

Quantitative Genetic Parameters for Yield, Drought Tolerance and some Quality Traits in Tea (*Camellia sinensis* L.) O. Kuntze

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ABSTRACT

The genetic parameters for eight agronomic and quality traits in tea (*Camellia sinensis*) were estimated using a 4 x 4 full diallel analysis. There were significant family and clonal variations for the traits among the progenies and their parents. The mid-parent heterosis (MPH) and better-parent heterosis (BPH) averaged across the families, were high for fermentability (MPH: 108.5%; BPH: -12.82), and drought tolerance (MPH: 16.33%; BPH: 2.30%) but low for yield (MPH: 2.17%; BPH: -5.09%) and total polyphenols (MPH: -2.81%; BPH: -5.71%). The heritability estimates for yield ($h^2 = 0.44 \pm 0.16$; $H^2 = 0.56 \pm 0.15$), drought tolerance ($h^2 = 0.61 \pm 0.06$; $H^2 = 0.96 \pm 0.01$) and fermentability ($h^2 = 0.45 \pm 0.04$; $H^2 = 0.98 \pm 0.01$) were high indicating that the three traits are highly heritable and further hybridization or judicious clonal selection can lead to improvement. Correlations analyses among the traits were significant among drought tolerance and black tea quality, suggesting control by either linked or pleiotropic genes, indicating possibility of simultaneous selection of more than one trait. Moderate genetic gains are achievable from selection based on clonal means for characters that traditionally have received improvement attention like yield and fermentability at 14.1% and 8.9%, respectively, while traits such as drought tolerance and pubescence realized considerable gains at 20.6%, and 30%, respectively. The results emphasize the importance of reliance on genetic parameters for enhanced tea improvement programmes. Selecting mating cultivars with high tolerance to drought, high pubescence and yield could lead to new cultivars with higher economic potentials.

Key words: Tea, *Camellia sinensis*, Heritability, Heterosis, Genetic gains

Since the introduction of tea in Kenya at the turn of the 20th century, area under tea has continued to expand with the land under tea cultivation now exceeding 149,000 ha (Tea Board of Kenya Statistics, www.teaboard.or.ke). The tea industry in Kenya is largely based in the rural areas where vast majority of Kenyans live. Over 62% of the crop is produced by the smallholder sub-sector offering direct source of livelihood to over 3 million people (Mbadi & Owuor, 2008). The contribution of tea towards poverty alleviation and infrastructural development in the rural areas has therefore been enormous. In 2008, Kenya produced 345,817 metric tonnes, being the fourth largest producer after China, India and Sri Lanka, with an average annual production per hectare of 2193 Kg made tea, which is among the largest in the world (Tea Board of Kenya Statistics, www.teaboard.or.ke). The successful development of the tea industry in Kenya has been attributed in part to the tremendous efforts put in tea improvement research and favourable climatic conditions (Othieno, 1981; 1991). The pioneer tea plantations comprised seedling tea populations with low

productivity and quality. These plantations had heterogeneous plants that made management and quality maintenance difficult. This elicited research and development of vegetative propagation techniques in the early 1960s that resulted in development of single whole-leaf cutting of tea as a propagule and later, release for commercial use of clonal teas (Green, 1964). The early tea improvement efforts saw the release of better yielding but poor to moderate black tea quality or high quality but low yielding clonal teas compared to the existing seedling teas. Although efforts to recombine the two traits in one genotype through hybridization have gained significance (Kamunya, 2003), the prerequisite genetic information meant to guide breeding activities has been lacking. A recent study revealed significant but variable general and specific combining abilities for some desirable agronomic attributes (Kamunya *et al.*, 2009). Besides, the changing global climate with unprecedented weather phenomenon and worsened by extension of tea growing in areas not traditionally meant for tea, have resulted in emergence of new or increase in virulence of

endemic diseases and pests as well as prolonged drought periods (Otieno *et al.*, 2002). There is therefore need to develop clonal teas with combined high yields, acceptable black tea quality and tolerance to abiotic and biotic stresses.

Owing to its long generation time from seed to flower, allogamous nature and large genome ($n=15$), development of a new elite tea variety is a protracted process. For example, it takes about 21-26 years to obtain an improved seedling population, while superior clonal plants may take 8-10 years to be extracted from such a population (Gazi, 1978). Additionally, it takes 21-30 years for tea to attain optimum yield potential (Gazi, 1978). While selfing would largely result in creation of hybrids for autogamous crops, tea has evolved self-incompatibility mechanisms (Rogers, 1975; Wachira and Kamunya, 2005) to constrain selfing that may result in inbreeding depression. Information on inheritance patterns of quantitative traits in tea is scanty. Availability of such information influences the choice of progenitors, size of breeding population and the design of seed orchards. As most of the agronomic traits of tea are quantitative and governed by several to many genes, they may not be amenable to easy manipulations in breeding programmes without elaborate and long-term field testing, often in several environments to determine their inheritance, adaptability and stability. Such field experiments are expensive to maintain in terms of manpower, time and shrinking land resources. Hence, there is need to understand the type of gene action governing the most important attributes to form a solid foundation for rationalized and fruitful breeding programme.

Diallel cross was used to study genetic variation, heritability, heterosis, correlation coefficients and genetic gains for three important agronomic traits; yield, bud weight and drought tolerance, five traits related to black tea quality, fermentability, total polyphenols, theaflavins and thearubigins and pubescence. Pubescence is a trait relevant for processing of quality orthodox teas with “silvery tips”

(Wight & Barua, 1954; Kamunya & Wachira, 2006) and orthodox teas (Venkataramani & Padmanabhan, 1963). The implications of the relative magnitudes of the genetic parameters and potential gains on breeding strategies and clonal selection are elucidated in regard to their usefulness in tea improvement.

MATERIALS AND METHODS

Test material and experimental field design:

A 4x4 full diallel cross trial was established in the year 2000 at the Timbilil Estate (0° 22' S, 35° 21' E and 2180 m above mean sea level) of the Tea Research Foundation of Kenya (TRFK), Kericho. The sixteen clonal full-sib families and four parental clones (AHP S15/10, TRFK 6/8, TRFCA SFS 150, EPK TN14-3) were set up in a randomized complete block design with three replications in plots of 30 plants spaced at 0.61 m within rows and 1.22 m between rows (i.e. 13448 plants/ha). The four parental clones used in the diallel cross are amongst popular Kenyan commercial tea cultivars that were selected based on diverse attributes as summarized in Table-1.

The 16 clonal full-sib families were derived from a series of full diallel crosses carried out between 1983 and 1993 involving the four parental clones. Each cross was represented by five randomly selected full-sib clonal progeny except for two crosses (selfs of TRFK 6/8 and EPK TN14-3) that had two full-sibs each. Seed arising from the crosses were used to establish single-bush progeny tests, which were maintained for six years. Cuttings were collected from selected progeny, rooted and raised in the nursery for one year prior to field transplanting. Each replicate was surrounded by a guard row of clone TRFK 303/1199. The trial received 150 Kg N per hectare per year in the form of NPKS 25:5:5:5 compound fertilizer and brought into bearing following the recommended management practices (Anonymous, 2002). The following traits were scored in the test families, parental and control clones.

Table 1: Attributes of progenitor clones used in the full diallel mating design

Clone	Varietal type	Special attributes
EPK TN14-3	Kenyan Chinariy local selection	Tolerant to high soil pH and cold but susceptible to red crevice mites (<i>Brevipalpus phoenicis</i>) with moderate levels of caffeine (2.7%)
TRFCA SFS150	Malawian Assam type	Drought, cold and pest tolerant with moderate levels of caffeine (2.9%)
AHP S15/10	Assam type Kenyan local selection	High yielding, highly pubescent but susceptible to water stress with moderate levels of caffeine (3.0%)
TRFK 6/8	Assam type Kenyan local selection	High black tea quality (fast fermentability and high levels of polyphenols), low yielding and susceptible to water stress with low levels of caffeine (1.7%)

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Crop yields:

Yield data collection of the plucked two leaves and a bud was from February, 2001 up to December, 2007. Harvesting was done at 7 to 10 days intervals, depending on availability of crop. The cumulative yield data was converted from green leaf weight to annual mean yield by dividing it with the number of years since first plucking. The green leaf yield was converted into made tea per hectare by a conversion factor of 0.225 (Anonymous, 2002).

Total polyphenolic contents of green leaf:

The total polyphenol contents from 0.5 g of steam-milled fresh tea shoots collected from each of five randomly selected bushes of each clonal full-sib progeny were determined as outlined in British Standard ISO document (Anonymous, 2005). Actual values were determined from a standard curve generated using gallic acid, and were expressed as the amount of gallic acid equivalent, expressed as per cent by mass on a dry matter basis.

Fermentability of green leaf:

Chloroform test (Sanderson, 1963) was carried out on harvested two leaves and a bud sampled from five randomly selected bushes per plot to determine the fermentability of the test array as well as the parent clones and one inherently non-fermenting clone, TRFK 12/2 as control. Fermentability was scored based on the change in colour after four hours using a 4-point scale as: 1-bright red brown (fast fermenting); 2-dull brown (moderate fermenting); 3-greenish tinge (poor fermenting); 4-green (non-fermenting).

Drought damage assessment:

Drought damage was assessed during periods of severe water stress in January to April, 2003 and November 2005 to April 2006. Damage due to drought was scored on five randomly selected plants per plot using a 5-point scale as 1 (0-10% scorch with prolific flushing, no dormant shoots), 2 (11-25% scorch and wilting with few dormant, few flushing shoots and some leaf fall), 3 (26-50% scorch with many dormant shoots, wilting leaves and moderate leaf fall), 4 (51-75% scorch with many dormant shoots, wilting leaves, severe leaf defoliation and die back), 5 (76-100% scorch with severe defoliation and die back, all shoots dormant and sometimes death) on five randomly selected plants per plot.

Black tea processing, total theaflavins (TF) and thearubigins determinations:

Black tea quality analysis was conducted from miniature manufactured tea samples (Owuor *et al.*, 1986; 2006) obtained from each plot. The tea leaf (600 gm) was withered at room temperature for 18 hours. Upon “cut, tear and curl” (CTC) maceration, the tea was fermented for 90 minutes under ambient temperature (22-26°C) and relative humidity. A bench top fluid drier (Teacraft) was utilized in firing the tea. Total theaflavins (TF) were determined by the Flavognost method as described by Hilton (1973). Total

thearubigins (TR) for the miniature manufactured tea samples were determined following protocol by Roberts and Smith (1963).

Bud pubescence and weight:

The degree of pubescence on the leading bud (“tip”) and under surface of the leaf is an important morphological marker for quality especially in orthodox tea. This character was scored on buds from three randomly selected bushes using a modified 5-point scale (Wight and Barua, 1954). The assessment of pubescence was carried out under a light dissecting microscope as follows: 1 for glabrous buds and leaves with hair only on the mid-rib; 2 for buds and leaves with a few scattered hairs on the lamina; 3 for hairiness extending about halfway to the margin; 4 for leaves and buds with entire surface of lamina pubescent; 5 for leaves and buds where pubescence formed a dense indumentum. Bud weight was recorded as dry weight for 20 randomly selected buds among 50 plucked buds which had been dried at 70°C for 48 hours to attain constant weight.

Analysis of statistical and genetic parameters:

The various genetic parameters were estimated according to Griffing’s diallel Model II assuming random effects (Method 1) (Griffing, 1956). The model enabled derivation of components due to general and specific combining abilities effects, which in turn were used to compute the corresponding genetic components namely; σ_g^2 and σ_s^2 (Becker, 1984; Singh & Chaudhary, 1985). As σ_A^2 is $2\sigma_g^2$ and σ_s^2 equals to σ_D^2 , both narrow-sense (h_{ns}^2) and broad-sense (h_{bs}^2) heritabilities could be estimated. Data were analyzed on DIAL98 statistical software by Ukai (2002) based on the assumptions of absence of non-allelic interaction and independent distribution of genes among the parents.

Heterosis was calculated as: absolute mid-parent heterosis (AMPH): $AMPH = F_1 - P$; absolute better-parent heterosis (ABPH): $ABPH = F_1 - P_{max}$. Mid-parent value ($MPV = P$) was derived from the means of the two parents involved in a cross [i.e. $(P_1 + P_2)/2$]. In addition, calculations were done for the relative mid-parent heterosis (MPH) as $MPH = 100 * (F_1 - P)/P$ and relative better-parent heterosis (BPH) as $BPH = 100 * (F_1 - P_{max}) / P_{max}$ where P_{max} refers to the better performing parent while F_1 is the family mean. For drought tolerance and fermentation, however, the relative mid-parent heterosis and better-parent heterosis were calculated as $(P - F_1)/P * 100$ and $(P_{min} - F_1)/P_{min} * 100$, respectively, where P_{min} refers to the better parent in terms of the two traits whose lower score would indicate better performance. The contrasts were tested with the appropriate two-tailed t tests (Snedecor & Cochran, 1974). Correlation coefficients among the nine characters were calculated according to Zobel and Talbert (1984). Genetic gains arising from expected family and clonal selection for the same characters were calculated using their respective phenotypic standard deviation, heritability, selection intensities, family and

clonal means (Williams and Matheson, 1994). Selection intensities based on family means were calculated by obtaining the means of families with comparable performance to the better parent less the overall family means. On the other hand, clonal mean based selection intensities were derived by calculating the means of within-family clones performing at least 1.5 times better than the better parent less the overall family mean (population mean). The data for genetic gain is

presented as a percentage of means for the characters evaluated. The following formulae applied:

$$G = i\sigma_p h^2$$

Where G is the genetic gain, i is selection intensity which is the difference between the mean of the selected individuals and the overall mean and σ_p is the phenotypic standard deviation.

Table 2: Family means (F₁), for yield, percent total polyphenols, fermentability, drought tolerance, theaflavins, thearubigins, pubescence and bud weight in the 16 hybrids of *C. sinensis*

Family code	Pedigree	Family mean (F ₁)							
		Yield	%TP	FERM	DT	TF(μmol/g)	TR (%)	Pubescence	Bud wt(gm)
467	TRFK 6/8 X TRFK 6/8	2347	21.07	1.50	2.00	19.99	15.94	3.00	0.37
475	TRFK 6/8 X AHP S15/10	2486	22.33	1.50	1.80	22.21	15.23	4.00	0.40
482	TRFK 6/8 X TRFCA SFS150	2440	21.53	1.05	1.30	21.72	15.82	1.80	0.36
476	TRFK 6/8 X EPK TN14-3	2381	23.90	1.53	1.50	22.85	16.99	3.00	0.38
456	AHP S15/10 X TRFK 6/8	2609	20.70	1.21	1.97	22.53	14.52	2.60	0.39
478	AHP S15/10 X AHP S15/10	2499	23.63	1.09	2.00	19.85	15.15	2.60	0.44
485	AHP S15/10 X TRFCA SFS150	2375	21.60	1.11	1.40	19.40	15.12	2.20	0.44
474	AHP S15/10 X EPK TN 14-3	2533	22.20	1.30	1.63	20.05	15.52	3.80	0.36
420	TRFCA SFS150 X TRFK 6/8	2525	22.23	1.39	1.46	22.47	15.93	1.80	0.37
463	TRFCA SFS150 X AHP S15/10	2451	20.60	1.20	1.57	18.57	14.98	3.80	0.47
471	TRFCA SFS150 X TRFCA SFS150	2171	21.93	1.40	1.80	18.68	14.95	3.00	0.38
430	TRFCA SFS150 X EPK TN14-3	2470	21.30	1.15	1.13	18.83	15.75	2.47	0.30
443	EPK TN14-3 X TRFK 6/8	2510	22.63	1.77	1.70	23.66	16.53	2.20	0.32
447	EPK TN14-3 X AHP S15/10	2434	21.20	1.32	1.63	21.71	16.60	4.20	0.38
488	EPK TN14-3 X TRFCA SFS150	1966	20.53	1.00	1.27	25.63	15.50	3.40	0.36
490	EPK TN14-3 X EPK TN14-3	2102	20.33	1.50	2.33	20.46	15.27	3.30	0.32
Overall mean		2394	21.06	1.31	1.66	21.16	15.61	2.95	0.38
Significance of t-test (p = 0.05)		S	S	S	S	S	S	S	S
Parents' performance									
	TRFK 6/8	1708	24.30	1.27	2.00	23.03	17.74	1.00	0.38
	AHP S15/10	2556	20.60	1.83	2.80	18.73	15.58	5.00	0.49
	TRFCA SFS150	2699	22.40	1.40	1.30	18.86	15.53	3.00	0.36
	EPK TN14-3	2478	22.30	1.00	2.00	22.44	17.01	3.00	0.44

TP =percent total polyphenols, FERM = fermentability, DT = drought tolerance, TF = theaflavins, TR = thearubigins

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Table 3: Ranges of clonal means within families for yield, percent total polyphenols, fermentability, drought tolerance, theaflavins, thearubigins, pubescence and bud weight in the 16 hybrids of *C. sinensis*

Family code	Pedigree	Range of traits within family							
		Yield	%TP	Ferm	DT	TF (μmol/g)	TR (%)	Pubescence	Bud wt(gm)
467	TRFK 6/8 X TRFK 6/8	1483-2654	20.10-22.80	1.0-2.0	1.0-2.6	16.56-25.8	16.56-25.80	3.0-3.0	0.22-0.33
475	TRFK 6/8 X AHP S15/10	1834-2790	18.60-26.00	1.0-2.0	1.3-2.0	14.45-27.24	14.45-27.24	3.0-5.0	0.18-0.42
482	TRFK 6/8 X TRFCA SFS150	1516-3050	19.10-24.20	1.0-1.1	1.0-1.7	15.83-30.67	15.83-30.67	3.0-3.0	0.18-0.37
476	TRFK 6/8 X EPK TN14-3	1340-3086	19.40-22.00	1.0-3.0	1.2-2.0	16.80-29.65	16.80-29.65	1.0-3.0	0.17-0.50
456	AHP S15/10 X TRFK 6/8	1794-3458	18.10-24.20	1.0-2.0	1.4-2.2	17.06-30.20	17.06-30.20	3.0-5.0	0.11-0.51
478	AHP S15/10 X AHP S15/10	1631-3002	20.10-26.20	1.0-1.4	1.8-2.2	13.36-26.02	13.36-26.02	1.0-3.0	0.20-0.42
485	AHP S15/10 X TRFCA SFS150	1407-3268	17.90-24.50	1.0-1.3	1.2-2.6	12.15-24.72	12.15-24.72	3.0-5.0	0.11-0.40
474	AHP S15/10 X EPK TN 14-3	2006-3104	18.80-25.80	1.0-2.5	1.0-2.3	15.95-24.23	15.95-24.23	1.0-5.0	0.17-0.43
420	TRFCA SFS150 X TRFK 6/8	1691-3041	18.70-24.90	1.1-1.6	1.1-1.7	26.67-15.19	15.19-26.67	1.0-5.0	0.19-0.32
463	TRFCA SFS150 X AHP S15/10	502-3528	18.90-23.20	1.0-2.0	1.4-2.0	14.40-21.57	14.40-21.57	5.0-5.0	0.24-0.55
471	TRFCA SFS150 X TRFCA SFS150	1120-2415	19.90-24.60	1.0-2.0	1.6-1.9	13.93-25.18	13.93-25.18	1.0-5.0	0.19-0.38
430	TRFCA SFS150 X EPK TN14-3	759-3044	18.00-26.50	1.0-1.6	1.0-1.3	14.47-21.90	14.47-21.90	1.0-5.0	0.16-0.29
443	EPK TN14-3 X TRFK 6/8	1634-3023	18.60-28.50	1.4-2.3	1.3-2.0	18.09-32.66	18.09-32.66	1.0-3.0	0.15-0.35
447	EPK TN14-3 X AHP S15/10	1885-2986	17.20-25.20	1.0-1.5	1.2-1.7	13.68-30.52	13.68-30.52	3.0-5.0	0.17-0.32
488	EPK TN14-3 X TRFCA SFS150	1450-2398	17.00-23.80	1.0-1.0	1.2-2.0	17.06-31.14	17.06-31.14	3.0-3.0	0.22-0.41
490	EPK TN14-3 X EPK TN14-3	796-2212	19.80-22.10	1.0-2.0	1.5-1.7	14.32-25.15	14.32-25.15	1.0-3.0	0.14-0.33

TP =percent total polyphenols, FERM = fermentability, DT = drought tolerance, TF = theaflavins, TR = thearubigins

RESULTS

Phenotypic Variation for Yield, Total polyphenols, Drought Tolerance and Fermentation:

There was significant phenotypic variation ($P \leq 0.05$) for all the traits measured (Table-2) among the progeny and their parents. Progeny from cross AHP S15/10 X TRFK 6/8 had superior fermentability whereas crosses TRFK 6/8 X TRFCA SFS150, TRFCA SFS150 X EPK TN14-3 and TRFCA SFS150 X TRFK

6/8 produced offspring that were both highly drought tolerant and fast-fermenting. A self of EPK TN14-3 gave the lowest yield although it was moderately drought resistant progeny. It also fermented at significantly ($P \leq 0.05$) slower speed than its parent. There was a wide range in performance of nearly all the crosses for all the traits assessed (Table-3). For yield, the widest and narrowest ranges were indicated by crosses TRFK 6/8 X TRFK 6/8 and AHP S15/10 X AHP

S15/10, respectively, both of which are selfs. The widest range for total polyphenols was depicted by TRFK 6/8 X TRFCA SFS150, while the narrowest resulted from cross TRFK 6/8 X TRFK 6/8, a self. Fermentability was the least variable trait for almost all crosses. The widest range was shown by cross TRFK 6/8 X EPK TN14-3, while the narrowest arose from

cross TRFK 6/8 X TRFCA SFS150. Drought tolerance exhibited the greatest variability of the four traits. Crosses TRFK 6/8 X TRFK 6/8 and AHP S15/10 X TRFCA SFS150 produced the most variable progeny while crosses TRFCA SFS150 X TRFCA SFS150 and TRFCA SFS150 X EPK TN14-3 gave the least variable progeny.

Table 4: Mid-parent value for yield, percent total polyphenols, fermentability, drought tolerance, theaflavins, thearubigins, pubescence and bud weight in the 16 hybrids of *C. sinensis*

Family code	Pedigree	MPV							
		Yield	%TP	Ferm	DS	TF(μmol/g)	TR (%)	Pubescence	Bud wt(gm)
467	TRFK 6/8 X TRFK 6/8	1708	24.30	1.50	2.00	23.03	17.74	1.00	0.38
475	TRFK 6/8 X AHP S15/10	2132	22.45	1.50	2.40	20.88	16.66	3.00	0.44
482	TRFK 6/8 X TRFCA SFS150	2204	23.35	1.05	1.65	20.95	16.64	2.00	0.37
476	TRFK 6/8 X EPK TN14-3	2093	23.30	1.53	2.00	22.74	17.38	2.00	0.41
456	AHP S15/10 X TRFK 6/8	2132	22.45	1.21	2.40	20.88	16.66	3.00	0.44
478	AHP S15/10 X AHP S15/10	2556	20.60	1.09	2.80	18.73	15.58	5.00	0.49
485	AHP S15/10 X TRFCA SFS150	2628	21.50	1.11	2.05	18.80	15.56	4.00	0.43
474	AHP S15/10 X EPK TN 14-3	2517	21.45	1.30	2.40	20.58	16.30	4.00	0.47
420	TRFCA SFS150 X TRFK 6/8	2204	23.35	1.39	1.65	20.95	16.64	2.00	0.37
463	TRFCA SFS150 X AHP S15/10	2628	21.50	1.20	2.05	18.80	15.56	4.00	0.43
471	TRFCA SFS150 X TRFCA SFS150	2699	22.40	1.40	1.30	18.86	15.53	3.00	0.36
430	TRFCA SFS150 X EPK TN14-3	2589	22.35	1.15	1.65	20.65	16.27	3.00	0.40
443	EPK TN14-3 X TRFK 6/8	2093	23.30	1.77	2.00	22.74	17.38	2.00	0.41
447	EPK TN14-3 X AHP S15/10	2517	21.45	1.32	2.40	20.58	16.30	4.00	0.47
488	EPK TN14-3 X TRFCA SFS150	2589	22.35	1.00	1.65	20.65	16.27	3.00	0.40
490	EPK TN14-3 X EPK TN14-3	2478	22.30	1.50	2.00	22.44	17.01	3.00	0.44
Overall mean		2360	22.40	1.31	2.03	20.77	16.47	3.00	0.42
Significance of t-test (p = 0.05)		S	S	S	S	S	S	S	S

TP =percent total polyphenols, FERM = fermentability, DT = drought tolerance, TF = theaflavins, TR = thearubigins

Heterosis:

Tables 4 to 6 show the relative magnitude of heterosis against the respective family means for the eight traits. While significant mid-parent value ($P \leq 0.05$) were observed for all traits (Table-4), no significant mid-parent heterosis were detected for yield, total polyphenols, theaflavins and pubescence. The converse was true for fermentability, drought tolerance, thearubigins, and bud weight (Table-5). Similarly, there were no significant better-parent heterosis for yield,

fermentability, drought tolerance, theaflavins and pubescence, while the same was significant for percent total polyphenols. The mid-parent heterosis means for fermentability, drought tolerance, thearubigins and bud weight were significantly high at 108%, 16%, -5.13% and -9.56%, respectively. The mean better-parent heterosis for yield (-5.09%), total polyphenols (-5.7%), fermentation (-12.82%) and pubescence (-10.4%) were markedly lower than the better parent. The clones TRFK 6/8 and AHP S15/10 whether used as female or

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male parents gave progenies with high better-parent heterosis for most of the traits but were inconsistent for theaflavins, thearubigins and pubescence. The highest better-parent heterosis for fermentability coincided with AHP S15/10 when crossed to itself. The availability of transgressive segregants among various hybrids as exhibited by high better-parent heterosis is notable for yield for crosses TRFK 6/8 x TRFK 6/8 (37.41%), AHP S15/10 x TRFK 6/8 (2.07%), percent total polyphenols, fermentability and drought tolerance (DT) for AHP S15/10 x AHP S15/10 (14.71%, 40.44% and 28.57%, respectively), theaflavins (14.22%) (Table-6). Possible

existence of heterotic crosses can be revealed by the ranges for each family in the diallel (Table-3). Considering family and parental means (Table-2) for each trait, crosses outperforming the best performing parents (i.e. best-parent heterosis) by 30.7%, 17.3%, 30%, 41.8% for yield, percent total polyphenols, drought tolerance and theaflavins, respectively in the upper range performance for these traits (Table-3) were apparent. Clones arising from such crosses need exposure to other tea growing regions with farmers' participation to test their adaptability and stability prior to release and large-scale commercialization.

Table 5: Mid-parent heterosis for yield, percent total polyphenols, fermentability, drought tolerance, theaflavins, thearubigins, pubescence and bud weight in the 16 hybrids of *C. sinensis*

Family code	Pedigree	Mid-parent heterosis							
		Yield	%TP	FERM	DT	TF(μ mol/g)	TR (%)	Pubescence	Bud wt(gm)
467	TRFK 6/8 X TRFK 6/8	37.41	-13.29	84.67	0.00	-13.20	-10.15	200.00	-2.63
475	TRFK 6/8 X AHP S15/10	16.60	-0.53	103.33	25.00	6.37	-8.58	33.33	-9.09
482	TRFK 6/8 X TRFCA SFS150	10.71	-7.79	127.62	21.21	3.68	-4.93	-10.00	-2.70
476	TRFK 6/8 X EPK TN14-3	13.76	2.58	74.51	25.00	0.48	-2.24	50.00	-7.32
456	AHP S15/10 X TRFK 6/8	22.37	-7.80	128.10	17.92	7.90	-12.85	20.00	-11.36
478	AHP S15/10 X AHP S15/10	-2.23	14.71	167.89	28.57	5.98	-2.76	-48.00	-10.20
485	AHP S15/10 X TRFCA SFS150	-9.63	0.47	145.95	31.71	3.19	-2.83	-45.00	2.33
474	AHP S15/10 X EPK TN 14-3	0.64	3.50	109.23	32.08	-2.58	-4.79	-5.00	-23.40
420	TRFCA SFS150 X TRFK 6/8	14.56	-4.80	96.40	11.52	7.26	-4.27	-10.00	0.00
463	TRFCA SFS150 X AHP S15/10	-6.74	-4.19	135.00	23.41	-1.22	-3.73	-5.00	9.30
471	TRFCA SFS150 X TRFCA SFS150	-19.56	-2.10	100.00	-38.46	-0.95	-3.73	0.00	5.56
430	TRFCA SFS150 X EPK TN14-3	-4.60	-4.70	104.35	31.52	-8.81	-3.20	-17.67	-25.00
443	EPK TN14-3 X TRFK 6/8	19.92	-2.88	64.41	15.00	4.05	-4.89	10.00	-21.95
447	EPK TN14-3 X AHP S15/10	-3.30	-1.17	107.58	32.08	5.49	1.84	5.00	-19.15
488	EPK TN14-3 X TRFCA SFS150	-24.06	-8.14	120.00	23.03	24.12	-4.73	13.33	-10.00
490	EPK TN14-3 X EPK TN14-3	-15.17	-8.83	66.67	-16.50	-8.82	-10.23	10.00	-27.27
Overall mean		3.17	-2.81	108.48	16.44	2.06	-5.13	12.56	-9.56
Significance of t-test (p = 0.05)		NS	NS	S	S	NS	S	NS	S

TP =percent total polyphenols, FERM = fermentability, DT = drought tolerance, TF = theaflavins, TR = thearubigins

Heritability estimates and other genetic parameters:

The heritability estimates are presented in table-7. The narrow sense and broad sense heritabilities estimated for most of the traits measured were high. But the narrow-sense heritability estimate for total

polyphenols was low. Generally, the high heritabilities for the traits measured indicate that they are highly heritable and significant strides are likely to be achieved if judicious breeding and clonal selection were to be undertaken.

Table 6: Better-parent heterosis for yield, percent total polyphenols, fermentability, drought tolerance, theaflavins, thearubigins, pubescence and bud weight in the 16 hybrids of *C. sinensis*

Family code	Pedigree	Better-parent heterosis							
		Yield	%TP	Ferm	DT	TF($\mu\text{mol/g}$)	TR (%)	Pubescence	Bud wt(gm)
467	TRFK 6/8 X TRFK 6/8	37.41	-13.29	-18.11	0.00	-13.20	-10.15	200.00	-2.63
475	TRFK 6/8 X AHP S15/10	-2.74	-8.11	-18.11	10.00	-3.56	-14.15	-20.00	-18.37
482	TRFK 6/8 X TRFCA SFS150	-9.60	-11.40	17.32	0.00	-5.69	-10.82	-40.00	-5.26
476	TRFK 6/8 X EPK TN14-3	-3.91	-1.65	-53.00	25.00	-0.78	-4.23	0.00	-13.64
456	AHP S15/10 X TRFK 6/8	2.07	-14.81	4.72	1.50	-2.17	-18.15	-48.00	-20.41
478	AHP S15/10 X AHP S15/10	-2.23	14.71	40.44	28.57	5.98	-2.76	-48.00	-10.20
485	AHP S15/10 X TRFCA SFS150	-12.00	-3.57	20.71	-7.69	2.86	-2.95	-56.00	-10.20
474	AHP S15/10 X EPK TN 14-3	-0.90	-0.45	-30.00	18.50	-10.65	-8.76	-24.00	-26.53
420	TRFCA SFS150 X TRFK 6/8	-6.45	-8.52	-9.45	-12.31	-2.43	-10.20	-40.00	-2.63
463	TRFCA SFS150 X AHP S15/10	-9.19	-8.04	14.29	-20.77	-1.54	-3.85	-24.00	-4.08
471	TRFCA SFS150 X TRFCA SFS150	-19.56	-2.10	0.00	-38.46	-0.95	-3.73	0.00	5.56
430	TRFCA SFS150 X EPK TN14-3	-8.48	-4.91	-15.00	13.08	-16.09	-7.41	-17.67	-31.82
443	EPK TN14-3 X TRFK 6/8	1.29	-6.87	-77.00	15.00	2.74	-6.82	-56.00	-27.27
447	EPK TN14-3 X AHP S15/10	-4.77	-4.93	-32.00	18.50	-3.25	-2.41	-16.00	-22.45
488	EPK TN14-3 X TRFCA SFS150	-27.16	-8.35	0.00	2.31	14.22	-8.88	13.33	-18.18
490	EPK TN14-3 X EPK TN14-3	-15.17	-8.83	-50.00	-16.50	-8.82	-10.23	10.00	-27.27
Overall mean		-5.09	-5.70	-12.82	2.30	-2.71	-7.84	-10.40	-14.71
		NS	S	NS	NS	NS	S	NS	S

TP =percent total polyphenols, FERM = fermentability, DT = drought tolerance, TF = theaflavins, TR = thearubigins

Genetic gains:

Genetic gains estimated from h^2 and H^2 for the traits measured are presented in table-8. Generally, genetic gain that arose from family selection were markedly lower compared to those realized from within family (clonal) selection. Additionally, the magnitude of response to selection would be higher under broad sense heritability than narrow-sense heritability. Lower magnitudes of genetic gain were achieved for traits that have hitherto been receiving attention than those that began receiving attentions recently owing to global climatic changes like drought and need to diversify tea products like percent total polyphenols, and pubescence. The lower magnitude of genetic gain for fermentation under h^2 may be attributed to narrow genetic variability which gives very little room for selection. Higher genetic gains are tenable owing to the high H^2 estimates shown by the eight characters coupled with high clonal selection intensity imposed by use of adequate effective population size.

Correlation coefficients among the nine traits:

Linear correlation coefficients (r) among the traits that were significant included; yield and percent total polyphenols (0.61, $P < 0.01$), percent total polyphenols and fermentability (0.54, $P < 0.05$), percent total polyphenols and percent thearubigins (0.66, $P < 0.01$), fermentability and drought tolerance (0.67, $P < 0.01$), fermentability and percent thearubigins (0.67, $P < 0.01$) (Table-9). The rest were weakly correlated (e.g. yield and drought tolerance: 0.23, yield and fermentability: 0.31, and theaflavins and pubescence: 0.24).

DISCUSSION

The mating analysis method employed, gave good indicators of the genetic parameters governing the traits measured within the moderate sample size used. Certain progenitors were more associated with superior traits than others. For example, TRFK 6/8 and AHP S15/10 gave superior progeny for high yields, fermentability, and drought tolerance, while the progeny with best

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better-parent heterosis for total polyphenols resulted from AHP S15/10 either as female or male parent. This implies that efforts meant to improve these traits should involve these progenitors in the hybridization programme. The present study reveals genetic effects

rather than environmental factors to be the underlying cause of the observed heterosis. The considerable variation revealed in the test for the eight traits combined with high heritability serve to emphasize the prevalence of great room for selection.

Table 8: Percent genetic gains of the measured traits based on narrow and broad-sense heritabilities

Trait	percent genetic gain			percent genetic gain		
	$h^2 \pm$ s.e.	family mean	clonal mean	$H^2 \pm$ s.e.	family mean	clonal mean
Yield	0.44 ± 0.16	2.8	14.1	0.56 ± 0.15	3.5	17.9
%TP	0.09 ± 0.07	1.2	2.5	0.88 ± 0.04	11.3	24.0
Ferm	0.45 ± 0.04	6.7	8.9	0.98 ± 0.01	14.2	19.5
DT	0.61 ± 0.06	11.6	20.6	0.96 ± 0.01	18.5	32.4
TF(μ mol/g)	0.28 ± 0.12	4.6	13.1	0.71 ± 0.09	11.7	33.2
TR (%)	0.29 ± 0.15	2.0	29.5	0.62 ± 0.13	4.4	61.3
Pubescence	0.43 ± 0.04	16.8	30.0	0.98 ± 0.00	38.2	68.1
Bud dry wt	0.74 ± 0.09	11.0	27.3	0.81 ± 0.06	13.9	29.8

NB: s.e. designates standard error.

The significance of heterosis in breeding is best exhibited by better-parent heterosis, which directly illustrates the superiority of a hybrid over the best performing parent under cultivation. The importance of mid-parent heterosis has been emphasized (Barth *et al.*, 2003), especially as regards the expected quadratic relationship to the parental genetic distance under a simple genetic model. The mean data revealed that the best progeny for yield was only marginally worse (better-parent heterosis of -5.09%) than the better parent TRFCA SFS150, hence the shift of focus to mid-parent heterosis. The highest better-parent heterosis (2.30) was recorded for drought tolerance. Black tea quality improvement in Kenya has only been relying on sensory evaluation and fermentability (Seurei, 1996). Recently efforts to develop reliable black tea parameters to assist in selection of elite black tea quality cultivars based on correlation between tea green leaf polyphenols, and black tea theaflavins, thearubigins and tasters' scores were reported (Owuor *et al.*, 2006 and Wright *et al.*, 2000). Such studies have pointed to the positive contribution of theaflavins towards valuation of Kenyan black teas (Owuor *et al.*, 1986; 2006 and Owuor & Obanda, 2007). Similar results have been obtained in Malawi (Cloughley, 1981; Wright *et al.*, 2002), North East India (Deb & Ullah, 1968) and Sri Lanka (Roberts and Fernando, 1980). Thearubigins are responsible for colour and thickness of black tea.

A better-parent heterosis for total polyphenols, fermentation, pubescence and bud weight (Table-6) were low under family mean criteria but the scenario were different within-family variability. The possibility

that better-parent heterosis entirely improves when the best full-sib clonal progeny means are considered indicates that a lot of caution need to be taken while judging the performance of the progeny based solely on family means.

The significant mid-parent heterosis values for fermentability, and drought tolerance, and to a lesser extent, pubescence (Table-5) served to emphasize the availability of elite quality cultivars which can be exploited to improve quality of tea. Yield only scored a mid-parent heterosis of 3.17%. This is an indication that despite the allogamous nature of tea crop, the trait was approaching a ceiling in its improvement unless new sources of germplasm are identified or biotechnological approaches such as mutation breeding are employed to cause further higher yields while possibly compromising other characters. The amount of heterosis is much smaller in autogamous than in allogamous crops (Melchinger and Gumber, 1998). However, dearth in knowledge of heterosis in *Camellia* sp. is evident by lack of previous studies, except one (Bezbaruah, 1974) in which the heterotic response for tea yield ranged from 21% to 85% over the mid-parental values while the quality of made tea approached the mid-parent value for F₁ hybrids of most seedling populations of tea. While four hybrids were comparable to results of Bezbaruah (1974) for yield, majority of the crosses had over 25% mid-parent heterosis for fermentation and drought tolerance, (Table-5). Many of the crosses

involving TRFK 6/8 had significantly higher mid-parent heterosis than others. Those crosses also scored high mid-parent heterosis for, theaflavins. The fact that the parents involved in our study were good performing clones in commercial plantations (Wachira, 2002) and coupled with overemphasis on improving yields and fermentation as the traditional primary traits indicates that further progress of these traits could be approaching their ceiling. The use of disparate parental materials in the current study notwithstanding, heterotic hybrids could only be observed within families but not between families. The ease of propagation of tea using vegetative propagation, however, allows for considerable progress if judicious clonal selection

within families is imposed. Drought tolerance was the most variable character. This is not surprising as breeding for drought tolerance was previously not considered as a trait for improvement of tea in Kenya. Following the severe drought incidence in 1997 when huge clonal tea fields were wiped out in Kenya, drought tolerance has become an important trait in selection of tea cultivars. Additionally, the freak frost incidence in Kenya of 2000 further emphasized the need to develop drought and frost tolerant cultivars. The marked genetic variability both within and between crosses coupled with high heritability serve to confirm that considerable in roads can be achieved in the breeding for drought tolerance trait.

Table 9: Correlation coefficients among the measured nine traits

	Yield	%TP	FERM	DT	TF(μmol/g)	TR (%)	Pubescence	Bud wt(gm)
Yield	1	0.612*	0.313	0.225	0.392	0.253	0.462	0.441
%TP		1	0.541*	0.215	0.276	0.664**	0.460	0.356
FERM			1	0.667**	0.373	0.67**	0.329	0.585*
DT				1	0.399	0.545*	0.502*	0.276
TF(μmol/g)					1	0.616**	0.237	0.531*
TR (%)						1	0.212	0.637**
Pubescence							1	0.436
Bud wt(gm)								1

NB: *, ** and *** denote significance levels at $P < 0.05$, $P < 0.001$ and $P < 0.0001$, respectively

The heritability estimates, additive and dominance variances for yield indicate that the character was controlled by additive genes and further progress can be realized if selection is cautiously undertaken. The other traits namely total polyphenols, fermentability, drought tolerance, theaflavins, thearubigins, pubescence and bud weights reveal non-additive gene action to be influential in the expression of the traits. The apparent dominant nature of the fermentability character was also observed (Toyao, 1982) in a study of inheritance of non-fermenting trait in tea plant and the consistency of the results obtained in the present study confirmed that this trait is governed predominantly by non-additive genes. Yield is a polygenic character, although non-additive gene effects are occasionally observed. Comparative results have been observed in cacao (Dias and Kageyama, 1995) where the effects of specific combining ability (SCA) (read non-additive effects) were greater than general combining ability (GCA) (read additive effects) for yield. Thus, in seed gardens composed of many parents, accumulation of favourable alleles with additive genetic effects on yield in the improved generations is likely to be successful.

The strong non-additive genetic effects that are also characterized by high broad-sense heritabilities for majority of the traits, coupled with considerable clonal variation and moderate mid-parent heterosis, may imply that the straight forward procedure of selecting suitable clones and allowing them to pollinate randomly even in properly designed polyclonal seed orchards (baries) might not result in improved performance in the traits. Thus, improvement efforts for traits showing strong influence by non-additive genes might call for a different breeding approach such as controlled crosses or establishment of biclinal seed orchards. The improved biclinal seedlings can then be multiplied by vegetative means following progeny testing and clonal selection and used to establish new plantations. The broadened genetic base of commercial cultivars would mitigate attendant risks normally associated with monocropping. As heritability estimates vary with age, season and environment in which genetic tests are conducted (Zhang *et al.*, 1996), their applicability is limited to the environment in which the study was undertaken. There is need, to replicate the same experiment in other sites with different environmental

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components in order to strengthen the reliability of the derived genetic variances. Further, clones arising from crosses with marked best parent heterosis for economic traits need to be comparatively exposed to other tea growing regions in order to test their adaptability and stability prior to their release for commercial utilization.

Among the significant correlation coefficients, the most important ones were yield and percent total polyphenols (0.61, $P < 0.01$), percent total polyphenols and fermentability (0.54, $P < 0.05$), percent total polyphenols and percent thearubigins (0.66, $P < 0.01$), fermentability and drought tolerance (0.67, $P < 0.01$) and suggest that the traits could be controlled by linked genes or genes with pleiotropic effects, and therefore improving on one trait may lead to improvement of the others. These traits need to be rationalized in a breeding programme for the possibility of simultaneous improvement point to development of novel variety for specialty tea products. The weakly correlated traits like yield and drought, yield and fermentability suggest lack of significant genetic relationship between any two of the measured characters. Efforts to recombine all or any two traits into one clone simultaneously are unlikely to be easy. More studies are needed to confirm this conclusion. Besides, selection for one trait may

adversely affect or might not enhance the performance of the other. This kind of relationship nevertheless may allow for selection of traits in tandem beginning with the most important attributes followed by the others. Further studies in different environments are required to confirm this proposition. Genetic correlation studies involving even more traits will reveal which characters are synergistic (positively linked) and can be packaged into a single genotype and which ones are antagonistic and hence cannot be recombined easily.

The present study showed that moderate gains can be registered for all the traits if the appropriate clonal selection criterion is instituted based on heritabilities obtained. The values compared favourably with those reported (Lin and Zsuffa, 1993), for biomass production based on individual ramets and clonal means in *Salix eriocephala*. Greater gains are obtainable through manipulating the selection differential and selecting only individuals that meet set minimum criteria for all traits of interest. Faster progress could be realised if more precise selection tools are developed and by employing appropriate methods of indirect selection (Wright, 1976; Falconer 1981) and marker-assisted selection as has been proposed in other studies (Hackett *et al.*, 2000; Wachira *et al.*, 1995; 1997; 2001).

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Table 7: Genetic parameters and their standard errors for yield, percent total polyphenols, fermentability, drought tolerance, theaflavins, thearubigins, pubescence and bud weight in the 16 hybrids of *C. sinensis*

Parameter	Yield		Total polyphenols		Fermentability		Drought tolerance		Theaflavin		Thearubigins		Pubescence		Bud dry weight	
	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.
D (Additive variance)	10764.71	16035.96	1.88	0.64	0.04	0.01	0.12	0.03	-0.32	1.12	-0.02	0.29	0.04	0.02	0.00	0.00
H1 (Dominance variance 1)	10491.04	24598.87	5.01	1.33	0.24	0.03	0.16	0.03	5.93	3.63	0.81	0.76	1.50	0.15	0.00	0.00
H2 (Dominance variance 2)	9498.81	19339.78	3.52	0.94	0.17	0.02	0.13	0.03	5.27	2.99	0.69	0.61	1.03	0.10	0.00	0.00
D/(D+E) (Heritability by parents)	0.56	0.86	0.93	0.03	0.96	0.02	0.97	0.01	-0.56	3.48	-0.10	3.18	0.83	0.12	0.83	0.14
h ² b (Heritability for diallel in a broad sense)	0.56	0.15	0.88	0.04	0.98	0.01	0.96	0.01	0.71	0.09	0.62	0.13	0.98	0.00	0.81	0.06
h ² n (Heritability for diallel in a narrow sense)	0.44	0.16	0.09	0.07	0.45	0.04	0.61	0.06	0.28	0.12	0.29	0.15	0.43	0.04	0.74	0.09
Mean of Parents	2354.60	44.70	21.74	0.18	1.37	0.02	1.77	0.03	19.75	0.47	15.33	0.23	2.82	0.04	0.38	0.01
Mean of F ₁ s	2431.80	25.20	21.73	0.11	1.37	0.01	1.53	0.02	21.62	0.28	15.71	0.13	2.94	0.03	0.38	0.01
Overall means	2412.50	22.00	21.73	0.09	1.37	0.01	1.59	0.02	21.15	0.25	15.61	0.12	2.91	0.02	0.38	0.01
Variance of Parents	18997.50	15886.39	2.02	0.64	0.04	0.01	0.12	0.03	0.57	1.09	0.18	0.28	0.05	0.02	0.00	0.00
Variance of F ₁ s	11772.68	6555.41	0.63	0.19	0.08	0.01	0.05	0.01	2.04	0.83	0.44	0.19	0.49	0.04	0.00	0.00

Quantitative Genetic Parameters for Yield