron mínimos. No se observaron efectos importantes del $O_3$ en la concentración foliar de nutrientes, en la eficiencia fotoquímica del PSII (índice $F_v/F_m$) y otros parámetros de la emisión de fluorescencia, ni en las tasas de fotosíntesis, el crecimiento y la biomasa final.

En la concentración foliar de pigmentos, el $O_3$ produjo diferencias en función de la edad de las acículas, con una tendencia a la disminución de la concentración de clorofila en las acículas más jóvenes y la tendencia opuesta en las más maduras. Sin embargo, el conjunto de resultados no es suficientemente importante como para concluir un efecto fotooxidativo del $O_3$ en las hojas más jóvenes de la planta. También se observaron algunos efectos del $O_3$ en las tasas medias de conductancia estomática en verano cuando la disponibilidad de agua estuvo limitada en el suelo, con un aumento significativo de éstas, de la transpiración acumulada a lo largo del día y una disminución de la eficiencia en el uso del agua. Los resultados son insuficientes para extraer conclusiones, pero son interesantes porque apuntan a una posible desregulación estomática inducida por el $O_3$ en combinación con el estrés hídrico.

Por tanto, la duración y las concentraciones de $O_3$ no fueron, en nuestras condiciones de experimentación, suficientes para desencadenar efectos importantes en los aspectos estudiados. Esa ausencia de efectos puede atribuirse al corto plazo de tiempo (una estación de crecimiento), a unas concentraciones realistas pero relativamente bajas, o bien a una tolerancia genética de *Pinus halepensis*, quizá propiciada por la xerofilia de la especie, con unas tasas de conductancia estomática bajas que obstaculizan la entrada del contaminante en la acícula. No obstante, resultados obtenidos en el mismo experimento por otro miembro del equipo (Moliner et al., datos no publicados) revelaron la existencia de mecanismos de destoxificación de radicales libres generados por el contaminante, lo que abre la posibilidad de efectos del $O_3$ a más largo plazo. En todo caso, la dosis acumulada aplicada en nuestra experimentación (AOT40 = 57 ppm·h), muy por encima del umbral de daño establecido por el Worshop de Kuopio (1996) en 10 ppm·h, indica la necesidad de una

mediterránea.

**4.- Efectos de la mezcla de $SO_2$+$O_3$**

Los resultados obtenidos en el estudio presentado no apoyan la existencia de efectos interactivos de los dos contaminantes, al menos con las concentraciones empleadas y en nuestras condiciones de experimentación. Los efectos de la mezcla de $SO_2$ y $O_3$ se pudieron explicar por la suma de efectos de los contaminantes por separado en la mayor parte de los aspectos estudiados: la concentración foliar de nutrientes y de pigmentos, la eficiencia fotoquímica del PSII, el crecimiento y la acumulación de biomasa.

Únicamente se obtuvieron efectos interactivos asociados a las medidas de intercambio gaseoso en verano con una disponibilidad de agua restringida en el suelo. En tal caso, el tratamiento con $SO_2$+$O_3$ produjo una disminución de la asimilación diaria de $CO_2$ respecto a los gases por separado, aunque el descenso respecto al control no fue significativo. Los resultados parecen de nuevo, como en el caso del $O_3$, sugerir posibles interacciones de los contaminantes con el estrés hídrico, de particular interés en el clima mediterráneo.

**5.- Extrapolación a condiciones naturales y posibles futuras líneas de investigación**

Como en otros estudios realizados en condiciones distintas a las naturales, existen dificultades a la hora de extrapolar los resultados obtenidos a condiciones reales. La complejidad de los ecosistemas forestales, el gran tamaño de los árboles adultos y su ciclo de vida largo hacen imposible su recreación en sistemas con cierto grado de artificialidad. Como se ha discutido a lo largo de la Memoria, el efecto de la propia cámara OTC y las condiciones de cultivo en maceta son también factores a tener en cuenta para evitar interpretaciones y extrapolaciones inapropiadas. Por otra parte, como muchos autores han señalado, el comportamiento de individuos jóvenes frente a los contaminantes no suele predecir adecuadamente el comportamiento de árboles adultos, ya que existen diferencias morfológicas, anatómicas y ecofisiológicas entre ellos.

Sin embargo, el tipo de estudios realizados en condiciones experimentales de OTCs pueden ser muy útiles para ayudar a comprender los mecanismos de acción de los contaminantes y de la respuesta de las plantas a éstos; y por tanto a interpretar los fenómenos que se observan en la realidad. En ese sentido, resultan interesantes las

conclusiones más importantes de nuestro trabajo, ya que sugieren la existencia de fenómenos con posibles consecuencias ecológicas en condiciones naturales. Entre ellos cabe destacar:

- fenómenos de aclimatación de las plantas al estrés producido por el $SO_2$, que incluyen una redistribución de recursos que ayudan a contrarrestarlo. Pero al mismo tiempo tales procesos pueden limitar la resistencia de las plantas a la sequía, de particular importancia en el entorno mediterráneo.

- fenómenos de destoxificación del $SO_2$ en la planta, con la acumulación de ciertos cationes y posible disminución o agotamiento de éstos en el suelo, conduciendo a deficiencias nutricionales en las plantas a largo plazo.

- inversión de energía y poder reductor en esos procesos de destoxificación, no disponibles por tanto para el crecimiento, la reproducción y la supervivencia frente a otros fenómenos adversos.

- importancia de las características fisiológicas y morfológicas de especies forestales mediterráneas, con su incidencia a la hora de establecer niveles umbrales de daño de los contaminantes como la AOT40 en el caso del $O_3$. No obstante, aunque *a priori* tales niveles podrían ser superiores para especies mediterráneas respecto a especies de otros ámbitos, es necesario también tener en cuenta la posible interacción con el estrés climático típico de estas áreas, como por ejemplo los indicios de desregulación estomática producida por el $O_3$, sólo o en mezcla con el $SO_2$, en combinación con el estrés hídrico.

Sería interesante conectar las líneas futuras de investigación acerca del fenómeno del declive de los bosques con el conjunto de fenómenos que se ha dado en denominar "cambio global". Las investigaciones podrían abarcar las siguientes aproximaciones:

- aproximación experimental, sometiendo a diversas especies forestales mediterráneas a niveles realistas de gases, en consonancia con las previsiones futuras, la legislación y los compromisos actuales de los países de la Unión Europea: aumento de los niveles de $O_3$ y de $CO_2$, disminución paulatina de los niveles de $SO_2$. Por otra parte, es necesario en nuestra opinión un mayor acercamiento a las condiciones naturales, con cultivo de plantas directamente en el suelo, y ubicación de

resultaría interesante profundizar en las interacciones de los gases con el estrés hídrico en las especies mediterráneas y recoger, particularmente en el caso del ozono, los posibles efectos acumulativos a lo largo de más de un período vegetativo.

- esfuerzo de investigación en la modelización de la respuesta de los árboles a los gases con identificación de los factores que fundamentalmente controlan su entrada en la planta, encaminado fundamentalmente a la predicción de la respuesta de individuos adultos a partir del comportamiento observado en plantas jóvenes.

- aproximación al estudio de los efectos de los gases en condiciones naturales, con delimitación de áreas con concentraciones de fondo de éstos bien contrastadas e identificación de los indicadores de estrés más importantes observados en las OTC. En definitiva, los experimentos en condiciones controladas no son sino una fase más en el intento de contribuir a conocer la respuesta de los bosques a una atmósfera cambiante en sus condiciones reales y complejas, conocimiento necesario para una adecuada gestión de los ecosistemas forestales.

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