Interspecific Differences of the Capacities of Waterlogging and Drought Tolerances among Summer Cereals*

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The interspecific estimation for both tolerance capacities of each crop species to waterlogging condition and a limited soil moisture (drought) one are significant in agricultural practices. However, they have not been investigated so thoroughly. There are found frequently contradictory descriptions on the capability of waterlogging and drought tolerances of some crop species among various textbooks. For instance, on finger millet, OHARA's textbook⁹⁾ describes both cultivation practices in paddy and upland field, in contrast, PURSEGROVE's¹¹⁾ one describes that it cannot tolerate to waterlogging.

In an attempt to throw light to both tolerance capacities to waterlogging and drought conditions of each crop species, it is useful that transpiration coefficients which expressed the efficiency in use of water of crops, as well as ratios of each yield under both extreme soil moisture regimes to the yield under an optimum soil moisture condition, are compared with each other. However, transpiration coefficient is greatly influenced by edaphic and climatic environmental factors as well as plant growth phase^{3,4,5,12,14)}. Therefore, this value of each crop species which was measured at the same season and under the same condition, should be used for the comparison.

In the present study, the capabilities of dry matter production and transpiration coefficients in nine species of summer cereals, when grown under waterlogging and drought conditions, were investigated. The results

obtained were discussed in relation to interspecific differences on the capacities of waterlogging and drought tolerances.

Materials and Methods

Four experiments were carried out under glasshouse conditions in Nagoya University (Table 1). The cultivars of each species shown in Table 2 is common to all the experiments. The cultivars of each species used for comparison of varietal difference in Exp. 3 are listed in Table 5. Each experiment was duplicated. The order of species in all figures and tables of this paper was in conformity with the Hotta's classification⁷⁾.

1. *Experiments 1, 2 and 3*: Plastic Wagner pots (1/5000 a) were filled with 4 kg per pot of an air-dried Kisogawa sandy loam soil mixed with 1.2g of compound fertilizer (N, 16%; P, 18%; K, 12%) as a base manure and 1g of slake lime for pH adjustment. Prior to sowing, the soil of each pot was moistened by addition of 1 liter of water. Five to ten pregerminated seeds per pot according to their sizes were sown at the center of pot. Seedlings were given to 400ml water per pot at every 4 days for the first 8 to 12 days after sowing. On the 10th to 14th day after sowing when the weight of each pot came to around 4.7 kg,

Table 1. Date of sowing, start of treatment and harvest in each experiment.

Experiments	Sowing	Start of treatment	Harvest
1. (1977)	Jun. 29	Jul. 13	Full-ripe stage*
2. (1977)	Aug. 10	Aug. 23	Sep. 17
3. (1978)	Jun. 26	Jul. 6	Aug. 7
4. (1981)	Jul. 1	Jul. 16	Full-ripe stage*

Note. *Harvest dates of each cereal are shown in Tables 2 and 3, respectively.

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Fig. 1. Comparison of influences of waterlogging and drought conditions on the average intervals of leaf emergence among nine species of summer cereals. It was calculated as follows; Average interval of leaf emergence=Days from the start of treatment to the heading/Number of leaves which emerged for this period. This average intervals of W- and D-plots were shown in percentage to that of M-plot. The numerals in parenthesis on the top of histogram of each cereal mean the average interval of leaf emergence in its M-plot.

seedlings were thinned into two plants each for sorghum and maize, and into three plants for the other species, then treatments were started. Treatments were as follows; waterlogging plot (W-plot) was established by paddy condition and each pot weight was adjusted to 6.0 kg by addition of water. Soil moisture of moderate moisture plot (M-plot) was prepared to 62.7 percent of maximum water holding capacity (37.5%) and each pot weight was adjusted to 5.4 kg by addition of water. Soil moisture of drought plot (D-plot) was prepared to 22.7 percent of maximum water holding capacity and each pot weight was adjusted to 4.8 kg by addition of water.

To prevent evaporation from the soil surface, each pot was covered with opaque vinyl sheet. Evaporation from pot soil surface was prevented perfectly. Each pot was weighed with a platform scale daily or every other day, and the amount of water lost through transpiration was added to maintain the original weight of pots in each treatment plot. One gram of the compound fertilizer as mentioned before per pot was top-dressed on Aug. 20 in Exp.1. No top-dressing was done in Exps.2 and 3.

The sum of water added for a given measurement period was assumed to be the total

amount of transpiration for the period of measurement. Plant dry matter production was the balance of dry weight between initial and final days of each experiment.

2. *Experiment 4*: In order to ascertain again the effects of the different soil moisture conditions on the ear and plant dry matter production of each cereal, this experiment was done by use of larger pots. Pregerminated seeds were sown in plastic Wagner pots (1/2000a) containing 11.0 kg of the same sandy loam soil used in Exps. 1, 2 and 3, with 3.3g of the compound fertilizer as base manure and 2.7g of slake lime for pH adjustment. Soil moisture of each pot was conditioned to the field capacity before sowing. Seedlings were allowed to grow in this water retained soil for the first 14 days after sowing. On the 15th day after sowing, seedlings were thinned in the same way as in Exps. 1, 2 and 3, then treatments were started. The treatments were as follows; W-plot was kept paddy condition. M-plot was prepared to field capacity by immersion of each pot into a deep tank for one hour once a week up to Aug. 20 and after that at every 2 to 3 days, respectively. D-plot was prepared by addition of 900 ml water per pot once a week up to Aug. 20 and after that at every 2 to 3 day, respectively. Three grams of the

Table 2. Changes in heading date, flag leaf position, amount of transpiration and dry matter production of nine species of summer cereals when grown under different soil moisture regimes (Exp. 1).

Species (cv/source)	Plot	Heading date	Flag leaf position	Amount of tran- spiration (g/plant)	Dry matter production (g/plant)			
					Ear	L.C. *	Root	Total
Upland rice (Norin No. 11) (<i>Oryza sativa</i> L.)	W	Sep. 16	15.0	5695	5.2	6.5	3.7	15.4
	M	Sep. 24	15.0	6433	3.7	8.2	3.8	15.7
	D	Oct. 1	14.0	2915	0.5	6.5	2.0	9.0
Finger millet (Gifu) (<i>Eleusine coracana</i> Gaertn.)	W	Sep. 17	33.3	5472	3.9	12.9	5.4	22.2
	M	Sep. 12	28.3	5506	4.6	13.7	5.7	24.0
	D	Sep. 24	25.0	2619	2.1	7.9	2.0	12.0
Job's tears (Kyoto) (<i>Coix lacrima-jobi</i> L.)	W	Aug. 23	16.0	4035	2.0	9.7	3.3	15.0
	M	Aug. 24	16.0	3193	1.5	7.7	3.3	12.5
	D	Sep. 1	14.0	1375	0.3	3.5	1.8	5.6
Japanese barnyard millet*** (Okayama) (<i>Echinochloa utilis</i> Ohwi et Yabuno)	W	Sep. 2	20.7	3779	3.3	6.9	4.4	14.6
	M	Sep. 1	20.3	4661	3.8	11.9	4.5	20.2
	D	Sep. 5	20.0	2410	2.3	8.0	2.3	12.6
Common millet (Saitama) (<i>Panicum miliaceum</i> L.)	W	Aug. 17	14.0	1007	1.3	2.8	0.9	5.0
	M	Aug. 16	16.0	3000	5.5	7.3	2.8	15.6
	D	Aug. 13	13.0	1550	4.0	3.2	1.6	8.8
Pearl millet (Miyazaki Univ.) (<i>Pennisetum typhodeum</i> L.)	W	Aug. 30	17.0	1125	1.2	2.6	0.5	4.3
	M	Aug. 22	17.0	3968	5.5	9.7	2.8	18.0
	D	Aug. 24	17.0	1995	3.8	4.7	2.2	10.7
Foxtail millet (Saitama) (<i>Setaria italica</i> Beauv.)	W	Aug. 18	14.0	675	0.3	0.2	0.2	0.7
	M	Aug. 16	18.0	4070	7.8	9.0	2.8	19.6
	D	Aug. 24	17.0	2193	4.5	6.2	1.8	12.5
Sorghum (Saitama) (<i>Sorghum bicolor</i> Moench)	W	Sep. 9	16.0	3225	3.3	9.0	2.8	15.1
	M	Aug. 19	16.0	5538	8.8	14.5	5.0	28.3
	D	Aug. 24	14.0	3755	6.0	10.0	4.0	20.0
Maize (Aichi) (<i>Zea mays</i> L.)	W	Sep. 12**	21.0	1845	0.3**	5.5	1.0	6.8
	M	Sep. 10**	23.0	5125	1.2**	18.6	6.3	26.1
	D	Sep. 15**	20.0	2428	0.9**	9.1	4.0	14.0

Note. * shows leaves and culms. ** shows heading date and weight of tassel. Measurement was done for a period from Jul. 13 (14th day after sowing) to 30 days after heading of every species, except for maize which was harvested on Sep. 16, because of damage by corn borer.

*** Confer Reference 12.

compound fertilizer as mentioned before was top-dressed on Aug. 25.

3. *Harvest*: At harvest of all experiments, top part of the plant was cut apart at the soil surface, then roots were sampled after the soil in pot was washed away by gentle stream of water. Plant parts were then dried in an electric oven at 90°C for 3 days, and their dry weight was measured. Dried root samples were ashed in a muffle furnace at 550°C for 24 hours. The cooled ash was treated with hot N-hydrochloric acid, and then dried at 105°C for 24 hours, and weighed. The net root dry weight was gained by subtracting the ash residue weight from the original root dry weight, assuming that the weight of the ash residue represents the weight of the unsolved soil particles in the root sample²⁾.

Results and Discussion

1. Interval of leaf emergence

Results of Exps. 1 and 4 in which measurements were done up to the full-ripe stage, were shown in Tables 2 and 3. No species used withered and failed to head under the waterlogging condition as well as the drought one. As compared with M-plot, heading dates of all the species in D-plot delayed, excepting common millet which prematured. The flag leaf positions of main stem of each cereal lowered in D-plot, except for pearl millet which did not modify. In contrast, both extents of changes of heading dates and flag leaf positions of main stem of each cereal in W-plot varied with species, in comparison with those of M-plot.

For the purpose of comparing a growth response of each cereal to waterlogging and drought conditions, the average interval of leaf emergence (day/leaf) was calculated from data of days from the start of the treatment to the heading and number of leaves which

Fig. 2. Comparison of both capacities of waterlogging and drought tolerances among summer cereals. Both tolerances of each cereal were shown in the percentages of ear dry weight of W- and D-plots to that of M-plot, respectively.

Fig. 3. Comparison of both capacities of waterlogging and drought tolerances among summer cereals. Both tolerances of each cereal were shown in the percentages of plant dry matter weight of W- and D-plots which were produced for a period of treatment to that of M-plot, respectively.

emerged for this period. In Fig.1, these of W- and D-plots were shown as relative values to those of M-plot in each cereal. The results of both Exps. clearly indicate that the intervals of all the species in D-plot are longer than those in M-plot, and also based on whether their intervals, as compared with M-plot, under the waterlogging condition were prolonged or not, a distinct demarcation can be drawn between

the species from lowland rice to Japanese barnyard millet and the species from common millet to maize in the order named in Fig.1.

2. Evaluation of capacities of waterlogging and drought tolerances based on dry matter production

Generally speaking, the optimum soil moisture regime for the growth of cereals is the field capacity^{4,14)}, around 60 to 70 percent to

Fig. 4. Comparison of both capacities of waterlogging and drought tolerances among summer cereals. Both tolerances of each cereal were shown in the percentages of seedling dry weight of W- and D-plots which were produced for a period of treatment to that of M-plot, respectively. *This histogram was drawn by the data of common cultivar of each cereal to Exps. 1 to 4. **Mean values of cultivars in each cereal were used.

the maximum water holding capacity. Assuming that the yield of each cereal in M-plot (62.7% to maximum water holding capacity) represents a result of its optimum growth response, the ratios of the plant dry matter production in W- and D-plots to that in M-plot can be considered as an index of the capacities to waterlogging and drought tolerances, respectively. These ratios based on dry matter production almost agreed with those based on ear dry weight. We will designate the species having a higher W/M ratio than D/M one in plant dry matter and ear production, as the species having large waterlogging tolerance capacity (LWTC), and the species which are in the reverse relation between both ratios, as the species having large drought tolerance capacity (LDTC), respectively.

As following this designation, the species used were divided into LWTC species from lowland rice to Japanese barnyard millet, and LDTC species, from common millet to maize, in the order named in Figs. 2 and 3. At Exps. 2 and 3 which were tested for seedling stage, the similar results were also obtained in both natures of each cereal in common cultivars to Exps. 1 and 4, except for finger millet in Exp. 2 (Fig. 4).

Varietal differences of both capacities of

waterlogging and drought tolerances were examined in Exp. 3. The results were shown in Table 5. Varietal differences in almost all the species were small. However, in finger millet and common millet, there were great varietal differences. The cultivars of finger millet, Gunma and Okayama, and those of common millet, Gifu and Shinano No. 1, showed just opposite of the respective specific natures which they are supposed to have, characterized by the dry matter production mentioned above, although their leaf emergence intervals gave full play to their natures of LWTC and LDTC species, respectively. In addition, Niigata, a cultivar of Job's tears which belonged to LWTC species, and Aichi, that of sorghum which belonged to LDTC species, showed about the same ratios of W/M and D/M in the plant dry matter production. Exp. 3 was done so a short period 32 days. Therefore, judging from that the cultivars of the other species clearly established their natures in the plant dry matter production of LWTC or LDTC species to which each species belonged, under waterlogging or drought conditions for this period, such results may indicate that they require more time to ameliorate their growth to waterlogging or drought conditions. The exceptional growth response of finger millet

Table 3. Changes in heading date, flag leaf position and dry matter production of nine species of summer cereals when grown under different soil moisture regimes (Exp. 4).

Species (cv/source)	Plot	Heading date	Flag leaf position	Dry matter production (g/plant)			
				Ear	L.C.*	Root	Total
Lowland rice (Kinmaze)	W	Aug. 30	15.0	8.3	11.3	4.0	23.6
	M	Sep. 5	14.8	3.8	8.0	3.0	14.8
	D	Sep. 16	13.1	0.9	6.5	2.1	9.5
Upland rice (Norin No. 11)	W	Sep. 15	15.0	10.9	11.8	5.0	27.7
	M	Sep. 20	15.0	7.2	11.5	4.4	23.1
	D	Sep. 28	14.0	0.8	10.6	3.9	15.3
Finger millet (Gifu)	W	Sep. 12	32.6	8.9	15.9	3.8	28.6
	M	Sep. 10	28.5	8.4	15.6	4.4	23.1
	D	Sep. 20	25.0	6.5	10.6	3.9	21.0
Job's tears (Kyoto)	W	Aug. 20	16.0	7.4	18.0	9.0	34.4
	M	Aug. 20	16.0	4.6	13.6	4.3	22.5
	D	Aug. 29	14.5	1.8	6.3	5.8	13.9
Japanese barnyard millet (Okayama)	W	Aug. 28	21.0	12.4	20.3	9.9	42.6
	M	Aug. 29	20.5	12.3	22.1	7.9	42.3
	D	Sep. 1	20.0	4.9	5.3	1.9	12.1
Common millet (Saitama)	W	Aug. 15	14.1	2.4	5.3	1.8	9.5
	M	Aug. 15	16.0	8.9	12.4	3.3	24.6
	D	Aug. 10	13.5	6.8	5.5	1.0	13.3
Pearl millet (Miyazaki Univ.)	W	Aug. 28	17.0	3.3	6.3	1.6	11.2
	M	Aug. 20	17.0	8.9	18.4	4.1	31.4
	D	Aug. 22	17.0	4.8	7.0	2.0	13.8
Foxtail millet (Saitama)	W	Aug. 20	14.0	0.1	0.8	0.3	1.2
	M	Aug. 18	18.0	11.4	11.6	3.1	26.1
	D	Aug. 25	16.5	6.4	5.1	1.0	12.5
Sorghum (Saitama)	W	Sep. 5	16.3	7.5	13.5	8.5	29.5
	M	Aug. 20	16.0	24.8	30.5	10.8	66.1
	D	Aug. 25	15.1	12.5	15.0	6.5	34.0
Maize** (Aichi)	W	Sep. 15	20.5	0.5	5.5	1.5	7.5
	M	Sep. 11	23.2	17.5	30.5	9.5	57.5
	D	Sep. 18	20.1	4.9	10.8	5.5	21.2

Note. *See Table 2. ** shows heading date of tassel. Treatment was done for a period from Jul. 9 (15th day after sowing) to 30 days after heading of every species.

and Job's tears in Exp. 2 to waterlogging condition also may be so, though the late sowing is the point to be duly considered.

In the ear production of each cereal as shown in Fig. 2-C, the order of large capacity of waterlogging tolerance was: (1) lowland rice, upland rice and Job's tears; (2) finger millet and Japanese barnyard millet; (3) common millet, pearl millet and sorghum; (4) foxtail millet and maize, and the order of large capacity of drought tolerance was: (1) common millet; (2) finger millet, Japanese barnyard millet, pearl millet, foxtail millet and sorghum; (3) lowland rice, upland rice, Job's

tears and maize.

In the comparison of capacities of waterlogging and drought tolerance among cereals based on plant dry matter production, it is reasonable to use data of Exps. 1 and 4 rather than those of Exps. 2 and 3, since the interspecific differences in time needed for amelioration of growth complicated the interpretation of the data in Exps. 2 and 3. In plant dry matter production of each cereal as shown in Fig. 3-C, the order of large capacity of waterlogging tolerance was the same with that in ear production, while the relationship of large drought tolerance capacity between the

Table 4. Changes in plant age in leaf number, amount of transpiration and dry matter production of seedlings of nine species of summer cereals when grown under different soil moisture regimes for a period of 25 days (Exp.2).

Species (cv/source)	Plot	Plant age		Transpiration (g/plant)	Dry matter production (g/plant)		
		S*	H*		L.C.**	Root	Total
Upland rice (Norin No. 11)	W	3.4	9.9	898	2.06	0.95	3.01
	M	3.5	9.9	1025	1.82	0.76	2.58
	D	3.5	8.7	488	0.70	0.34	1.04
Finger millet (Gifu)	W	5.E	13.E	268	0.82	0.33	1.15
	M	5.E	13.E	693	2.51	0.95	3.46
	D	5.E	13.E	512	2.10	1.00	3.10
Job's tears (Kyoto)	W	4.E	12.E	705	2.35	1.09	3.44
	M	4.E	12.E	663	2.35	0.81	3.16
	D	4.E	12.E	813	3.32	1.15	4.47
Japanese barnyard millet (Okayama)	W	4.E	12.E	557	2.63	1.49	4.12
	M	4.E	13.E	942	4.46	2.68	7.14
	D	4.E	11.E	422	1.97	0.98	2.95
Common millet (Saitama)	W	3.E	7.E	127	0.27	0.13	0.40
	M	3.E	8.E	488	2.09	0.42	2.51
	D	3.E	8.E	307	1.49	0.38	1.87
Pearl millet (Miyazaki Univ.)	W	4.E	8.E	105	0.38	0.14	0.52
	M	4.E	13.E	956	4.93	1.18	6.11
	D	4.E	12.E	460	2.86	0.70	3.56
Foxtail millet (Saitama)	W	3.E	9.E	72	0.17	0.04	0.21
	M	3.E	12.E	602	3.20	0.47	3.67
	D	3.E	12.E	358	2.00	0.29	2.29
Sorghum (Saitama)	W	4.E	8.E	208	0.77	0.36	1.13
	M	4.E	9.E	748	4.10	1.28	5.38
	D	4.E	8.E	338	1.97	0.67	2.64
Maize (Aichi)	W	3.E	9.E	168	0.34	0.15	0.49
	M	3.E	12.E	988	3.81	1.43	5.24
	D	3.E	10.E	255	0.83	0.39	1.22

Note. * S and H mean the plant age in leaf number at start of treatment and harvest, respectively. n.E shows the emergence of the n-th leaf.

** See Table 2. Measurement was done for a period of Aug. 23 (13th day after sowing) to Sep. 17.

two bases was not very clear.

Adaptability of each cereal to waterlogging condition depends on the capability of respiration by plant roots under a decreasing oxygen concentration in the soil and the capability of plant roots to tolerate some toxic substances, such as hydrogen sulfide, which are produced with decreasing the soil oxidation-reduction potentials¹⁶⁾. The former capability is closely connected with the development of aerenchyma as a ventilating system for oxygen supply to roots, which passes through leaves via stem to roots^{1,16)}.

In general, plants which demonstrate high tolerance capacity to waterlogging have a low

ventilating pressures and the ability to induce the aerenchyma to develop well. ARIKADO¹⁾ reported that decreasing extent of ventilating pressure of maize was 2 times lower than that of sorghum, when grown under waterlogging condition. It could not be explained only by the differences of ventilating pressure between the two species that sorghum was always larger than maize in W/M ratio of dry matter production, which was shown in the present study. PURSEGLOVE¹¹⁾ describes that the sorghum has a nature which permits it to survive physiological drought produced by waterlogging when root functions are temporarily impaired. Japanese farmers also had pointed

Table 5. Changes in plant age in leaf number, amount of transpiration and dry matter production of seedlings of nine species of summer cereals when grown under different soil moisture regimes for a period of 32 days (Exp.3).

Species (cv/source)	Plot	Plant age		Transpiration (g/plant)	Dry matter production (g/plant)		
		S*	H*		L.C.**	Root	Total
Lowland rice Kinmaze	W	4.2	11.2	1092	2.00	0.79	2.79
	M	3.9	11.0	879	1.47	0.44	1.91
	D	4.0	8.9	497	0.75	0.20	0.95
Nipponbare	W	4.7	10.7	1342	2.47	1.16	3.63
	M	4.4	9.9	920	1.60	0.69	2.29
	D	4.8	9.7	433	0.70	0.22	0.92
Koshihikari	W	3.8	11.0	1095	1.84	0.76	2.60
	M	4.0	11.0	810	1.30	0.42	1.72
	D	4.0	8.9	383	0.45	0.11	0.56
Upland rice Norin No. 11	W	4.0	10.0	1285	2.10	1.19	3.29
	M	4.0	10.0	1032	1.97	1.12	3.09
	D	4.0	9.0	578	1.17	0.69	1.86
Norin No. 21	W	4.0	9.8	1505	2.47	1.19	3.29
	M	4.3	9.7	1248	2.20	0.99	3.19
	D	4.0	9.0	687	1.48	0.57	2.05
Norin No. 7	W	3.8	9.8	1007	2.25	0.99	3.24
	M	3.8	9.3	743	1.52	0.64	2.16
	D	4.0	9.0	495	1.07	0.29	1.36
Finger millet Gifu	W	8.E	17.E	500	1.29	0.90	2.19
	M	8.E	16.E	984	2.59	1.53	4.12
	D	8.E	12.E	529	1.25	0.48	1.73
Gunma	W	8.E	15.E	596	0.99	0.79	1.78
	M	8.E	16.E	983	2.32	1.33	3.65
	D	8.E	14.E	570	1.54	0.62	2.16
Okayama	W	8.E	18.E	560	1.14	0.69	1.83
	M	9.E	18.E	1105	3.22	1.40	4.62
	D	8.E	16.E	625	1.69	0.68	2.37
Job's tears Kyoto	W	4.E	11.E	725	1.51	0.56	2.07
	M	4.E	11.E	963	2.56	0.79	3.35
	D	4.E	10.E	583	1.38	0.48	1.86
Niigata	W	4.E	12.E	617	1.48	0.59	2.07
	M	4.E	13.E	1080	3.31	1.09	4.40
	D	4.E	10.E	593	1.48	0.53	2.01
Japanese barnyard millet Okayama	W	5.E	14.E	1157	3.91	1.54	5.45
	M	5.E	14.E	1000	3.70	1.48	5.18
	D	5.E	13.E	469	1.61	0.58	2.19
Iwate	W	5.E	14.E	1111	3.76	1.82	5.59
	M	5.E	14.E	1116	4.12	1.27	5.39
	D	5.E	13.E	442	1.45	0.59	2.07
Gifu	W	6.E	14.E	1019	3.55	1.62	5.17
	M	5.E	13.E	1025	3.42	1.57	4.99
	D	5.E	12.E	618	1.82	1.04	2.86
Common millet Saitama	W	4.E	10.E	374	1.49	0.40	1.89
	M	5.E	12.E	996	4.37	1.03	5.40
	D	4.E	11.E	730	2.89	0.84	3.73
Gifu	W	5.E	11.E	545	1.97	0.55	2.52
	M	4.E	14.E	1019	4.44	0.92	5.36
	D	5.E	12.E	475	1.99	0.49	2.48
Shinano No. 1	W	5.E	11.E	450	1.67	0.54	2.21

	M	5.E	13.E	989	4.07	1.29	5.36
	D	5.E	11.E	404	1.62	0.50	2.12
Pearl millet	W	4.E	13.E	452	0.89	0.41	1.30
Miyazaki Univ.	M	5.E	13.E	1448	5.19	1.88	7.10
	D	5.E	13.E	867	2.96	0.99	3.95
Foxtail millet	W	4.E	11.E	240	0.49	0.10	0.59
Saitama	M	5.E	16.E	835	3.23	0.75	4.07
	D	5.E	13.E	580	1.93	0.53	2.46
Gifu	W	5.E	11.E	438	0.98	0.13	1.11
	M	6.E	15.E	878	3.62	0.86	4.48
	D	6.E	13.E	417	1.62	0.45	2.07
Yachiyomochi	W	6.E	14.E	270	0.74	0.11	0.85
	M	6.E	16.E	893	3.57	0.98	4.55
	D	5.E	14.E	419	1.74	0.50	2.24
Sorghum	W	6.E	11.E	1282	3.19	1.20	4.39
Saitama	M	5.E	12.E	1401	6.94	1.80	8.74
	D	5.E	11.E	785	3.87	0.87	4.74
Hazera-726	W	6.E	9.E	823	2.44	0.62	3.06
	M	5.E	14.E	1778	8.49	2.02	10.51
	D	5.E	13.E	808	3.39	0.52	3.91
Aichi	W	4.E	10.E	667	2.22	0.75	2.97
	M	5.E	12.E	1317	7.09	1.64	8.73
	D	4.E	11.E	497	2.47	0.53	3.00
Maize	W	4.E	9.E	268	0.35	0.13	0.48
Aichi	M	5.E	13.E	927	2.60	2.07	4.67
	D	4.E	13.E	480	1.06	0.77	1.83
Koshyushyu	W	6.E	12.E	1670	3.47	2.08	5.55
	M	5.E	16.E	3845	9.95	7.58	17.53
	D	6.E	11.E	1555	3.87	3.13	7.00
Golden cross	W	5.E	13.E	2006	3.54	1.54	5.08
bantam	M	5.E	13.E	2980	7.86	3.42	11.08
	D	5.E	10.E	940	3.62	1.24	4.86

Note. * See Table 4. ** See Table 2. Measurement was done for a period of Jul. 6 (10th day after sowing) to Aug. 7.

out this nature of sorghum from their experience of cultivation practices¹⁵⁾. The difference of the capacities of waterlogging tolerance between sorghum and maize may be due to both interspecific differences of tolerance capacity of roots to toxic substances and capacity to increase the number of adventitious roots which develop rapidly along near the soil surface, when grown under waterlogging condition.

On the other hand, adaptability of cereals in field to limited soil moisture conditions depends on the capability of water absorption by plant root system as well as utilization efficiency of absorbed water by plants^{6,10)}. PURSEGLOVE¹¹⁾ describes that looking at rice, maize, sorghum and millets, the order of production in terms of decreasing rainfall is: (1) rice; (2) maize; (3) finger millet; (4)

sorghum; (5) bulrush millet (pearl millet); (6) some of the small millets. In terms of decreasing order of drought tolerance capacity based on either production of ear or plant dry matter, the order mentioned above did not necessarily agree with the result of the present study. This disagreement may be related to the limit of space by pot culture, which did not allow the root system to develop to its maximum extent. This divergence may derive from the interspecific differences of development of root system, which is considered to be largely responsible for the capability of water absorption and consequently drought tolerance of a given species¹⁰⁾.

Thus, the capacities of waterlogging tolerance and drought one are under the control of quite different factors from each other. Therefore, a cereal having a large waterlog-

Table 6. Comparison of both tolerance capacities of waterlogging (W/M) and drought (D/M), and transpiration coefficient of summer cereals grown under different soil moisture regimes (Exp. 3).

Species (cv/source)		Dry matter ratio(%)		Transpiration coefficient		
		W/M	D/M	W-plot	M-plot	D-plot
Lowland rice	Kinmaze	146	50	546 (391)	597 (460)	663 (523)
	Nipponbare	159	40	543 (370)	575 (402)	619 (471)
	Koshihikari	151	33	595 (421)	623 (471)	851 (684)
	Mean	152	41	561 (394)	598 (421)	711 (559)
Upland rice	Norin No. 11	106	60	621 (391)	524 (334)	494 (311)
	Norin No. 21	115	64	609 (411)	567 (391)	464 (335)
	Norin No. 7	150	63	448 (311)	489 (344)	463 (364)
	Mean	124	62	556 (371)	527 (356)	474 (337)
Finger millet	Gifu	53	42	388 (228)	380 (239)	423 (306)
	Gunma	49	59	602 (335)	424 (269)	370 (264)
	Okayama	40	51	491 (306)	343 (239)	370 (264)
	Mean	47	51	494 (290)	382 (249)	388 (278)
Job's tears	Kyoto	62	56	480 (350)	376 (287)	422 (313)
	Niigata	47	46	417 (298)	326 (254)	401 (295)
	Mean	55	51	449 (324)	351 (266)	412 (304)
Japanese barnyard millet						
	Okayama	105	42	296 (212)	270 (193)	291 (214)
	Iwate	104	38	295 (199)	271 (207)	305 (214)
	Gifu	104	57	287 (197)	300 (205)	340 (216)
	Mean	104	46	293 (203)	280 (202)	312 (215)
Common millet	Saitama	35	69	251 (198)	228 (184)	255 (196)
	Gifu	47	46	277 (216)	230 (190)	239 (192)
	Shinano No. 1	41	40	269 (204)	243 (186)	248 (193)
	Mean	41	52	266 (206)	234 (186)	248 (193)
Pearl millet	Miyazaki Univ.	18	56	508 (348)	279 (204)	293 (219)
Foxtail millet	Saitama	15	60	490 (407)	252 (186)	301 (236)
	Gifu	25	46	447 (395)	243 (196)	257 (201)
	Yachiyo-mochi	19	49	365 (318)	250 (196)	241 (187)
	Mean	20	52	434 (373)	248 (193)	266 (208)
Sorghum	Saitama	50	54	402 (294)	202 (160)	203 (166)
	Hazera-726	29	37	337 (269)	209 (169)	238 (207)
	Aichi	34	34	300 (225)	186 (151)	201 (166)
	Mean	38	42	346 (263)	199 (160)	214 (180)
Maize	Aichi	10	39	766 (558)	357 (199)	453 (262)
	Koshyushyu	32	40	481 (301)	386 (219)	402 (222)
	Golden cross bantam	46	44	567 (395)	379 (269)	260 (193)
	Mean	29	41	605 (418)	374 (229)	372 (226)

Note. Transpiration coefficients were shown by dry weight based on shoot dry weight (TCs) which was produced for a period of treatment. Numerals in parenthesis indicate transpiration coefficients based on dry weight of plant as a whole (TCp) which was produced for treatment period.

ging tolerance capacity is not always the one having a small drought tolerance capacity and *vice versa*.

3. Transpiration coefficients of cereals grown under different soil moisture regimes

Transpiration coefficient of each cereal in every plot was calculated from the amount of transpiration and the plant dry matter production during the treatment. Results are listed in Tables 6 and 7. When estimating transpiration coefficient, the weight of shoot part is widely used as that of plant dry matter production,

excluding tuber-crops³⁾. However, it is only fair to add the weight of roots to that of plant dry matter production. Therefore, transpiration coefficients which based on whole plant (TCp) and ear dry weight (TCe) as well as shoot dry weight (TCs), were used in our study. TCp values were 10 to 40% lower than TCs ones. No definite relationship between the two coefficients in any species and plots was found.

SHANTZ and PIEMEISEL¹²⁾ have already reported the transpiration coefficients based on

Table 7. Transpiration coefficient of common cultivar of each species to all the treatments.

Species (cv/source)	plot	Exp. 1			Exp. 2		Exp. 3	
		ear	shoot	plant	shoot	plant	shoot	plant
Lowland rice (Kinmaze)	W	—	—	—	—	—	546	391
	M	—	—	—	—	—	597	460
	D	—	—	—	—	—	663	523
Upland rice (Norin No. 11)	W	1095	487	370	436	298	612	391
	M	1739	590	410	563	397	524	334
	D	5830	416	324	697	469	494	311
Finger millet (Gifu)	W	1403	326	246	327	233	388	228
	M	1197	300	229	276	200	380	239
	D	1247	262	218	244	165	423	306
Job's tears (Kyoto)	W	2018	345	269	300	205	480	350
	M	2129	347	255	282	210	376	287
	D	4583	362	246	244	182	422	313
Japanese barnyard millet (Okayama)	W	1145	370	259	212	135	296	212
	M	1227	297	231	211	132	270	193
	D	1048	234	191	214	143	291	214
Common millet (Saitama)	W	775	246	201	470	318	251	198
	M	545	234	192	233	194	228	184
	D	388	215	176	206	164	255	196
Pearl millet (Miyazaki Univ.)	W	938	296	264	276	202	508	348
	M	721	279	220	194	156	279	204
	D	525	235	186	161	129	293	219
Foxtail millet (Saitama)	W	2250	1350	964	424	343	490	407
	M	522	242	208	188	164	252	186
	D	487	205	175	179	156	301	236
Sorghum (Saitama)	W	977	262	214	270	184	402	294
	M	629	238	196	182	139	202	160
	D	626	235	188	172	128	203	166
Maize (Aichi)	W	n.d.	318	271	494	343	766	558
	M	n.d.	259	196	259	189	357	199
	D	n.d.	243	173	307	209	453	262

Note. Transpiration coefficients were shown by the dry weights based on ear (TCe), shoot (TCs) and plant as a whole (TCp) which were produced for treatment periods.

shoot dry matter and grain weights of several summer cereals, which presumed to be grown under a soil moisture regime in relatively dry condition as compared with the M-plot of the present study. The average TCs values of these cereals which they determined were 682 for rice (1 cultivar), 267 for common millet (3 cultivars), 360 for foxtail millet (5 cultivars), 305 for sorghum (9 cultivars) and 349 for maize (23 cultivars). These values of common millet and maize are almost accord with those in M-plot of our experiments, but the values of rice, foxtail millet and sorghum are fairly larger than those of ours. The average values of transpiration coefficients based on grain weight which they determined were 567 for common millet (2 cultivars), 959 for foxtail

millet (3 cultivars), 868 for sorghum (5 cultivars) and 1,405 for maize (3 cultivars). Their values and our TCe can not be compared with each other since our TCe based on ear dry weight. Transpiration coefficients of rice which were determined in Japan¹⁴⁾ were 211 to 300 (waterlogging condition) and 307 to 329 (soil moisture of 50 to 70% to maximum water holding capacity) for lowland rice, and 347 to 364 for upland rice (soil moisture of 50 to 70% to maximum water holding capacity). Recently MARUYAMA et al. reported the transpiration coefficients of rice plants⁸⁾. However, our results were found to be rather higher as compared with their data.

TCs of every species in Exps. 1 and 3 almost agreed with each other, excepting maize,

although those of M-plot of Exp. 2 were slightly smaller as compared with those of Exps. 1 and 3. Similarly, TCp in M-plot of every species in Exps. 1 and 3 nearly coincided with each other, except for upland rice and Japanese barnyard millet, and as a rule those of Exp. 2 were less than those of Exps. 1 and 3. These results suggested that the transpiration coefficient of each cereal is strongly influenced by the difference of growing season rather than the differences of year and plant growth stage.

Generally, the transpiration coefficients of C₄-plants, such as the species from finger millet to maize in the order named in tables, are less than those of C₃-plants such as lowland rice and upland rice. However, this rule applies only when the cereals were grown under the M- and D-plots. When cereals were grown under W-plot, for instance, TCs of foxtail millet in Exp. 1, that of common millet in Exp. 2 and those of maize in Exps. 2 and 3 were larger than those of lowland rice and upland rice.

In Table 7, TCe of LWTC species in M- and D-plots were clearly larger than those of LDTC ones. This tendency also was generally evident in TCs and TCp through all the experiments except for Japanese barnyard millet whose TCs and TCp in M- and D-plots were small in spite of a member of LWTC species.

TCs and TCp of lowland rice were measured only in Exp. 3. Those of all the three cultivars used increased as the soil moisture decreased. On the contrary, those of cultivars of upland rice in Exp. 3 decreased with decreasing the soil moisture, though this pattern was obscure in Norin No. 7. This result suggests that lowland rice and upland rice are different at least in water economy at seedling stage.

4. *Evaluation of capacities of waterlogging and drought tolerances based on TC ratios*

Fig. 5 shows the transpiration coefficients of W- and D-plots expressed by the percent to those of M-plot. Those of all the species in D-plot were almost equal to or less than those of M-plot, exclusive of upland rice and Job's tears in Fig. 5-(A), and lowland rice in Fig. 5-(C). This result signifies that the efficiency in use of water of most summer cereals examined is scarcely affected by drought condition¹⁰⁾.

In contrast, water economy of summer cereals when grown under waterlogging condition varied among the species. Especially the extents of decrease in the efficiency in use of water in LDTC species were marked in both productivities of ear and plant dry matter as a whole. For TCp, common millet only showed the similar level to LWTC species (Fig. 5-(B) and (C)).

SHANTZ and PIEMEISEL¹²⁾, who measured transpiration coefficients of 66 species of crops and native weeds over a seven years period, pointed out that any departure from the optimum growth conditions would increase the transpiration coefficient. Therefore, their view leads to the assumption that the farther W/M or D/M ratio of a given species exceeds 1.00, the more unfavorable waterlogging or drought condition is for the growth of the species.

As shown in Fig. 5-(A), such TCe ratios as far above 1.00 were found in upland rice (3.00) and Job's tears (2.00) in D-plot, and in common millet (1.50), pearl millet (1.40), foxtail millet (4.40) and sorghum (1.55) in W-plot. In contrast to these species, TCe ratios of finger millet and Japanese barnyard millet in W- and D-plots were around 1.00.

In Fig. 5-(B) which showed TCp ratios based on mature plant dry weight, the ratios in D-plot were below 1.00 in all the species. On the contrary, TCp ratios in W-plot were above 1.00 in all the species, except for upland rice (0.85). Especially the species which had the high ratio were pearl millet (1.30), foxtail millet (4.40) and maize (1.60). TCp ratios based on seedling weight were shown in Fig. 5-(C). The ratios in D-plot were slightly above or near 1.00 in all the species, except for lowland rice (1.30). Similar to Fig. 5-(B), in W-plot particularly high ratios were found in pearl millet (1.90), foxtail millet (2.00), sorghum (1.60) and maize (1.80).

In all the species except for foxtail millet, TCp ratios of W- and D-plots in Fig. 5-(B) at mature plant stage became smaller than those in Fig. 5-(C) at seedling stage. Only in foxtail millet the ratio increased from 1.00 at seedling stage to 4.40 at mature plant stage. Regarding the extent of decrease in TCp ratio of each cereal from seedling stage to mature stage as a capability of amelioration in water economy to waterlogging and drought conditions, that of foxtail millet to waterlogging condition may be

Fig. 5. Interspecific differences of changes in transpiration coefficient of plants grown under different soil moisture regimes. Transpiration coefficient ratio in A, B and C are based on ear dry weight (Exp. 1), plant dry weight at full-ripe stage (Exp. 1) and plant dry weight at seedling stage (mean values of cultivars of the species in Exp. 3), respectively.

the least among the summer cereals examined.

It is likely that the ecological habit of a given species to soil moisture environment is more clearly expressed by TCe ratio based on ear production which are thickly related to survival and integrity of the species, when the effects of waterlogging and drought conditions on the water economy of each cereal are evaluated. Additionally, this evaluation is also quite significant from the viewpoint of agronomy.

Looking at changes in TCe ratio of each cereal as shown in Fig.5- (A), the order of large capacity of waterlogging tolerance was: (1) upland rice, Job's tears and Japanese barnyard millet; (2) finger millet; (3) common millet, pearl millet and sorghum; (4) foxtail millet, and the order of large capacity of drought tolerance was; (1) common millet and pearl millet; (2) Japanese barnyard millet and foxtail millet; (3) finger millet and sorghum; (4) upland rice and Job's tears. Judging from Fig.2- (C), Fig.5- (B) and Fig.5- (C), lowland rice and maize may belong to (1) and (3) group in capacity of waterlogging tolerance, and to (3) and (4) group in capacity of drought tolerance, respectively. These orders were almost in accord with the order in W/M and D/M ratios based on ear dry weight, as mentioned before.

On the basis of the large extent of either W/M ratio or D/M one in yield, summer cereals used were divided into two groups, LWTC and LDTC. In addition to these yield ratios, when TCe ratio, *i. e.*, stability of the efficiency in the use of water, is used as a criterion in evaluation of the capacities of waterlogging and drought tolerances of each cereal, LWTC group and LDTC one also can be divided into two subgroups, respectively. The former group is divided into (1) the species which are the most susceptible to drought condition and the most stable to waterlogging condition, lowland rice, upland rice and Job's tears, and (2) the species which are relatively stable to drought and waterlogging conditions, finger millet and Japanese barnyard millet. The latter group is divided into (1) the species which are more susceptible to waterlogging condition and stable to drought condition, common millet, pearl millet, sorghum and maize, and (2) the species which are the most susceptible to waterlogging condition and stable to drought condition, foxtail millet.

Summary

The extents of alteration in intervals of leaf emergence, dry matter production and transpiration coefficients in nine species of summer cereals, when grown under waterlogging (W),

moderate soil moisture (M) and drought (D) conditions, were compared.

The intervals of leaf emergence of all the species in D-plot were longer than those in M-plot. However, in W-plot, the intervals of the species such as lowland rice, upland rice, finger millet, Job's tears and Japanese barnyard millet were shorter, while those of the species such as common millet, pearl millet, foxtail millet, sorghum and maize were prolonged, as compared with those in M-plot.

Based on whether W/M ratios in plant and ear dry matter production were larger than D/M ones or *vice versa*, the cereals were divided into two groups. The species having higher W/M ratios than D/M ones were lowland rice, upland rice, finger millet, Job's tears and Japanese barnyard millet, and the species which were in the reverse relation between the two ratios were common millet, pearl millet, foxtail millet, sorghum and maize. The former and the latter groups were designated as the species having large waterlogging tolerance capacity (LWTC) and as the species having large drought tolerance capacity (LDTTC), respectively.

Transpiration coefficients of the cereals grown under W-, M-, and D-plots, which based on whole plant (TCp) and ear dry weight (TCe) as well as shoot dry weight (TCs), were determined.

Comparing the ratios of TCp and TCs values in W- and D-plots to those in M-plot, both ratios of most cereals were around 1.00 in D-plot, while in W-plot, those ratios varied among the species. From SHANTZ and PIEMEISELS' view¹²⁾, the following assumption can be led that the farther W/M or D/M ratio of TCe in a given species exceeds 1.00, the more unfavorable waterlogging or drought condition is for the growth of the species. On the basis of this assumption, the capacities of waterlogging and drought tolerances of each cereal were evaluated and the following results were obtained. 1) the order of large capacities of waterlogging and drought tolerances were almost in accord with that in W/M and D/M ratios based on ear dry weight, 2) LWTC group and LDTTC one could be further divided into two subgroups, respectively. The former group was divided into (1) the species which were the most susceptible to D-condition and the most stable to W-condition, lowland rice,

upland rice and Job's tears, and (2) the species which were relatively stable to W- and D-conditions, finger millet and Japanese barnyard millet. The latter group was divided into (1) the species which were more susceptible to W-condition and stable to D-condition, common millet, pearl millet, sorghum and maize, and (2) the species which were the most susceptible to W-condition and stable to D-condition, foxtail millet.

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* In Japanese.

** In Japanese with English summary.

〔和 文 摘 要〕

夏作イネ科作物の耐湿性・耐旱性程度に関する種間比較

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湛水 (W)・適湿 (M)・乾燥 (D) の土壌条件下で、生育させた 9 種類の夏作イネ科作物の出葉間隔、乾物生産と蒸散係数の変化の程度を、4 回の実験を通じて比較検討した (第 1 表)。

M 区に比べて D 区では、すべての種の出葉間隔が長くなったが、W 区では水稻・陸稻、シコクビエ、ハトムギ、ヒエで短くなり、キビ、トウジンビエ、アワ、モロコシ、トウモロコシで長くなった (第 1 図)。

植物体と穂の乾物重にもとづく W/M 比が、D/M 比より大きいか、またその逆の関係かどうかによって、供試作物は 2 群に大別された (第 2, 3, 4 図、第 2, 3, 4, 5 表)。その一つは、D/M 比よりも W/M 比の方が大きい群で、水稻・陸稻、シコクビエ、ハトムギ、ヒエを含む。他の一つは、W/M 比よりも D/M 比の方が大きい群で、キビ、トウジンビエ、アワ、モロコシ、トウモロコシを含む。前者の群を耐湿性程度が大きい群 (LWTC 群)、後者の群を耐旱性程度が大きい群 (LDTC 群) とした。

W・M・D 区の各作物の蒸散係数を、地上部乾物重当り (TCs) だけでなく、植物体全乾物重当り (TCp) と穂乾物重当り (TCe) でも求めた (第 6, 7 表)。各作物の TCs と TCp にもとづく D/M 比は、約 1.00 であったが、W/M 比は種によって変異を示した (第 5 図 B, C)。SHANTZ と PIEMEISEL の知見にもとづいた「TCe における W/M 比または D/M 比が、1.00 を大きく上回れば上回るほど、湛水または乾燥条件はその種の生育にとって不適当な環境であることを示す」とする假説によって、各作物の耐湿性・耐旱性程度を評価した (第 5 図 A)。この評価法による各作物の耐湿性と耐旱性程度の大きさの順位は、穂乾物重の W/M 比と D/M による順位とほぼ一致した。そして、この評価法によって LWTC 群と LDTC 群は、さらに 2 つの亜群に分けえた。LWTC 群は、(1) 湛水条件でもっとも安定しているが、乾燥条件に対する感受性をもっとも高い種である水稻・陸稻、ハトムギを含む亜群と、(2) 湛水条件でも乾燥条件でも比較的安定している種であるシコクビエ、ヒエを含む亜群に分かれた。一方、LDTC 群は、(1) 湛水条件に対する感受性は比較的高いが、乾燥条件では安定している種であるキビ、トウジンビエ、モロコシ、トウモロコシを含む亜群と、(2) 湛水条件に対する感受性をもっとも高いが、乾燥条件では安定している種であるアワを含む亜群に分かれた。