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Full Length Research Paper

Quantitative genetic parameters in tea (*Camellia sinensis* (L.) O. Kuntze): I. combining abilities for yield, drought tolerance and quality traits

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The combining abilities for yield, drought tolerance and quality related traits in *Camellia sinensis* were estimated using a 4 x 4 full diallel mating design. There was significant phenotypic variation for the nine traits measured among the progeny and their parents. Generally, parents with good combining ability produced progeny with above average performance for all the traits evaluated. The general combining ability (GCA) effects were significant for all but one black tea quality trait, TF:TR, while specific combining ability (SCA) effects were significant for fermentability, pubescence and bud weight. All the traits but TF:TR however were predominantly governed by additive gene effects. Strong maternal influence for all traits was evident except for thearubigins and bud weight signifying the importance of the choice of female parents in tea breeding programmes targeting yield, abiotic stress related traits and processing of black tea and special tea products like the silvery tips. Significant non-additive effects were demonstrated by all traits apart from yield, TF:TR and bud weight. However, only drought tolerance, TF and pubescence exhibited unidirectional dominance effects. The results show that the assessed traits are highly heritable and guided breeding and judicious clonal selection would lead to further tea improvement. Although no trait can be treated singly, utilization of open pollinated seed targeted towards improvement of yield and black tea quality traits particularly high levels of total polyphenols and pubescence aimed at developing a designer clone for specialty tea product would suffice given judicious choice and inclusion of suitable progenitors in seed orchards. It is inferred that the basic information about combining abilities is valuable for breeding of elite cultivars.

Key words: Tea, *Camellia sinensis*, general combining ability, specific combining ability

INTRODUCTION

Tea (*Camellia sinensis* (L.) O. Kuntze) is the most widely consumed non-alcoholic beverage in the world, and consequently the most important crop species in the genus *Camellia*, which has over 200 species reported so far (Chang and Bartholomew, 1984) . Tea is consumed either as a black (fermented), green (non-fermented) or oolong (semi-fermented) beverage with the process of manufacture for each type varying (Hampton, 1992; Takeo, 1992). The manufacture process of black tea, in particular, normally entails an oxidation of the polyphenolic compounds (fermentability) during which certain chemical changes take place (Hampton, 1992).

Other tea products include the orthodox teas, decaffeinated tea, specialty and herbal teas and silvery tips (Banerjee, 1992; Gill, 1992). Quality of each type of tea product is largely dependent upon the type of tea cultivar, which provides the raw material for its manufacture. Studies undertaken to evaluate quality of black tea by chemical means have revealed theaflavin (TF) and thearubigin (TR) to be major components that are largely responsible for briskness, brightness, strength and colour of black tea (Roberts, 1958, 1962; Woods and Roberts,

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

Clone	Varietal type	Special attributes
EPK TN14-3	Kenyan Chinary local selection	Tolerant to high soil pH and cold but susceptible to red crevice mites (*Brevipalpus phoenicis*) 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%)

1964) . Thus, when tea liquor is termed as bright and brisk, usually such teas fetch high market value. Thus, quality improvement in addition to other important attributes of tea has been an essential component of tea breeding.

The tea plant is a highly out crossing, strongly but not absolutely self-incompatible tree species (Rogers, 1975; Wachira and Kamunya, 2005), owing to which it is highly heterogeneous and heterozygous (Banerjee, 1992). The allogamous characteristic of tea coupled with its perennial nature implies that development of true hybrids via conventional means is an onerous task if not nearly impossible.

Although significant strides have been made in tea improvement over the last three decades, faster progress in the development of improved cultivars would have been realized had it not been for the dearth of knowledge in gene action responsible and combining abilities for the primary desirable traits like yield and quality as well as other secondary attributes. As such, the success of obtaining desirable crosses is unpredictable as crossing activities are based on chance rather than informed choices. The acquisition of information on combining abilities for the most important traits is a prerequisite in determining the most suitable mating designs and appropriate parents to involve in the hybridization programmes. By analyzing the combining abilities, clues of the nature of gene action and desirable parents for the target traits will be revealed (Can et al., 1997).

A number of methods that help in deciphering the inheritance pattern of economically important quantitative traits exist. Amongst the most popularly used are the mating designs suggested by Kempthorne (1957) (that is, Line x Tester), partial diallel (Kempthorne and Curnow, 1961) and full diallel (Grifffing, 1956; Hayman, 1954a; Hayman, 1954b). The GCA and SCA variances and their effects derived from these designs could be useful in devising breeding strategies for crop plants. Although scant data from these designs exist for tea, studies employing diallel analysis have been reported (Ikeda and Amma, 2004). Their study, however, only addressed the inheritance of resistance to Anthrancnose disease in tea involving 5 clonal cultivars using a full diallel analysis. From the study, they were able to tell which cultivars could be harbouring dominant and recessive genes as well as elucidated the influence of additive and non-additive effects in the resistance of the disease.

The role of good combiners in all aspects of crop improvement including the use of heterosis in tea breeding has rarely been emphasized, a prerequisite that cannot be ignored, considering the role of tea industry in improving livelihoods of resource poor farmers in tea growing countries. Related to this is the genetic distance of the target parents. Fortunately for tea, numerous such data (Wachira et al., 1995, 1997, 2001) exist and thus integrated breeding approaches are likely to yield encouraging results.

In this study, a diallel cross was used to study the combining abilities for three important agronomic traits; yield, bud weight and drought tolerance, four traits related to the quality of black tea namely fermentability, total polyphenols, theaflavins and thearubigins and pube-scence which is a trait relevant for processing of a specialty tea product widely called “silvery tips”. A full diallel design was employed to generate information on GCA, SCA, maternal and non-maternal effects in the expression of the traits among the crosses. The implications of the genetic parameters studied and their utilization in tea breeding strategies and clonal selection are discussed.

MATERIALS AND METHODS

Test material

A 4 x 4 full diallel cross trial was established in the year 2000 at the Timbilil estate (0° 22’ S, 35° 21’ E and at an altitude of 2180 m a.m.s.l.) of the Tea Research Foundation of Kenya (TRFK), Kericho. The sixteen clonal full-sib families and four parental clones used 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 (that is, 13448 plants/ha). The four parental clones involved in the diallel cross are amongst the most popular Kenyan commercial tea clones 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 had been receiving 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 (Anon., 2002). The following traits were scored in the test families, parental and control clones.

Crop yields

Yield data collection of the plucked two leaves and a bud commenced in February, 2001 and continued up to December, 2007. Harvesting was carried out at average intervals of 7 to 10 days 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 prior to statistical analyses.

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 from a standard curve generated using gallic acid, and were expressed as the amount of gallic equivalent. The total polyphenol content was expressed as per cent by mass on a dry matter basis following procedures out - lined in British Standard ISO document (BS ISO 14502-1:2005(E)).

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 fermenter); 2- dull brown (moderate fermenter); 3- greenish tinge (poor fermenter); 4- green (non-fermenter).

Drought damage assessment

Drought damage was conducted during periods of severe water stress that is normally accompanied by frost incidence such as that which occurred in January to April, 2003 and November, 2005 to April, 2006, rendering the plants to suffer widespread drought damage and marked drop in production of green leaf. Thus, 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.

Total theaflavins (TF) content

Black tea quality analysis was conducted from miniature manufactured tea samples obtained from each of the clones represented in the trial. The tea leaf was withered at room temperature for 18 h. Upon maceration, the tea was fermented for 90 min under ambient temperature (22°C) and relative humidity. The fluid drier system was utilized in firing the tea, initially at 120°C for about 20 min then lowered to 100°C for 10 min. Total TF were determined by the flavognost method as described by Hilton (1973).

Total Thearubigins (TR)

Total TR were calculated 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 that was first described by Wight and Barua (1954). Thus, assessment of pubescence was carried out under a light dissecting microscope as follows: 1 for glabrous buds and leaves with hair only on the midrib; 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 ones which had been dried at 70°C for 48 h.

Statistical analysis

The general combining ability (GCA), specific combining ability (SCA) and reciprocal effects were estimated according to Griffing’s diallel Model I that assumes fixed effects (Method 1) (Griffing, 1956), while partitioning of various genetic components namely, a (additive), b (non-additive, sub-divided further into b1, b2 and b3), c (maternal) and *d* (reciprocal) followed Hayman’s approach (1954a). Further analysis of %TP, FERM, TF and PUB data using Vr (variance of each cross) and Wr (covariance between parents and their progeny) approach of Hayman (1954b) was done because of significance of item b (non-additive variance) and their potential basis for tea product diversification. The distance between the origin and the point where the regression line cuts the *Wr* axis provided a measure of average degree of dominance (Singh and Chaudhary, 1985):

(i) $D > H_1$ (partial dominance) when intercept is positive;
(ii) $D > H_1$ (complete dominance) when line passes through the origin;

$D > H_1$ (overdominance) when intercept is negative, and
No dominance when the regression line touches parabola limit. Data were analysed on DIAL98 statistical software by Ukai (2002: http://www.asahi-net.or.jp/~fh6y.uki) based on the assumptions of absence of non-allelic interaction and independent distribution of genes among the parents.

RESULTS

Phenotypic variation for measured traits

There was significant phenotypic variation (P = 0.05) for all the traits measured (Table 2) among the progeny and

Table 2. Family means (F), for yield, %TP (percent total polyphenols, Ferm (fermentability), DT (drought tolerance), TF (theaflavins), TR (thearubigins), TF: TR, pubescence and bud weight in the 16 hybrids of *C. sinensis*.

		Family mean (F_1)								
Family No.	**Pedigree**	**Yield**	**%TP**	**Ferm.**	**DT**	**TF(umol/g)**	**TR (%)**	**TF:TR**	**Pubescence**	**Bud wt(gm)**
467	TRFK 6/8 X TRFK 6/8	2347	21.07	1.50	2.00	19.99	15.94	0.11	3.00	0.37
475	TRFK 6/8 X AHP S15/10	2486	22.33	1.50	1.80	22.21	15.23	0.11	4.00	0.40
482	TRFK 6/8 X TRFCA SFS150	2440	21.53	1.05	1.30	21.72	15.82	0.10	1.80	0.36
476	TRFK 6/8 X EPK TN14-3	2381	23.90	1.53	1.50	22.85	16.99	0.10	3.00	0.38
456	AHP S15/10 X TRFK 6/8	2609	20.70	1.21	1.97	22.53	14.52	0.11	2.60	0.39
478	AHP S15/10 X AHP S15/10	2499	23.63	1.09	2.00	19.85	15.15	0.10	2.60	0.44
485	AHP S15/10 X TRFCA SFS150	2375	21.60	1.11	1.40	19.40	15.12	0.09	2.20	0.44
474	AHP S15/10 X EPK TN 14-3	2533	22.20	1.30	1.63	20.05	15.52	0.10	3.80	0.36
420	TRFCA SFS150 X TRFK 6/8	2525	22.23	1.39	1.46	22.47	15.93	0.09	1.80	0.37
463	TRFCA SFS150 X AHP S15/10	2451	20.60	1.20	1.57	18.57	14.98	0.09	3.80	0.47
471	TRFCA SFS150 X TRFCA SFS150	2171	21.93	1.40	1.80	18.68	14.95	0.09	3.00	0.38
430	TRFCA SFS150 X EPK TN14-3	2470	21.30	1.15	1.13	18.83	15.75	0.08	2.47	0.30
443	EPK TN14-3 X TRFK 6/8	2510	22.63	1.77	1.70	23.66	16.53	0.11	2.20	0.32
447	EPK TN14-3 X AHP S15/10	2434	21.20	1.32	1.63	21.71	16.60	0.09	4.20	0.38
488	EPK TN14-3 X TFFCA SFS150	1966	20.53	1.00	1.27	25.63	15.50	0.12	3.40	0.36
490	EPK TN14-3 X EPK TN14-3	2102	20.33	1.50	2.33	20.46	15.27	0.11	3.30	0.32
	Overall mean	2394	21.06	1.31	1.66	21.16	15.61	0.10	2.95	0.38
	Significance of t-test (p = 0.05)	S	S	S	S	S	S	S	S	S
	Parents' performance									
	TRFK 6/8	1708	24.30	1.27	2.00	23.03	17.74	0.09	1.00	0.38
	AHP S15/10	2556	20.60	1.83	2.80	18.73	15.58	0.08	5.00	0.49
	TRFCA SFS150	2699	22.40	1.40	1.30	18.86	15.53	0.08	3.00	0.36
	EPK TN14-3	2478	22.30	1.00	2.00	22.44	17.01	0.09	3.00	0.44

their parents. Results on mean yield indicate that progeny from crosses AHP S15/10 x TRFK 6/8, AHP S15/10 x EPK TN14-3 and TRFCA SFS150 x TRFK 6/8 were more superior whereas the cross EPK TN14-3 x TRFCA SFS150 and inbred crosses of EPK TN14-3 and TRFCA SFS150 were inferior in that order. The inbred cross of AHP S15/10 gave comparable yield performance to other hybrids such as TRFK 6/8 x TRFCA SFS150 and TRFCA SFS150 x EPKTN14- 3. Crosses TRFK 6/8 x AHP S15/10, AHPS15/10 x TRFK 6/8 and EPK TN14-3 x TRFK 6/8 had a combination of superior performance for at least four attributes namely yield, percent total polyphenols, fermentability, drought tolerance, TF, and bud weight. Based on family means alone, none of the crosses produced progeny that had outstanding performance for yield, total polyphenols, TR, pubescence

Table 3. Recapitulation of MS for the genetic parameters of the measured traits

		Mean squares								
Source	**df**	**Yield**	**%TP**	**FERM**	**DT**	**TF(umol/g)**	**TR (%)**	**TF:TR**	**PUB**	**Bud Wt(gm)**
Rep	2	80672	0.6	0.02	0.03	7.54	10.97	0.030	0.04**	0.005
a	3	129600**	1.7*	0.4**	0.67**	13.83**	2.62*	0.008*	2.4**	0.02*
b	6	37390	5.7**	0.3**	0.2**	10.42**	1.6*	0.003	1.56**	0.002
b1	1	53631	0.0	0.0	0.5**	31.51**	1.28	0.005	0.13**	0.00002
b2	3	36841	9.4**	0.4**	0.23**	7.35	1.48	0.001	2.87**	0.001
b3	2	30094	2.8**	0.1**	0.0	4.48	1.93	0.005	0.31**	0.01*
c	3	100287*	1.8*	0.1**	0.05**	17.43**	0.52	0.008*	2.14**	0.001
d	3	54071	1.9**	0.017*	0.02	7.92*	0.49	0.009*	0.95**	0.005
Error	30	24698	0.4	0.0058	0.01	2.69	0.61	0.002	0.02	0.0024
Total	**47**									

NB: * and ** denote significance at $P < 0.05$ and $P < 0.01$, respectively; a denotes additive variance, b non-additive and is sub-divided into b1, b2 and b3 indicating directional dominance, extent of directional dominance and residual dominance, respectively, c maternal and d reciprocal differences other than maternal. Genetic parameters were derived using the method of Hayman (1954a).

Table 4. Recapitulation of MS for combining abilities of the measured traits.

		Mean squares								
Source	**df**	**Yield**	**%TP**	**FERM**	**DT**	**TF(umol/g)**	**TR (%)**	**TF:TR**	**PUB**	**Bud Wt(gm)**
Rep	2	17028	0.7	0.04	0.02	7.89	4.88	0.004	0.0045	0.01
gca	3	109402**	5.1**	0.8***	0.54**	19.46**	3.54*	0.001	5.13***	0.01**
sca	6	30147	2.8**	0.1**	0.004	4.49	1.93	0.001	0.31**	0.01**
Reciprocal	6	77179**	1.8*	0.1**	0.04*	12.68*	0.5	0.002**	1.55**	0.003
Error	22	11086	0.5	0.011	0.01	2.59	0.61	0.00044	0.0045	0.0017
Total	35									

[†] Combining abilities were determined using the method 1, model I of Griffing (1956).

and bud weight. The crosses with superior pubescence had AHP S15/10 either as female or male parent. Cross EPK TN14-3 x TRFCA SFS150 had significantly higher levels of TF and TF:TR indicating superior black tea quality even over the highest black tea quality clone TRFK 6/8.

Genetic effects

The ANOVAs for the various genetic components and combining ability effects are presented in Tables 3 and 4, respectively. All the traits demonstrated predominant additive gene effects ($P < 0.05$); non-additive effects were significant for all but yield, TF:TR and bud weight (Table 3). Table 4 further shows that SCA effects for yield, DT, TF, TR and TF:TR were not significant.. However, once SCA was dissected into individual components, significant dominance effects were observed for DT, TF and PUB as shown by b1, which indicates directional dominance (Table 3). Further, significant GCA effects were observed for all traits save for TF:TR (Table 4). Although GCA and SCA were mutually significant for %TP, FERM and PUB, these traits were predominantly influenced by additive genes as accentuated by GCA/SCA ratios of 1.8, 8 and 16.5, respectively. Variances of various crosses (Vr) were plotted against covariances between parents and their progeny (Wr) to reveal which parents harboured more dominant genes. Results of %TP, FERM, TF and PUB are presented in Figures 1 to 4, respectively. Based on the figures and considering the assumption of absence of non- allelic interaction and independent distribution of genes among parents (Jinks, 1954; Hayman, 1954b), trait-dependent interpretation could be derived. In the case of %TP (Figure 1) and FERM (Figure 2), parents 1 (TRFK 6/8) and 3 (TRFCA SFS150) displayed overdominance effects. Similarly, overdominance was expressed by parents 1 and 4 (EPK TN14-3) for TF (Figure 3). Contrary to what has always been assumed, parents 3 and 4 (Figure 4) seemed to carry more dominant genes for PUB, even though they are known to be least pubescent.

Significant maternal effects were revealed for all traits except TR and bud weight (Table 3) . Non-maternal effects were significant for %TP, FERM, TF, TF:TR and PUB (Table 4). Generally, the importance of reciprocal effects for yield, %TP, FERM, DT and PUB is confirmed

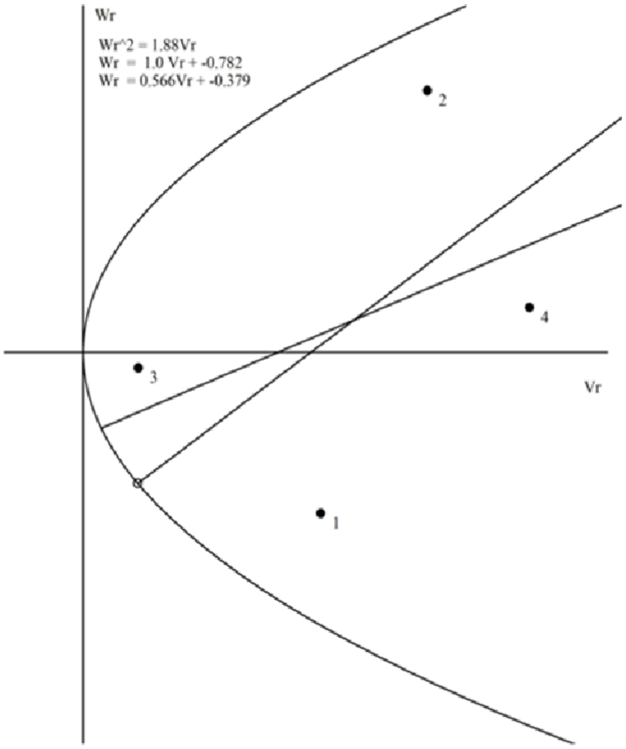

Figure 1. Relationship between Wr (covariance between parents and their progeny) Vr (variance of each cross) for %TP. Nos 1, 2, 3 and 4 denote TRFK 6/8, AHP S15/10, TRFCA SFS150 and EPK TN14-3 respectively.

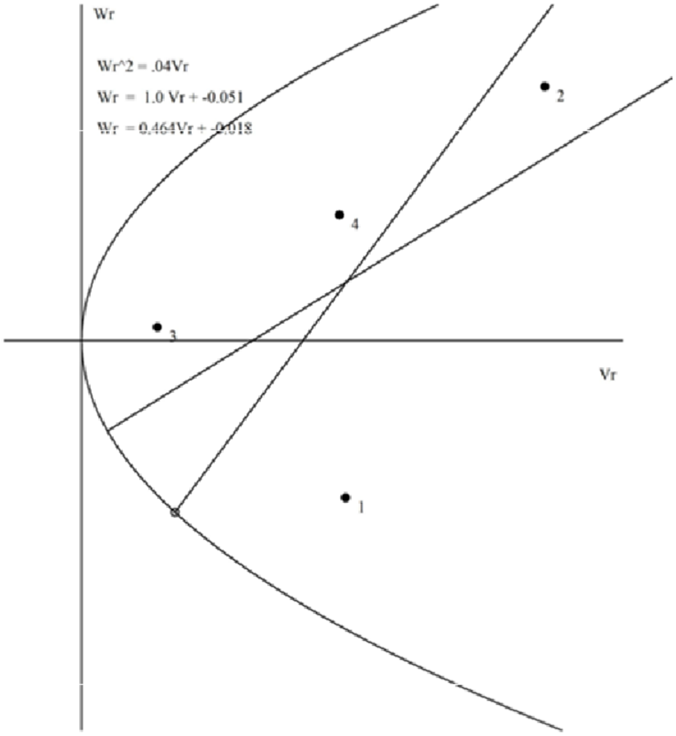

Figure 2. Relationship between Wr (covariance between parents and their progeny) Vr (variance of each cross) for FERM.

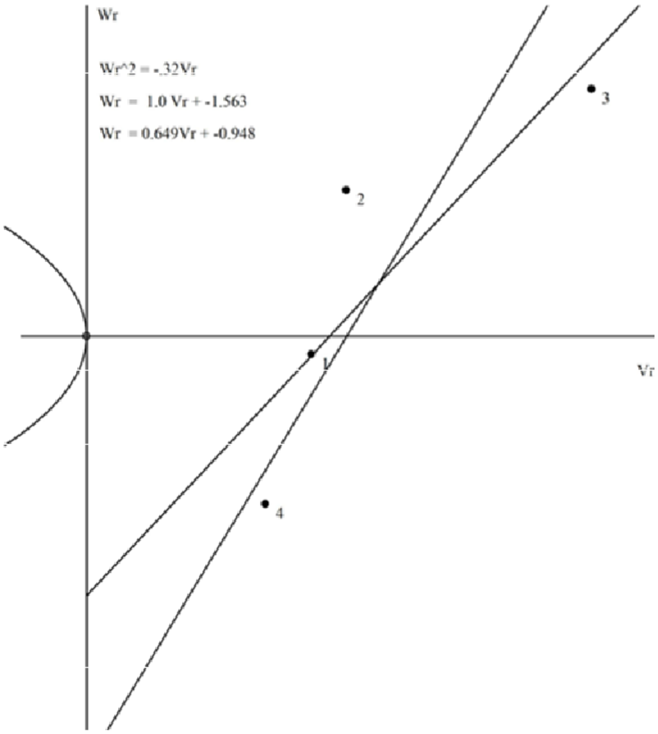

Figure 3. Relationship between Wr (covariance between parents and their progeny) Vr (variance of each cross) for TF.

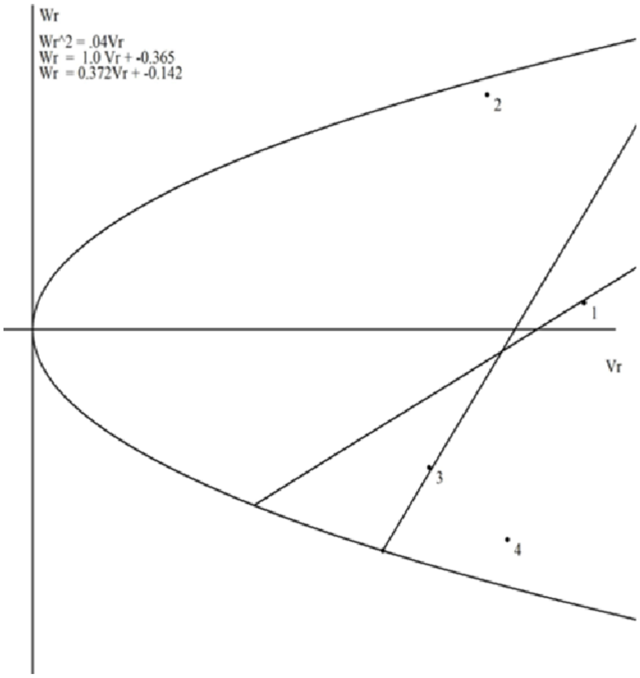

Figure 4. Relationship between Wr (covariance between parents and their progeny) Vr (variance of each cross) for PUB.

by their significance in the two approaches of analysis employed.

Table 5. General combining ability effects for the measured traits.

Parent	Yield	%TP	FERM	DT	TF(umol/g)	TR (%)	TF:TR	PUB	Bud Wt(gm)
TRFK 6/8	23.13	0.61	0.09	0.06	0.76	0.25	0.005	-0.25	-0.01
AHP S15/10	67.50	0.48	-0.08	0.10	-0.64	-0.33	-0.002	0.30	0.04
TRFCA SFS150	-45.75	-0.89	-0.08	-0.10	-0.67	-0.24	-0.006	-0.25	0.01
EPK TN14-3	-44.88	-0.20	0.07	-0.06	0.54	0.32	0.003	0.20	-0.04

Table 5 shows that all the GCA effects for yield, %TP and DT were contributed by AHP S15/10 and TRFK 6/8, as the other parents in the diallel, TRFCA SFS150 and EPK TN14-3, scored negative GCA values. Parents TRFK 6/8 and EPK TN14- 3 produced progeny with above average GCA effects for FERM, TF, TR and TF:TR. Above-average progeny for pubescence descended from parents AHP S15/10 and EPK TN14-3, while AHP S15/10 and TRFCA SFS150 gave above-average pro-geny for bud weight, as can be confirmed by their positive GCA.

DISCUSSION

The diallel mating design employed gave good indicators of the type of genes governing the traits measured in the crosses. The present study revealed that observed variation could be predominantly explained by genetic effects. The considerable variation revealed in the test for the measured traits combined with high additive and non-additive gene effects serve to emphasize the great room for selection and significant improvements if judicious breeding and clonal selection efforts were to be instituted.

The analysis by the Griffing's approach revealed significant GCA effects for all traits except TF:TR, while significant SCA (i.e. dominant and epistatic genetic effects) effects were detected for the %TP, FERM, PUB and bud weight. Significant reciprocal effects were demonstrated for all traits except TR and bud weight. The use of Hayman's (Hayman, 1954b) approach provided means of dissecting SCA effects and maternal/non-maternal effects into smaller entities so as to reveal which components contributed most variation. Thus, while significant b1 for drought tolerance, TF and PUB points to unidirectional dominance, the significance of *b2* for %TP, FERM and PUB indicated that extent of directional dominance varies among the four parents reflecting the fact that they carry different numbers of dominant alleles for the traits (Kearsey and Pooni, 1996). Clones TRFK 6/8 and EPK TN14-3, which the current study showed overdominance for %TP and FERM, are popular high quality cultivars, with TRFK 6/8 accounting to over 60% of the tea produced by smallholder sector (Wachira, 2002).

The significant variation in yield and DT presented herein could be attributed to additive and maternal effects. Maternal effects are attributed to non-nuclear genetic factors inherited through the cytoplasm (Barth et al., 2003). The observation that yield and DT are significantly influenced by maternal factors implies that some non-nuclear genetic factors on the traits are inherited from the maternal parents (Mousseau and Fox, 1998). All the other traits save for TR and bud weight similarly showed significant maternal effects. Significant SCA and reciprocal differences on the other hand could be revealed for %TP, FERM, TF, TF. TR and PUB, indicating influence by a combination of non-additive and non-nuclear genetic effects. Significant reciprocal effects have also been observed for height and stem straightness in maritime pine (Harfouche and Kremer, 2000) and for yield in pink stem borer infested and non-infested maize (Butron et al., 1999). The successful growth of F_1 hybrids depends largely on the nuclear and cytoplasmic genome with the latter being maternally inherited as well as the nutritional status of the seed parent, which the marked reciprocal effects appear to confirm (Nasrallah et al., 2000; Barth et al., 2003). In the present study, significant maternal effects for the various traits emphasize the importance of maternal parents in tea improvement programme. Although it is hard to predict the continuity of this effect in subsequent breeding efforts, in advanced tea improvement programmes, the choice of the female parent in hybridization programmes must be rationalized based on the breeding objectives.

In this study, significant GCA effects were revealed for all traits. However, the significance of additive effects relative to non-additive effects for yield, FERM, DT, TF, TR, pubescence and bud weight suggest that predominant additive genetic effects have stronger influence. The significance of both GCA and SCA implies the applicability of both natural and artificial hybridization process in tea improvement although the predominance of additive genetic effects for majority of the traits studied would be more favourable for open- pollination with only one known elite parent (Zobel and Talbert, 1984). The cost implications associated with artificial hybridization for perennial crops such as tea further underline the preferability of the later option (Anon, 2005). Faster progress may even be realized owing to ease of propagation by vegetative means (Green, 1964) that is preceded by judicious clonal selection in advanced stages of tea improvement. Non-additive genetic variance, however, can easily be captured through clonal propagation of selected biclonal progeny showing superior performance for a given trait or group of traits (Zobel and Talbert, 1984; Kamaluddin et al., 2007). Combining ability studies done for other perennial crops such as cocoa (*Theobroma* *cacao* L.) gave varied results. While Berry and Cilas (1994) showed GCA to be more important than SCA for yield, Dias and Kageyama (1995) found the contrary for the same trait. From the diallel analysis, AHP S15/10 and TRFK 6/8 had positive GCA effects for yield and total polyphenols implying that more often than not, they are likely to produce progeny with above average performance for the traits irrespective of which other parents are involved in the cross. Positive GCA posted by TRFK 6/8 and EPK TN14-3 for black tea quality traits (i.e. fermentability, TF, TR and TF:TR) emphasizes the importance of using these clones while targeting to improve or select for the two traits. Their inheritance pattern also indicates that the traits are either tightly linked or pleiotropic. As GCA refers to additive gene effects, collection of open-pollinated seed alone from these parents is likely to lead to improved populations for the respective traits. This observation is apparent in the TRFK tea improvement programme where 27 of 47 TRFK released clones had TRFK 6/8 as a common parent (Kamunya, 2003). Where GCA effect is more important, its utilization in seed gardens that are composed of many parents like in the polyclonal seed orchard of tea at TRFK becomes paramount. This may lead to accumulation of favourable alleles that have additive genetic effects in the phenotypes of the improved generations.

The apparent dominant nature of the fermenting character was also observed by Toyao (1982) in a study of inheritance of non-fermenters in tea plant and the corroboration of the results obtained in the present study confirms that this trait is largely governed by non-additive genes. Since SCA refers to non-additive gene effects, its utilization in polyclonal seed gardens is impracticable as open pollination results in many different combinations of alleles across gene loci. Thus, where SCA is more important, it can be utilized through vegetative propagation to produce commercial quantities of planting stock that are genetically identical to the plants or hybrids from which they were derived. Besides, biclonal specific crosses involvng parents with positive SCA effects for yield, fermentability and pubescence followed by prudent clonal selection may predictably result in marked progress in these traits (Zobel and Talbert, 1984; Cotterrill et al., 1987). Although efforts to utilize both GCA and SCA in tea improvement programme have been made, the composition of the various parents entered in the already designed and established seed orchards did not take cognizance of the combining abilities for all traits targeted for improvement. However, the results of the current study, small size of the diallel mating notwithstanding, will be handy in redesigning these orchards with improved ones earmarked for establishment by adopting progenitor clones with known combining abilities. The results show that the assessed traits are highly heritable and guided breeding and judicious clonal selection would lead to further tea improvement, and hence economic upturn of tea farmers, majority of whom, are smallholders. Generally, the current study shows that basic information on combing abilities is instrumental for breeding of elite cultivars.

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