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Pollination of Teak (Tectona grandis L.). 2.

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1. Introduction

Initial pollination investigations conducted in 1965—66 at the Teak Improvement Center, Thailand were reported in 1969 by Bryndum & Hedegart (1969).

The present paper summarises research activities during the period 1967—72. These concentrated on development of isolation and pollination procedures.

2. Natural Pollination

2.1 Pollinating insects

As previously suggested by Bryndum & Hedegart (1969) insects are believed to be the major agents of teak pollination. A closer examination of insects visiting teak flowers was undertaken in 1967 and 1968.

Observation scaffoldings were erected at four middle aged trees, the distance between the trees varying from 1.5 km to c. 16 km. The scaffoldings were visited frequently every day during the flowering period (July)-August-September. Records were kept of the number of flowers at each inflorescence marked for observation the temperature, wind and cover of clouds. During each visit 10 minutes were spent by each inflorescence counting the number of visiting insects according to the categories indicated in table 1. A number of insects were caught in small glass tubes. Five anthers, one from each of five flowers, were likewise collected from each inflorescence.

In the laboratory the insects were examined for pollen under microscope (25—50 X). A summary of the observations is presented in table 1.

A known amount of distilled water was added to each category of insects. After light shaking for two minutes, four drops were taken for examination of the quantities of pollen under the microscope (75 X). A "pollen index" was calculated from:

Amount of water (mm^3)/No. of insects (or anthers) X No. of pollen grains/Observation square (mm^2).

The same procedure was applied in calculating pollen indices for the collected anthers.

Figure *1* shows average pollen indices for anthers for the hours of the day, compared with the average number of visiting insects during the same periods.

In table *2* is calculated a "pollinator value" for each species (or group) of insects. These values are for each category based on the average pollen index for all insects caught and the average number of visiting insects during the 10-minute observation periods.

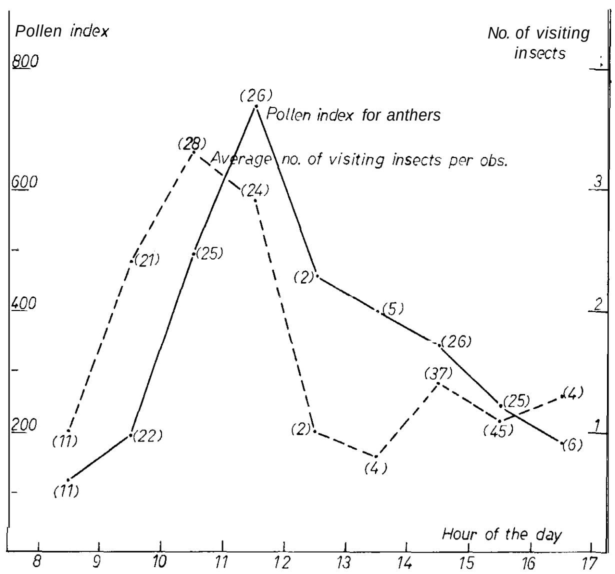

Figure 1. — Average pollen indices for anthers for the individual hours of the day, compared to average number of visiting insects per observation of 10 min. Pollen index = Amount of water (mm^3) / No. of anthers X No. of pollen grains / Observation square (mm^2). Figures in brackets indicate number of observations.

Table 1. — Insects visiting teak flowers distributed by the amount of pollen carried.

Insect species (or group)	Total no. examined	None No.	None %	A little No.	A little %	Much No.	Much %	Very much No.	Very much %
Heriades parvula	57	2	3.5	15	26.3	13	22.8	27	47.4
Ceratina hieroglyphica	18	3	16.7	7	38.8	3	16.7	5	27.8
Other bees	12	4	33.3	5	41.7	2	16.7	1	8.3
Ants	154	96	62.3	56	36.4	2	1.3	0	0
Other insects	106	71	67.0	34	32.1	1	0.9	0	0

Table 2. — Calculated "pollinator value" for insects visiting teak flowers.

Insect species (or group)	Total no. examined (1)	Average "pollen index" (2)	No. obs. during 145 10-min. observations (3)	"Pollinator value" 2 × 3/145 (4)	Remarks (5)
Heriades parvula	57	2579	18	320	
Ceratina hieroglyphica	18	1684	8	93	
Other bees	12	366	5	13	
Ants	154	140	222	214	Mainly selfings
Other insects	106	174	82	98	Many selfings

Pollen index = Amount of water (mm^3) / No. of insects × No. of pollen grains/Observation square (mm^2).

Figure 1 provides further evidence that teak is an insect pollinated species. The number of visiting insects is closely related to amount of pollen available in the flowers.

Tables 1 and 2 point to the 2 Apidae-species *Heriades parvula* and *Ceratina hieroglyphica* as being the most valuable teak pollinators. Calculations for the groups "other insects", which mainly consist of small beetles, and "ants" show high "pollinator values". These insects appear in great numbers and carry some pollen. It must however be remembered that these species will almost entirely be working in a single tree, and thus cause selfpollination. Since teak is known to have a high degree of self-incompatibility (see Bryndum & Hedegart, 1969 and the present paper *table 4),* the importance of these two insect groups is probably less than their "pollinator value" suggests.

2.2 Insect damaging teak flower buds

During the investigation period damage of teak flower buds by the larvae of the insect *Pagida salvaris* (Pyralidae) was observed. During 1967 and 1968 infestation was slight while attacks during 1969—71 increased in severity. In 1972 infestation was considerably reduced.

The larvae fed on young flower buds, causing failure of these to develop into flowers. Conditions inside big isolation bags, isolating whole inflorescences, seemed to favour the attack.

Investigations into the use of selective insecticides that will not kill pollinating insects have been started.

2.3 Fertilization percentage in natural pollination

Observations during 1969 showed a very low fertilization percentage in natural pollination (0.2%, or 13 fruits in 5570 flowers) compared to controlled crosspollination (12% or 235 fruits in 1973 flowers).

During 1970—72 fertilization percentages in natural pollination and handcrosspollinations of unisolated flowers were compared. The investigation also included comparison between emasculated and unemasculated flowers.

Observations were made on three trees the distance between these varying from about 100 m to 500 m. Pollen for handpollination was obtained from newly-cut flowers from a specific neighbouring tree and transferred by means of a small brush.

The results are presented in *table 3* which shows that the percentage of flowers developing into fruits due to pollination by natural agents is indeed low, varying between 0.4% and 5.1%, with an average of 1.3%. Handpollination of unisolated flowers considerably increased fertilization percentages. In more than half the cases the increase was above ten times. However, a few cases showed increases so low as 1.8, 2.8 and 3.4 times. *Table 3* also suggests that emasculation will reduce the success of pollination.

Table 3 clearly indicates that the low fertilization percentage in natural pollination is due to insufficient pollination. This again is believed due to an insufficient number of pollinating insects at the locality examined.

The decreased success after emasculation may be attributed to a reduced chance for selfpollination and — more important — damage to the style during the emasculation operation.

3. Controlled Pollination

The procedure for controlled pollination of teak, using small, numbered isolation bags isolating single flowers, as

Table 3. — Results from pollination investigations on unisolated flowers 1970, 1971 and 1972. Distance between trees varied from c. 100 m to c. 500 m. Emasculation was completed before 09.30 hrs. Handpollination took place between 11.30 and 12.30 hrs. Pollen was transferred from a specific neighbouring tree by means of a small brush.

Tree no. and year	Emasculated flowers: Handpollinated (crossings) Flowers No. (1)	Fruits No. (2)	Success % (3)	Emasculated flowers: Not handpollinated Flowers No. (4)	Fruits No. (5)	Success % (6)	Unemasculated flowers: Handpollinated (crossings) Flowers No. (7)	Fruits No. (8)	Success % (9)	Unemasculated flowers: Not handpollinated Flowers No. (10)	Fruits No. (11)	Success % (12)
Tree no.I 1970	108	19	17.6	108	1	0.9	96	12	12.5	97	2	2.1
Tree no.I 1971	208	23	11.1	208	0	0	76	28	36.8	76	1	1.3
Tree no.I 1972	58	9	15.5	67	3	4.5	120	11	9.2	136	7	5.1
Tree no.I 1970-72	374	51	13.6	383	4	1.0	292	51	17.5	309	10	3.2
Tree no.II 1970	372	25	6.7	396	1	0.3	297	28	9.4	315	4	1.3
Tree no.II 1971	637	61	9.6	637	8	1.3	251	72	28.7	251	1	0.4
Tree no.II 1972	596	136	22.8	610	7	1.1	623	175	28.1	658	5	0.8
Tree no.II 1970-72	1605	222	13.8	1643	16	1.0	1171	275	23.5	1224	10	0.8
Tree no.III 1970	228	9	3.9	228	1	0.4	126	10	7.9	127	1	0.8
Tree no.III 1971	386	17	4.4	386	5	1.3	301	34	11.3	301	5	1.7
Tree no.III 1972	593	130	21.9	796	2	0.3	494	126	25.5	633	8	1.3
Tree no.III 1970-72	1207	156	12.9	1410	8	0.6	921	170	18.5	1061	14	1.3
Total	3186	429	13.5	3436	28	0.8	2384	496	20.8	2594	34	1.3

well as big isolation bags, streched over a bamboo skeleton and isolating whole inflorescences, was previously described by BRYNDUM & HEDEGART (1969).

With anticipated clonal crossing series in mind, simplification of the slow procedure was considered necessary.

Table 4. — Results from pollination investigations on isolated flowers 1970, 1971 and 1972.
Distance between trees varied from c. 100 m to c. 500 m. Emasculation and isolation was completed before 09.30 hrs. Pollination took place between 11.30 and 12.30 hrs. Pollen was transferred from a specific neighbouring tree by means of a small brush.

	Emasculated flowers											
	Handpollinated (crossings)						Not hand pollinated					
	Sealed after poll.			Not sealed after poll.			Not opened up			Opened up		
	Flowers	Fruits	Success	Flowers	Fruits	Success	Flowers	Fruits	Success	Flowers	Fruits	Success
Tree no. and year	No. (1)	No. (2)	% (3)	No. (4)	No. (5)	% (6)	No. (7)	No. (8)	% (9)	No. (10)	No. (11)	% (12)
Tree no.I 1970	53	16	30.2	53	13	24.5	66	0	0	68	1	1.5
Tree no.I 1971	44	2	4.5	44	4	9.1	46	0	0	46	0	0
Tree no.I 1972	69	12	17.4	69	20	29.0	71	0	0	76	9	11.8
Tree no.I 1970-72	166	30	18.1	166	37	22.3	183	0	0	190	10	5.3
Tree no.II 1970	116	16	13.8	117	13	11.1	154	1	0.6	154	0	0
Tree no.II 1971	202	15	7.4	202	18	8.9	208	2	1.0	207	1	0.5
Tree no.II 1972	223	34	15.2	226	32	14.2	229	0	0	228	0	0
Tree no.II 1970-72	541	65	12.0	545	63	11.6	591	3	0.5	589	1	0.2
Tree no.III 1970	99	6	6.1	99	8	8.1	125	0	0	125	0	0
Tree no.III 1971	113	32	28.3	115	19	16.5	160	0	0	163	3	1.8
Tree no.III 1972	244	55	22.5	248	53	21.4	268	0	0	266	3	1.1
Tree no.III 1970-72	456	93	20.4	462	80	17.3	553	0	0	554	6	1.1
Total	1163	188	16.2	1173	180	15.3	1327	3	0.2	1333	17	1.3

	Unemasculated flowers											
	Handpollinated (crossings)						Not handpollinated					
	Sealed after poll.			Not sealed after poll.			Not opened up			Opened up		
	Flowers	Fruits	Success	Flowers	Fruits	Success	Flowers	Fruits	Success	Flowers	Fruits	Success
Tree no. and year	No. (13)	No. (14)	% (15)	No. (16)	No. (17)	% (18)	No. (19)	No. (20)	% (21)	No. (22)	No. (23)	% (24)
Tree no.I 1970	50	15	30.0	51	12	23.5	77	0	0	75	0	0
Tree no.I 1971	47	9	19.1	48	11	22.9	48	0	0	48	3	6.3
Tree no.I 1972	33	17	51.5	33	20	60.6	35	0	0	37	5	13.5
Tree no.I 1970-72	130	41	31.5	132	43	32.6	160	0	0	160	8	5.0
Tree no.II 1970	171	32	18.7	172	20	11.6	210	0	0	205	0	0
Tree no.II 1971	200	26	13.0	199	28	14.1	206	2	1.0	204	2	1.0
Tree no.II 1972	199	29	14.6	202	32	15.8	207	0	0	205	3	1.5
Tree no.II 1970-72	570	87	15.3	573	80	14.0	623	2	0.3	614	5	0.8
Tree no.III 1970	98	7	7.1	98	6	6.1	129	0	0	129	0	0
Tree no.III 1971	119	32	26.9	119	18	15.1	160	6	3.8	163	4	2.5
Tree no.III 1972	253	60	23.7	255	69	27.1	286	4	1.4	290	14	4.8
Tree no.III 1970-72	470	99	21.1	472	93	19.7	575	10	1.7	582	18	3.1
Total	1170	227	19.4	1177	216	18.4	1358	12	0.9	1356	31	2.3

Table 5. — Cutting test 1967 on 10 fruits per category from each of 4 trees. (Number of fruits containing 0—4 seeds.)

Category of fruits	No. of seeds per fruit 0	1	2	3	4	Total no. of seeds	Calculated no. of seeds in 100 fr.
Selfings	23	16	1	0	0	18	45
Open poll.	16	20	3	1	0	29	73
Crossings	20	13	4	3	0	30	75

3.1 Investigation procedure and results

The investigation involved the same three pairs of trees as under Section 2.3. Small, multicoloured and numbered isolation bags, isolating single flowers were used. Emasculation and isolation work was completed before 09.30, pollination was undertaken between 11.30 and 12.30. Pollen was transferred from newly cut flowers by means of a small brush.

Results for the years 1970—72 are presented in *Table 4.* Emasculated flowers are compared to unemasculated flowers; isolated, handcrosspollinated flowers are compared to isolated, but not handpollinated flowers; and isolation bags resealed after pollination are compared to isolation bags left unsealed after pollination.

3.2 Discussion

Table 4 indicates that emasculation of flowers will generally result in fewer successful pollinations. Damage to style during emasculation is the most likely explanation, since ability for self fertilization is generally low, although it does vary from one individual to another.

Table 5 shows that fruits resulting from self fertilization contain fewer seeds than fruits from crossings.

It is therefore proposed that the degree of self-incompatibility for each individual clone should be tested. If it is high, emasculation should be omitted.

Table 4 also shows that leaving the isolation bags unsealed after pollination did not consistently increase fertilization percentages, although columns 12 and 24 indicate that if the bagged flowers are not handpollinated, but the bags are opened up during the most favourable period for pollination, some contamination will take place. Tree no. I 1972 especially shows inexplicably high percentages.

Column 9 (Emasculated flowers in unopened bags) should ideally give a consistant zero fertility (disregarding apomixis, see BRYNDUM & HEDEGART, 1969). When the data do show some fertility, it may be ascribed to too late isolation, insufficient isolation and/or incomplete emasculation.

From the data presented in *Tables 3 and 4* three alternative isolation procedures are proposed, these three alternatives may, in accordance with the degree of self-incompatibility, be used with or without emasculation.

If complete control of the individual flower is desired, that is if registration of date and time of isolation/pollination is wanted and no risk for contamination is allowed, small, numbered isolation bags isolating single flowers are considered the most practical. Isolation of single flowers necessarily involves removal of many flower buds. During 1972 the number of isolations per inflorescence varied from 64 to 270, with an average of 136. Since the daily period available for emasculation/isolation work is limited to approximately 1½ hour, one man can handle only 50—80 flowers daily.

If control of the individual flower is not necessary, but complete isolation is still wanted, big isolation bags, streched over a bamboo skeleton, isolating whole inflorescences will probably prove most useful. The frequent removal and replacement of the bag may necessitate removal of parts of the inflorescence and will, of course, slow down pollination work. Breakage may be as high as 20—25% (BRYNDUM & HEDEGART 1969). Another notable disadvantage of the big isolation bag is that conditions inside the bag seem to favour attack by *Pagida salvaris*. For production of selfings, big isolation bags regularly supplied with bees are ideal.

In large scale series of crosspollinations however, omission of isolation is suggested because of the low contamination demonstrated (0.4% — 1.3% — 5.1%). Contamination in these series may be reduced further by handpollination of all open flowers during the optimum pollination period, and by dissuading visits by pollinating insects by means of insect repellants. Since no flowers are lost due to the isolation work and the breakages caused by isolation bag, all flowers appearing on the inflorescence (1000—3000) may be handled. One man may pollinate at least 1000 flowers daily, and the number of fruits available for progeny tests is consequently increased many times.

BRYNDUM & HEDEGART (1969) found the most favourable pollination period to be 11.30 to 15.00. *Figure 1* is in agreement with this observation, but suggests that the optimum period is limited to 11.30 to 13.00.

Pollen may be transferred from newly cut flowers by means of a small brush or by rubbing an anther gently against the stigma.

Table 4 shows that the success of controlled crosspollination may vary from c. 6% — c. 20% — c. 60%.

Variation between individuals is ambiguous, while variation between years indicate that 1970 and 1971 were inferior to 1972. A likely explanation is the severe infestation by *Pagida salvaris* during 1970 and 1971. An influence of climate on pollination conditions and periodicity in seed years can however not be ruled out.

An attempt to determine favourable climatic conditions for pollination work failed as daily pollination success varied widely for trees with a maximum spacing of c. 500 m.

4. Development and Harvest of Fruits

The development in fruit-size is shown in *Figure 2*. The figure shows that the fruit develops to full size approximately 50 days after pollination.

Figure 3 presents germination results for batches of fruits collected from tree tops by shaking. Fruits were collected at intervals of approximately two weeks from November 1971 to May 1972. The fruits were stored airtight until sowing in June 1972. The curve suggests that fruits may be picked from the tops of trees during January-February, that is 120—200 days after pollination. In March-April shedding of fruits takes place, and the curve indicates that the most viable fruits are the last to be shed.

Table 5 presents the result of a viability test on fruits from the 1967-investigation. The table clearly shows that fruits derived from selfpollination contain fewer seeds than those deriving from open pollination and controlled crosspollination.

Table 6 indicates that fruits deriving from selfpollination are smaller than those of open pollination and controlled crossings.

Acknowledgement

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Summary

Initial investigations on pollination of teak *(Tectona grandis* L.) carried out at the Teak Improvement Center, Thailand were reported in 1969 by BRYNDUM & HEDEGART (1969).

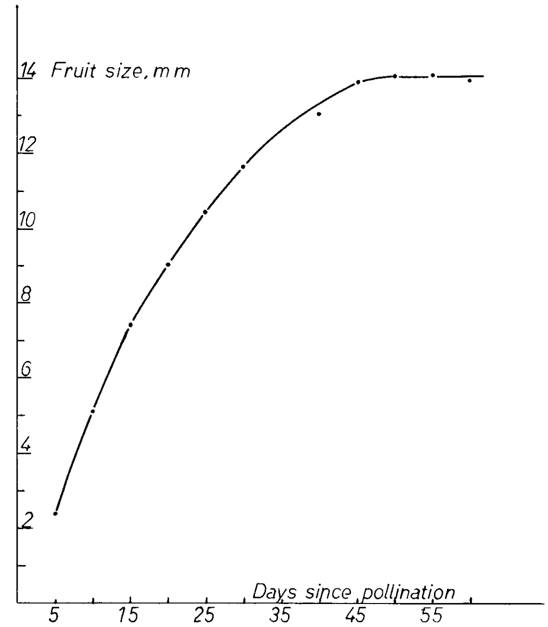

Figure 2. — Development of fruits (open pollination 1967). Averages of 10 fruits at each of 7 trees.

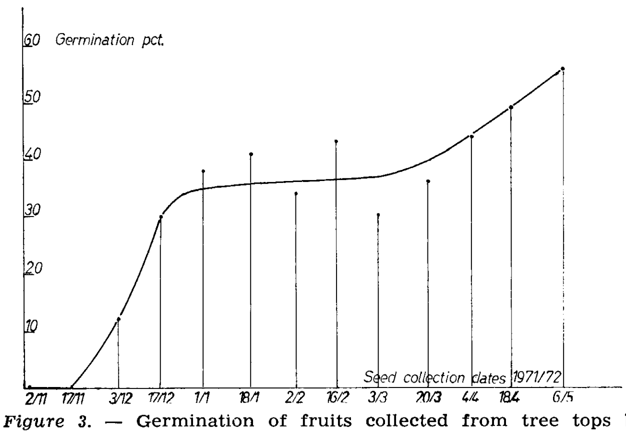

Figure 3. — Germination of fruits collected from tree tops by shaking of trees. Each point is based on 50 fruits collected randomly from 10 trees. All fruits stored airtight until sowing June 1972.

Table 6. — Fruit size. Average diameters of fruits above 6 mm.

	Category of fruits					
	Selfings		Open poll.		Crossings	
	No.	Diam., mm	No.	Diam., mm	No.	Diam., mm
1967, 6 trees	749	10.1	1088	10.8	181	11.2
1969, 3 trees	979	11.8	900	11.9	235	12.9

The present paper, based on investigations during 1967—72, provides further evidence that natural pollination in teak is undertaken by insects. Observations point to two Apidae-species *(Heriades parvula* and *Ceratina hieroglyphica)* as important pollinators.

The larvae of *Pagida salvaris* (Pyralidae) caused severe losses of teak flower buds during 1969—71, while infestation in 1972 was considerably reduced.

The fertilization percentage after natural pollination is generally low (0.4% — *1.3%* — 5.1%). The low percentage of flowers developing into fruits is ascribed to an insufficient number of pollinating insects.

Success of controlled handcrosspollinations was c. 6% — *c. 20%* — c. 60%. With large scale crossing series in mind the very slow procedure for controlled pollination described by Bryndum & Hedegart (1969) should be drastically simplified by omission of emasculation and even isolation. Omission of emasculation is justified by the risk of damaging the style during the operation and the high degree (c. 96% — 100%) of self-incompatibility. Omission of the slow isolation procedure increases the number of flowers handled from about 140 to c. 2000 per inflorescence, and from 50—80 to at least 1000 per man/day. This great increase in number of flowers handled — and consequently fruits harvested — justifies acceptance of 0.4% — *1.3%* — 5.1% contamination by natural agents. Handpollination of all open flowers during the most favourable pollination period will reduce contamination.

The optimum period for pollination is found to be 11.30 to 13.00 hours.

Fruits grow to full size about 50 days after pollination, but are not sufficiently ripe until 120—200 days after pollination. At this time (January-February) fruits may still be hand picked from the trees.

Key words: Tectona grandis, teak, pollination, breeding.

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Populationsgenetische Untersuchungen zur phänotypischen Selektion in Pflanzenbeständen mit Konkurrenz*)

Teil 3

Von M. Hühn**)

(Eingegangen im März 1973)

III. E. Approximationsansatz über Taylorreihen

a) Allgemeiner Ansatz

Im Gegensatz zu den doch relativ groben Abschätzungen *(69)* und *(72)* kommt man zu wesentlich genaueren Approximationen der durch phänotypische Selektion bewirkten Genfrequenzänderung Δp über die Anwendung von Taylorreihen und den daraus zu erhaltenden Näherungen durch Abbrechen dieser Reihen nach dem linearen bzw. dem quadratischen Glied.

Die exakte Formel für Δp war nach *(46)*:

$$\Delta p = \frac{pq}{s}\left[\sum_{v=0}^{8}\binom{8}{v} q^{8-v}p^{v}\left\{p\int_{\frac{h-(\gamma+(4-v)\delta+K)}{\sigma}}^{\frac{h-((4-v)\delta+K)}{\sigma}}\frac{1}{\sqrt{2\pi}}e^{-\frac{z^2}{2}}dz + q\int_{\frac{h-((4-v)\delta+K)}{\sigma}}^{\frac{h-(-\gamma+(4-v)\delta+K)}{\sigma}}\frac{1}{\sqrt{2\pi}}e^{-\frac{z^2}{2}}dz\right\}\right] \quad (73)$$

Für die in obiger Summe auftretenden beiden Integrale kann man unter Verwendung der üblichen Beziehungen (siehe *(64)*) schreiben:

$$\int_{\frac{h-(\gamma+(4-v)\delta+K)}{\sigma}}^{\frac{h-((4-v)\delta+K)}{\sigma}}\frac{1}{\sqrt{2\pi}}e^{-\frac{z^2}{2}}dz \quad (74)$$

$$= \Phi\left(\frac{h-((4-v)\delta+K)}{\sigma}\right) - \Phi\left(\frac{h-(\gamma+(4-v)\delta+K)}{\sigma}\right)$$

*) Von der Agrarwissenschaftlichen Fakultät der Christian-Albrechts-Universität in Kiel angenommene Habilitationsschrift.

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