Heterosis and Outbreeding Depression on Fertility and Biomass of Inter- and Intra-subspecies Crosses in Tetraploid Alfalfa

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Hybrids between the alfalfa (*M. sativa*) subspecies sativa and falcata show heterosis for biomass production (Riday and Brummer, 2002; 2005). However, the performance of subsequent generations of these hybrids, and the quantification of inbreeding depression has not been evaluated. Due to the differences in morphology, geological distribution, and growth habit between sativa and falcata, we hypothesize that cryptic chromosome rearrangements and/or the loss of favorable epitasis may occur and lead to decreased production in the later generations of F_1 hybrids, a phenomenon called outbreeding depression. In this experiment, we used 4 sativa and 4 falcata genotypes as parents to make a set of inter- and intra-subspecies crosses. For each cross, we measured the sib- and self-fertility and developed F1, F2, S1 and double-cross generations for biomass testing in the field. Parents were self-fertilized to create the PS1 generation. The objectives of this experiment were to test (1) whether the later generations of inter-subspecies crosses break down in fertility and/or biomass and (2) whether the double crosses show progressive heterosis for biomass. Fertility was evaluated in a greenhouse trial, and biomass was measured in replicated field plots at two locations in Iowa. Inter-subspecies crosses showed greater fertility than intra-subspecies crosses, which indicated that cryptic chromosome rearrangements probably don't exist between these subspecies. However, inter-subspecies crosses showed greater biomass depression on F2 and S1 generations than intra-subspecies crosses. Only the sativa by sativa double cross generation showed progressive heterosis, but only at one location, suggesting genotype by environment interaction. Busbice and Wilsie (1966) proposed that severe inbreeding depression in tetraploids might be due to the rapid loss of multiple allelic interactions. Inbreeding studies on two-allele tetraploid alfalfa suggested that heterozygosity *per se* (overdominance) is probably not the main cause of heterosis, while instead, complementary gene action, caused by dominance and/or epistasis, is the predominant contributor to heterosis (Bingham et al, 1994; Woodfield and Bingham, 1995; Kimbeng and Bingham, 1998). We fitted the biomass data from 3 generations (F1, F2 and S1) of 12 crosses and 4 generations (F1, F2, S1 and PS1*PS1) of 4 crosses to a set of linear models of expected inbreeding coefficients to test the significance of two, three, and four allelic interaction models as well as lack of fit to these models, suggestive of epistasis. The loss of two allelic interactions alone can explain the biomass depression only for three intra-subspecies crosses; the yield depression seen in all the other crosses is explained better by including the loss of multiple allelic interactions and/or epistasis in the model. These results suggest that multiple allelic (or linkat) interactions and epistasis likely contribute to biomass production in tetraploid alfalfa.

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