

## VI.- RESUMEN Y CONCLUSIONES

Esta Tesis constituye una parte de un intento de disección genética de la morfogénesis de la hoja. Con el objetivo de identificar el máximo número posible de los genes responsables del control del desarrollo de este órgano, se ha intentado la obtención y el análisis del máximo número posible de variantes con hojas anormales, tanto de origen natural como derivadas de experimentos de mutagénesis, en el sistema modelo *Arabidopsis thaliana*. Hemos seguido dos caminos paralelos, consistentes en el estudio de la variabilidad natural en la morfología de la hoja en estirpes silvestres y el análisis genético de mutantes preexistentes, obtenidos por autores anteriores.

Hemos realizado, en primer lugar, un análisis cuantitativo de la variación con respecto al tiempo de algunos de los parámetros que definen la forma y el tamaño de las diez primeras hojas vegetativas de Enkheim-2 (En-2), que se eligió como estirpe de referencia, ya que es el ecotipo originario de la gran mayoría de las líneas mutantes estudiadas en esta Tesis. Los resultados obtenidos permiten proponer la existencia de tres tipos de hojas en la roseta basal de la estirpe En-2: las juveniles (la primera y la segunda), las de transición (la tercera y la cuarta), y las adultas (de la quinta en adelante). El ritmo de crecimiento de todas ellas es más rápido en los estados tempranos de su expansión que en los postreros. Nuestros resultados cuantitativos en En-2 son coincidentes con las observaciones cualitativas de autores anteriores, realizadas en otros ecotipos.

Para analizar la variabilidad natural, hemos estudiado 188 ecotipos de *Arabidopsis thaliana*, estirpes silvestres aisladas por distintos investigadores en diferentes partes del planeta, integradas en una colección de dominio público, la del *Arabidopsis* Information Service, actualmente depositada en el NASC. Hemos constatado diferencias netas entre estos ecotipos en las proporciones y el tamaño del limbo de la hoja, en la estructura del margen de ésta, y en la organización de la roseta basal de la planta. La variabilidad intraecotípica encontrada ha sido mínima, lo que indica un reducido grado de polimorfismo para los *loci* implicados, en consonancia con la autogamia casi absoluta que caracteriza a *Arabidopsis thaliana*.

Los ecotipos a estudio fueron clasificados en 14 clases fenotípicas. Se seleccionaron aquéllos que exhibían variantes extremas de algunos caracteres de la arquitectura de la hoja, llevando a cabo 88 cruzamientos entre parejas que manifestaban un determinado rasgo en dos formas opuestas y extremas: margen aserrado y liso, limbo redondeado y lanceolado, y peciolo corto y largo. Sin embargo, los

individuos de la segunda generación filial de estos cruzamientos constituían un continuo de fenotipos, siendo prácticamente imposible la distinción de clases fenotípicas, por lo que se concluyó que la variabilidad natural observada era probablemente de origen poligénico y se interrumpió esta línea de trabajo.

Para el estudio de mutantes preexistentes, se obtuvieron del NASC y el ABRC 173 estirpes mutantes, aisladas por autores anteriores, 162 de las cuales forman parte de la colección denominada *Arabidopsis* Information Service Form Mutants, que ha recibido hasta ahora muy poca atención, hasta el punto de que se dispone de una muy sucinta información sobre su fenotipo y en algunos casos se ignora incluso el mutágeno que se empleó para obtenerlas. Procedimos a clasificar estos mutantes en base al fenotipo que manifestaban en nuestras condiciones de trabajo, concentrando nuestra atención en 116 líneas, que se agruparon en 13 clases fenotípicas. El modo de herencia de sus fenotipos se determinó en 78 casos, resultando todos ellos inequívocamente monogénicos, salvo uno, y recesivos, excepto tres (dos mutaciones semidominantes y una completamente dominante).

El análisis de complementación de 23 mutantes *incurvata*, cuyo rasgo fenotípico más característico es la curvatura del margen de las hojas vegetativas hacia el haz, nos ha permitido establecer que corresponden a 10 genes. Existe interacción entre dos de ellos, *ICU1* e *ICU2*, tal como se deduce de la sinergia de sus fenotipos mutantes. Hemos demostrado genéticamente que la actividad de *ICU1* e *ICU2* se requiere para controlar negativamente al gen floral *AGAMOUS* en la hoja. Hemos comprobado que las mutaciones *icu1* son alélicas del gen *CURLY LEAF*, cuya caracterización molecular por Goodrich *et al.* (1997) ha revelado que codifica para un factor de transcripción con homólogos en el reino animal, concretamente varios miembros del grupo Polycomb de *Drosophila melanogaster*. Estos resultados convierten a *ICU2* en candidato a formar parte de dicho grupo de genes en *Arabidopsis thaliana*.

En la clase Denticulata se incluyeron 29 mutantes que presentaban indentaciones en el margen de sus hojas vegetativas. El análisis de complementación de 15 de ellos reveló que correspondían a 14 genes. Este resultado y la heterogeneidad de la clase fenotípica en lo relativo a otras características morfológicas indican que son varios los procesos cuya perturbación causa modificaciones en la configuración marginal de las hojas, haciendo aparecer incisiones o prominencias, que pueden tener su origen tanto en una muerte celular localizada como en desajustes en el patrón silvestre de divisiones celulares. Al menos uno de ellos, *serrate*, parece un mutante heterocrónico en

el que la fase vegetativa temprana no se manifiesta, iniciando su desarrollo en un estadio equivalente al de la roseta madura del tipo silvestre. La administración de giberelinas al tipo silvestre produce fenocopias de *serrate*, lo que sugiere la implicación del gen *SE* en la síntesis o la percepción de estas hormonas.

Hemos establecido que las 45 estirpes mutantes cuyo fenotipo se denominó Compact rosette (Cro), por su densa roseta, corresponden a 13 genes. Siete de ellos (*CRO1-CRO7*) están representados por mutantes muy semejantes, enanos y con una inflorescencia arbustiva, y presentan relaciones de epistasia doble recesiva, lo que sugiere que su fenotipo se debe a la ausencia del producto final de una ruta metabólica en la que participan. Su comportamiento en la oscuridad y la constatación de que las mutaciones *cro1* son alelos del gen *DET2* apoyan la hipótesis de que los genes *CRO2-CRO7* participan en la síntesis o la percepción de los brasinosteroides.

La aproximación más habitualmente empleada para realizar contribuciones al análisis causal de un proceso de desarrollo es la concentración de esfuerzos en la caracterización estructural y funcional de un gen concreto. En esta Tesis, por el contrario, se ha optado por el análisis genético de una amplia colección de mutantes preexistentes, cuya caracterización se había limitado hasta ahora a una muy somera descripción de algunos de sus rasgos fenotípicos. Nuestro trabajo aporta una panorámica de las alteraciones en la morfología de la hoja de *Arabidopsis thaliana* que pueden obtenerse mediante mutaciones, a la vez que sienta las bases de los estudios centrados en genes específicos que serán realizados más adelante.

## VII.- BIBLIOGRAFIA

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