Genetic Analysis of Variation for Auxin-Induced Adventitious Root Formation Among Eighteen Ecotypes of Arabidopsis thaliana L. Heynh.

J. J. King and D. P. Stimart

Eighteen ecotypes and two inbred lines of Arabidopsis thaliana L. Heynh. were analyzed for variation in the number of adventitious roots formed (hereafter referred to as rooting) on seedling hypocotyls in response to auxin treatment. Mean root counts varied from 1.7 to 23.1. Stable high (HA) and low (LA) rooting lines selected from ecotype Columbia, a low rooting ecotype (Mt-0), and unselected Columbia populations were evaluated for vegetative and reproductive growth parameters to determine correlated phenotypic effects of selection for rooting response. High rooting in HA correlated with compact, highly branched shoot growth. Genetic analysis of HA, Mt-0, and their F1, F2, and reciprocal backcross generations indicated that high and low rooting responses in this population may be controlled by several genes acting independently in additive-dominance fashion. Genetic variance partitioned into principally additive effects, with dominance favoring low rooting.

Development of adventitious roots in higher plants involves perception of morphogenetic signals and de novo formation of root meristems by cells of shoots or leaves (Esau 1977). This process is the essential first step in forming root systems of lower vascular plants, monocots, and clonally reproduced forestry and horticultural crops (Davies et al. 1994; Esau 1977; Kovar and Kuchenbuch 1994; Ritchie 1994). In an agricultural sense, adventitious root formation on vegetative propagules allows clonal multiplication and rapid fixation of superior genotypes, expediting their incorporation into production or breeding programs. This strategy is often exploited for long-lived woody species. However, the inability to initiate adventitious roots on otherwise superior individuals in many species remains an obstacle to ubiquitous application of this procedure.

Competence to form adventitious roots is quantified as percent rooted cuttings or root count per rooted cutting, and economically important genotypes of Malus pumila Mill. (Alvarez et al. 1989), M. domestica L. (Harbage 1991), Eucalyptus (Grattapaglia et al. 1995), and other woody species are classified as easy or difficult to root. Although variation in ability to form roots is known in herbaceous species (Hardwick 1979), difficult-to-root genotypes are better characterized among woody species where clonal propagation is used more commonly as an alternative to breeding in these long-lived perennials.

Data from a limited number of genetic studies suggest that competence to form adventitious roots is a quantitative trait (Riemenschneider 1993). Four quantitative trait loci (QTL) were associated with percent rooted cuttings in Eucalyptus (Grattapaglia et al. 1995). Three of these were detected in an easy-to-root species—E. urophylla S. T. Blake—and the fourth was detected in a difficult-to-root species—Eucalyptus grandis W. Hill ex. Maiden. A narrow-sense heritability of 0.15 for percent rooted cuttings was calculated for Pinus taeda L. (Foster 1990), and broad-sense heritabilities for root count per rooted cutting were estimated to be 0.44–0.56 in Populus deltoides Bartr. (Wilcox and Farmer 1968) and 0.92 (Foster et al. 1984) and 0.30 (Pounders and Foster 1992) in Tsuga heterophylla (Raf.) Sarg. In the herbaceous species Phalaris arundinacea L., narrow-sense heritabilities were 0.36 for percent rooted nodes, and 0.78 for root count per node (Casler and Hovin 1980). Analysis of tissue culture responses in Trifolium pratense L. found mostly additive genetic variance for root count and percent rooting. Dominance effects were significant but accounted for only a small portion of genetic variance (Keyes et al. 1980).
Despite potential benefits of improved rooting ability in woody species, their long life cycles limit the acquisition of basic information on inheritance and the types of gene action involved in adventitious root formation. The shorter life cycles of herbaceous species permit more rapid development of family structures favoring genetic analyses. While dramatic structural and developmental differences exist between herbaceous and woody species, some basic information on root development is likely to be transferable between plant types.

Recent characterization of root development (Dolan and Roberts 1995), and identification of genes altering (Benfey et al. 1993; Cheng et al. 1995; King, et al. 1995) or associated with (Smith and Fedoroff 1995) this process in Arabidopsis thaliana has made this an attractive organism for analysis of adventitious root formation. The objectives of this study were to determine the extent of variation in auxin-induced adventitious root formation among ecotypes of A. thaliana, analyze the genetic basis of this variation, and characterize correlated phenotypic effects of this variation.

Methods

Plant Growth Conditions

For rooting assays, plants were grown on basal medium (Haughn and Somerville 1986) supplemented with 1% (w/v) sucrose, 0.6 mM thiamine hydrochloride, 0.28 mM myoinositol, and 0.7% (w/v) Difco Bacto agar. Hereafter referred to as media. 0.28 mM myoinositol, and 0.7% (w/v) Difco agar which flooded seedling cotyledons to a depth of 5 mm to induce adventitious root formation. Jars were resealed and placed at 23°C under a daily light regime from 0800 to 2400 h at 50 µE/m/s provided by cool-white fluorescent bulbs. After 14 days we counted emerged adventitious roots on seedling cotyledons. This procedure is hereafter referred to as the rooting protocol.

In the greenhouse, we grew plants in 1:1 soil:peat:perlite (v/v), hereafter referred to as potting mix. The greenhouse temperature was set to 20°C. A daily light regime, as above, at a minimum of 550 µE/m/s was provided by natural light supplemented by 1,000 W high-pressure sodium lamps.

Initial Selections

Adventitious roots on 100 randomly selected seedlings of A. thaliana ecotype Columbia were counted, and the lowest rooting individual (LA), with 1 root, and the highest rooting individual (HA), with 13 roots, were transplanted to potting mix and allowed to self-pollinate. We advanced these lines by single seed descent to S6. In each generation, 40 seedlings per line were evaluated and the lowest and highest rooting individuals in LA and HA lines, respectively, were selected and self-pollinated to produce the next generation.

Evaluation of Root Counts Among Ecotypes

To increase seed availability, we sowed approximately 50 seeds from each of 18 ecotypes of A. thaliana onto the surface of potting mix in 10 cm square plastic pots, arranged the pots in a greenhouse in a randomized complete block design with four blocks and one pot per ecotype per block. We allowed the plants to self-pollinate, then harvested and bulked seeds within each ecotype. Seeds derived from these self-pollinations were used to initiate rooting assays (as described above) on 36 seedlings of each ecotype, S6 families of HA and LA, and a bulk of self-pollinated seeds from 20 randomly selected Columbia seedlings that had passed twice through the rooting protocol (C235). We included C235 to detect changes in root counts due to factors other than selection for high or low rooting parents. The experiment was a randomized complete block design with 3 blocks and 12 samples per genotype per block. We selected individuals producing no adventitious roots from ecotype Mt-0, which produced the lowest mean root count, and the lowest and highest rooting individuals from LA and HA, respectively, transplanted these seedlings to potting mix, and allowed plants to self-pollinate in a greenhouse.

Evaluation of Multiple Trait Variation Among Selected Lines

To examine possible trait correlations with root count, phenotypic variation for 10 traits was quantified among the following five genotypes: S6 families of LA and HA; unselected ecotype Columbia, an S1 family of Mt-0, and self-pollinated progenies of 20 randomly selected Columbia plants that had passed through the rooting protocol (C335). Thirty-two seeds of each line were sown, one seed per pot, into potting mix in 10 cm square plastic pots. Pots were arranged in a greenhouse in a randomized complete block design with four blocks, each containing eight pots per genotype. Greenhouse conditions were as described above. We collected data for days corresponding to the following life-history traits—germination, visible flower bud, bolting, anthesis, and apical arrest [defined as “cessation of generative activity at the inflorescence meristems” (Hensel et al. 1993)]—and compared plant form and size based on rosette leaf counts and fresh and dry weights at anthesis, and height and lateral inflorescence branch counts at apical arrest. Data were subjected to analysis of variance.

In this experiment, plants of HA were short with many elongating lateral branches (suggesting weak apical dominance), whereas plants of Mt-0 were tall with few elongating lateral branches (suggesting strong apical dominance) (Figure 1). To ascertain the relationship between formation of lateral branches and adventitious roots, we counted adventitious roots in the rooting environment, then transplanted HA, Mt-0, and 71 F1 (synthesis described below) seedlings to 10 cm square plastic pots and grew them in the greenhouse as described above. When plants reached apical arrest, we counted the lateral inflorescence branches and performed a correlation analysis for root and branch counts.
Genetic Analysis of Root Count

We developed six populations for analysis of variation in rooting: parent 1 (P1) was HA at S1; parent 2 (P2) was Mt-0 at S1; F1 (HA × Mt-0), F2; backcross to parent 1 (BP1) was HA × [HA × Mt-0]; and backcross to parent 2 (BP2) was Mt-0 × [HA × Mt-0]. Ecotype Mt-0 was chosen because it yielded the lowest mean root count. The fact that the Mt-0 parent in the F1 was an S1 from the ecotype presents the possibility of heterozygosity at loci affecting root count and would therefore violate assumptions basic to a generation means analysis. We assumed homozygosity at these loci in Mt-0 based on three factors: the Mt-0 line used in these experiments had been maintained as a laboratory strain and propagated by self-pollinations for several generations; the variance for root count in the Mt-0 parental line was the lowest among the six generations tested, implying absence of segregation at loci affecting root count; and the Mt-0 line was homozygous at 20 microsatellite loci on four of the five Arabidopsis chromosomes (Innan et al. 1997). After determining that root counts were not different in F1 families derived from reciprocal crosses (data not shown), we chose HA × Mt-0 as the F1 parent because F1 plants were identical morphologically to Mt-0, but were distinctly different from HA. This allowed us to detect HA self-pollinated contaminants among putative F1 individuals. Flowers not crossed on the F1 plant were allowed to self-pollinate to generate the F2.

We counted adventitious roots on seedlings of each generation in two experiments, performed at different times, using randomized complete block designs consisting of four blocks with 10 to 20 samples per genotype per block depending on generation. More samples were counted for segregating generations (F2 and backcrosses) to equalize variances with non-segregating generations.

We transformed raw data as (root count + 1)^0.5, analyzed experiments separately, then tested for homogeneity of error variances to determine if data could be pooled across experiments. Generation × block/experiment variance was tested against sampling variance and, if significant, was used as the error term for testing generation and generation × experiment effects. We partitioned generation sum of squares into additive effects as (P1 − P2)/2 and dominance effects as F1 − (P1 + P2)/2, and discerned differences among generation means with Duncan’s multiple range test using Kramer’s modification for unequally replicated treatments (Kramer 1956). Using mean root counts for P1, P2, and F1, we calculated the degree of dominance according to Mather and Jinks (1977) as

\[
\text{Dominance} = \left( F_1 \text{ mean} - \text{Midparent value} \right) + \frac{1}{2} \left( \text{High parent mean} - \text{Low parent mean} \right)
\]

We performed a generation means analysis with an additive-dominance model for least squares estimation of generation root count means (Mather and Jinks 1977). Generation means were modeled in terms of mean effects (m), pooled additive effects (d), and pooled dominance effects (h). A joint scaling test (Cavalli 1952) was used to calculate a chi-square value to determine adequacy of the additive-dominance genetic model. The chi-square value was tested with three degrees of freedom with significance indicating inadequacy of the model.

Results

Mean root counts for LA, HA, C235, and the 18 ecotypes ranged from 1.7 to 23.1
Bulk of self-pollinated seed of 20 randomly selected plants of ecotype Columbia passed three times through the mini-mit, Mt-0 (Table 2). Heights of all genotypes were different statistically, with intervals between means of 2–6 cm. The smallest difference was between Columbia at 41.6 cm and C335 at 43.7 cm.

In the F2 population, counts of lateral inflorescence branches and adventitious roots correlated significantly (r = 0.31). Lateral branch counts ranged from 9 to 18 for HA, 4 to 9 for Mt-0, and 2 to 28 for the F1 (data not shown). The F1 distribution was unimodal and skewed positively, with a mean of 7.7. Branch count distributions of HA and Mt-0 overlapped at 9. Dividing the F2 population at this value yielded two segregating classes containing individuals with branch counts of 2 to 8 and 10 to 28 (n = 48 to 51 and 22 to 19, respectively, depending on placement of the three F2 individuals with branch counts of 9 into the high or low class). These distributions fit a 3:1 segregation ratio with chi-square values of 1.54, 0.93, 0.47, and 0.17, suggesting recessive, single-gene inheritance of the highly branched phenotype.

**Genetic Analysis of Root Count**

The root count distribution for P1 (HA at S0) ranged from 0 to 28, and the distribution for P2 (Mt-0 at S0) ranged from 0 to 15. Root count distributions for F1 and BP1 generations resembled the distribution for P1 (Figure 2). The F-test of error variances of the two separate experiments was not significant (P > .05) indicating homogeneity of variances, so data were pooled over experiments and analyzed (Table 3). In the pooled analysis, generation × block/experiment was significant and was used as the error term for testing generation and generation × experiment effects which were significant (P < .01) and not significant (P > .05), respectively. Partitioning generation sum of squares showed significant additive and dominance effects (Table 3).

Ranking of means by Duncan’s multiple range test did not differ between analyses of transformed and untransformed data. Therefore distributions (Figure 2) and means (Table 4) of untransformed data are presented. The mean adventitious root count for HA was 14.5 and for Mt-0 was 4.9 (Table 4). The F1 mean at 7.9 was 1.8 less than the midparent value of 9.7, yielding an estimate of −0.38 for degree of dominance. The BP1 mean at 10.5 was 0.8 greater than the midparent value. Means for F1, F2, and BP1 at 4.9, 4.7, and 4.9, respectively, were not significantly different, and ranked lowest among generation means.

The chi-square test of estimated generation means was nonsignificant (Table 5), indicating adequacy of an additive-dominance model for explaining rooting responses in this population. Estimated generation means were accurate to within 10% of observed means for all generations except the F1 and F2, where estimated means deviated from observed by 24% and 56%, respectively.

### Discussion

This study was initiated to evaluate genetic variation for auxin-induced adventitious root formation in *A. thaliana*. Among 21 genotypes, the number of adventitious roots formed in response to exogenous auxin ranged from 1.7 to 23.1. The generation means analysis for HA, Mt-0, and their F1, F2, BP1, and BP2 generations suggested that rooting response in this population is under relatively simple genetic control. An additive-dominance model predicted generation root count means accurately, indicating little or no epistasis. Phenotypic analysis of Columbia, C335, HA, LA, and Mt-0 distinguished HA and Mt-0 by the high leaf count and high fresh and dry weights at anthesis for Mt-0, and the high

**Table 1. Adventitious root counts at 14 days after treatment with 35 μM IBA for *A. thaliana* lines selected for high (HA) and low (LA) rooting, an unselected line from ecotype Columbia (C235), and unselected ecotypes.**

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Days to visible Bud</th>
<th>Days to bolting</th>
<th>Leaf count at anthesis</th>
<th>Fresh weight at anthesis (g)</th>
<th>Dry weight at anthesis (g)</th>
<th>Days to apical arrest</th>
<th>Branch count at apical arrest</th>
<th>Height at apical arrest (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Columbia</td>
<td>21.9±2.0</td>
<td>24.7±1.3</td>
<td>9.9±1.1</td>
<td>1.1±0.1</td>
<td>0.1±0.1</td>
<td>48.4±2.1</td>
<td>8.0±0.2</td>
<td>41.6±3.1</td>
</tr>
<tr>
<td>C335</td>
<td>21.9±2.0</td>
<td>25.1±1.3</td>
<td>8.9±1.1</td>
<td>1.1±0.1</td>
<td>0.1±0.1</td>
<td>48.8±2.1</td>
<td>7.8±0.3</td>
<td>43.7±3.1</td>
</tr>
<tr>
<td>HA-S6</td>
<td>24.0±2.0</td>
<td>26.7±1.3</td>
<td>9.8±1.1</td>
<td>1.2±0.2</td>
<td>0.2±0.2</td>
<td>52.6±2.1</td>
<td>15.1±3.1</td>
<td>31.6±3.1</td>
</tr>
<tr>
<td>LA-S6</td>
<td>23.1±2.1</td>
<td>26.4±1.3</td>
<td>8.7±1.0</td>
<td>0.8±0.2</td>
<td>0.1±0.1</td>
<td>53.0±2.1</td>
<td>7.6±0.3</td>
<td>35.9±3.1</td>
</tr>
<tr>
<td>Mt-0</td>
<td>23.4±2.1</td>
<td>25.9±1.3</td>
<td>11.0±1.0</td>
<td>2.2±0.2</td>
<td>0.3±0.3</td>
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<td>46.8±3.1</td>
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</table>

**Table 2. Days to visible flower bud, bolting, and anthesis; leaf counts and fresh and dry weights at anthesis; days to apical arrest; lateral branch counts; and height at apical arrest in *A. thaliana* ecotype Columbia and its derived line C335, and in lines selected for high (HA) and low (LA and Mt-0) rooting.**

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</table>

**Notes:**

- Values are means of 20 (Days to Bud and Bolting) or 16 (all other variables) observations.
- Duncan’s multiple range test rankings. Means within a column with same letter are not different at P < .05.
- Bulk of self-pollinated seed of 20 randomly selected plants of ecotype Columbia passed three times through the rooting protocol.
Adventitious root counts taken 14 days after application of 35 μM IBA to 6-day-old seedlings of A. thaliana representing generations derived from the cross of high (HA) × low (Mt-0) rooting lines

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment (E)</td>
<td>1</td>
<td>0.05</td>
<td>0.05</td>
<td>ns</td>
</tr>
<tr>
<td>Block/experiment (B/E)</td>
<td>6</td>
<td>3.21</td>
<td>0.54</td>
<td></td>
</tr>
<tr>
<td>Generation (G)</td>
<td>5</td>
<td>214.14</td>
<td>42.83</td>
<td>**</td>
</tr>
<tr>
<td>Additive effects</td>
<td>1</td>
<td>99.97</td>
<td>99.97</td>
<td>**</td>
</tr>
<tr>
<td>Dominance effects</td>
<td>1</td>
<td>3.36</td>
<td>3.36</td>
<td>*</td>
</tr>
<tr>
<td>Residual</td>
<td>3</td>
<td>110.82</td>
<td>36.94</td>
<td>**</td>
</tr>
<tr>
<td>Generation × experi-</td>
<td>5</td>
<td>3.69</td>
<td>0.74</td>
<td></td>
</tr>
<tr>
<td>ment</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G × B/E</td>
<td>30</td>
<td>21.62</td>
<td>0.72</td>
<td>**</td>
</tr>
<tr>
<td>Error</td>
<td>676</td>
<td>250.61</td>
<td>0.37</td>
<td></td>
</tr>
</tbody>
</table>

*Data transformed as (root count + 1)½.

ns, *, ** = not significant and significant at P = .05 or P = .01, respectively.

For only 1.6% of the sum of squares for generations, whereas additive effects accounted for 46.7% (Table 3). Similarly, in Trifolium pratense L., additive effects were the principal component of genetic variance for adventitious root count while dominance effects were significant but less important (Keyes et al. 1980). In Cucumis sativus L. (Ghaderi and Lower 1979) and in Phaseolus vulgaris L. (Fawole et al. 1982), root system dry weight was determined mainly by dominance effects. The root systems in these species include embryonic and lateral roots. The extent of genetic correlation among embryonic, lateral, and adventitious root formation is unknown, although in a few cases development of these root types has been uncoupled genetically (Zobel 1975).

Dominance gene action appeared to favor low rooting. This was suggested by similarities among root count means for P2, F2, and BP2 (Table 4); the F distribution being shifted toward P2 (Figure 2); and degree of dominance being −0.38. This calculation of degree of dominance likely represents a minimum estimate of dominance gene action because it cannot account for the situation in which opposite domi...
nance effects of multiple loci cancel (Mather and Jinks 1977).

High rooting in HA appears to be controlled by several independent genes and environmental influences. Multigene control is suggested by absence of high rooting segregants in the F₁, however, the shift of BP₁ toward high rooting implicates relatively few loci that could be introgressed through backcrossing. These conclusions for Arabidopsis are consistent with results of Grattapaglia et al. (1995) who found four QTL could account for 63% of the phenotypic variance for percent rooted cuttings in a cross of high × low rooting Eucalyptus species. While these two experiments quantified adventitious root formation differently (root counts in Arabidopsis; percent rooted cuttings in Eucalyptus), both of these measures could be valid assessments of competence to form adventitious roots, and could be detecting effects of analogous sets of genes.

The high lateral branch count in HA correlated significantly with high adventitious root count, and appeared to be controlled by a single recessive gene. The altered meristem program (amp1) mutant of A. thaliana produces more lateral shoots than wild type and contains elevated levels of endogenous cytokinin (Chaudhury et al. 1993). Cytokinins applied at low concentrations enhance responses to auxin (Dominov et al. 1992) including formation of lateral and adventitious roots (Biddington and Dearman 1982; Van Staden and Harty 1988). Cytokinins are also known to delay chlorophyll loss and leaf senescence (Galston and Davies 1970), and leaf retention has correlated positively with adventitious root counts in Phaseolus vulgaris L. and Glycine max L. Merrill (Hardwick 1979). Although not quantified, plants of HA were observed in the greenhouse to remain green longer than plants of other genotypes. If HA contains elevated cytokinin causing enhanced responsiveness to auxin, exogenous application of auxin in the rooting protocol may overcome root inhibitory effects of cytokinin and increase root initiation. Further analyses of HA could elucidate factors contributing to this phenotype.

The results reported here represent an initial characterization of variation for auxin-induced adventitious root formation in A. thaliana. Future analyses could benefit from expanding the genetic base being analyzed by intermingling within high and low rooting ecotypes, extracting unselected inbred lines from intermated populations, then characterizing and attempting to control the distribution of responses within inbreds before crossing between response groups. Analysis of multiple crosses would permit broader inferences about rooting in this species. Extraction of recombinant inbred lines from F₂ populations would provide greater degrees of freedom for more complex models of generation means analysis, allow estimation of heritability by parent offspring regression, and allow more accurate estimation of environmental variance from inbred lines.

References


Hensel LL, Grbic V, Baumgartner DA, and Bleecker AB, 1993. Developmental and age-related processes that in-


