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Yes, kin recognition in plants!

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Invited reply

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Klemens (2008) criticizes our evidence (Dudley & File 2007) that root allocation of plants depends on the kinship of neighbours. He objects to the statistical analysis, experimental setup and biomass results. Here we defend our statistical analysis and experimental setup, and show that Klemens misunderstands the study.

We used analysis of covariance (ANCOVA), an accepted technique in plant allometry (Muller *et al.* 2000; Cahill 2003), to assess root allocation. Our study met the conditions of McCoy *et al.* (2006) for unbiased ANCOVA because the covariate, leaf mass, could be measured with more accuracy than the dependent variable, root mass and the covariate ranges are greatly overlapping (table 1). Our major result is robust to whether the model includes same or separate slopes and raw or transformed data. We presented the analysis that gave homoscedastic residuals and a better model fit.

Littell *et al.* (2002) provides methodology for ANCOVA with separate slopes. Obtaining separate slopes indicates differences in allometric relationships (Müller *et al.* 2000). Thus, in finding a logleaf×kin effect, we found an effect of kin on root: leaf allometry.

However, the results of separate slopes ANCOVA must be interpreted cautiously. When the regression slopes differ, the treatment effect depends on the covariate. The main effect only measures the difference between treatments at the y-intercept (Littell *et al.* 2002). To assess the difference between kin and strangers, we compared the least-squares means (lsmeans), which estimate the treatment effects at the overall population mean for the covariate (figure 1), a value within the range of all our treatments. Klemens (2008) incorrectly asserts that lsmeans are derived assuming a common slope, but their derivation is based on the separate slopes (example in figure 1). A more complete and complex comparison can be made by examining the fitted equations over the range of the variables (table 1).

The role of pot size in explaining the apparent root competitor effects on root biomass and root allocation is a matter of current debate (Hess & De Kroon 2007). Since we can compare root allocation between groups of kin and groups of strangers within the same size pot, this is not a material objection to the basic result of kin recognition. The entangled roots of four plants could not be separated during harvesting, so we measured stand allocation rather than individual allocation.

Table 1. Parameters for the separate regression lines taken from the ANCOVA in Dudley & File (2007). (The overall population mean for logleaf (figure 1*a*; Dudley & File 2007) was 0.863.)

				log (leaf+1)	
root	kin	intercept	slope	minimum	maximum
solitary	kin	−0.045	0.534	0.268	1.223
solitary	strangers	0.077	0.396	0.152	1.044
neighbours	kin	−0.114	0.608	0.527	1.366
neighbours	strangers	0.012	0.519	0.206	1.489

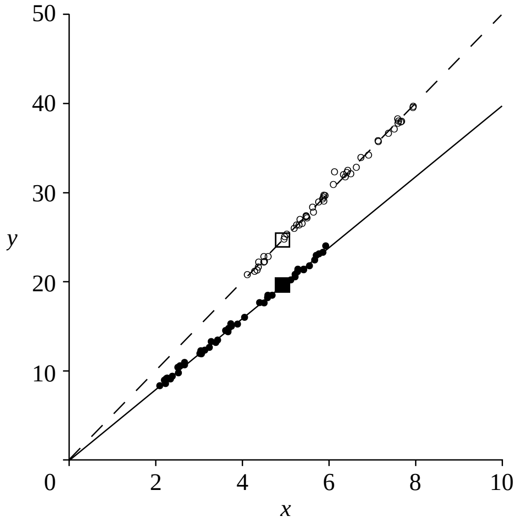

Figure 1. Scatter plot of a computer-generated dataset, where in group 1 (black filled circles), $y=4x+$error and in group 2 (open circles), $y=5x+$error. The dataset was analysed with a separate slopes ANCOVA (SAS PROC GLM), and the lsmeans (lsmean 1, black filled square and lsmean 2, open square) from this analysis are plotted against the overall mean for x.

Klemens' (2008) remarks on the biomass variability and the lack of competitive effects indicate a misunderstanding of the study. We focused our experimental design on determining root allocation for groups of kin and strangers, not assessing fitness consequences. No competitive effects were expected because we kept density and average soil volume constant per plant. We used natural populations planted into naturally high density; both increase within-treatment size heterogeneity. We harvested when plants were undergoing strong vegetative growth at the start of flowering. Annual plants vary in life-history strategies; some bet hedge by reproducing early at the cost of vegetative growth. We do not find variation in performance surprising because performance is determined by many environmental and genetic factors. The variance in size increased our power to measure root allocation.

Klemens (2008) claims that increased sibling biomass is a necessary consequence of kin recognition. This is not so. Others have measured fitness for groups of related and unrelated plants (Donohue 2003; Cheplick & Kane 2004), finding either increased fitness in sibling groups, suggesting kin selection or increased fitness in stranger groups, interpreted as niche partitioning. Both processes could co-occur. But no inferences concerning

The accompanying comment can be viewed on page 67 or at http://dx.doi.org/doi:10.1098/2007.0518.

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fitness should be made because we measured the plants at an early life-history stage, and there was no statistically significant size difference between kin and strangers (figure 1*b*; Dudley & File 2007).

We found kin recognition in one plant species. The best challenge to this result is further empirical work. Is the result methodology specific? Does it occur in other species, and in other traits? What are its fitness consequences?

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