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THE OCCURRENCE OF MIXED POPULATIONS OF DIFFERENT GENOTYPES OF THE LEMNA GIBBA – LEMNA MINOR COMPLEX

L. DE LANGE[1], A. H. PIETERSE[2] and I. VAN BAARSEN-BECKERS[2]

[1] Hugo de Vries Laboratorium, Universiteit van Amsterdam, Sarphatistraat 221, 1018 BX Amsterdam
[2] Koninklijk Instituut voor de Tropen, Afdeling Agrarisch Onderzoek, Mauritskade 63, 1092 AD Amsterdam

SUMMARY

It has been shown by means of cultivation in the presence of the gibbosity inducing agent EDDHA that mixed vegetations of potentially gibbous and flat genotypes of the *Lemna gibba – Lemna minor* complex commonly occur in The Netherlands. The taxonomic status of the different forms is discussed.

1. INTRODUCTION

It has generally been assumed that the gibbous and the permanently flat form of the *Lemna gibba – L. minor* complex, mostly referred to as *L. gibba* L. and *L. minor* L., occur in different habitats, the former preferring more eutrophic and/or brackish water (SEGAL 1966; DE LANGE & SEGAL 1968; WESTHOFF & DEN HELD 1969; DE LANGE 1972; LANDOLT 1975). This would imply that mixed vegetations of these species, at least as far as the gibbous form of *L. gibba* is concerned, are not likely to occur under natural circumstances. This assumption is supported by an investigation on competition, wherein *L. minor* was eliminated by a gibbous form of *L. gibba* within 3 months (REJMÁNKOVÁ 1975). However, in many cases it can be observed that gibbous plants are mixed with flat ones. Whether these plants are different growth forms – in this regard it has often been suggested that they are juveniles or winter forms – or genetically different forms which are unable to become gibbous, i.e. which according to general views would be *L. minor*, cannot be determined with certainty in the field. The problem is that, apart from the main characteristic, gibbosity, which varies under the influence of external circumstances, other differences between the two species in vegetative morphology are inconsistent (DE LANGE & PIETERSE 1973; DE LANGE 1975; PIETERSE 1975; KANDELER 1975; DE LANGE & WESTINGA 1979).

There are objections to the assumption that the flat plants in mixed vegetations are juveniles or winter forms as it has been emphasized that very young stages can already be markedly gibbous (DAUBS 1965; DE LANGE 1972) whereas winter forms, which are budded off in the autumn (GUPPY 1895), are unlikely to occur in the middle of the summer season. Moreover, DEN HARTOG (1968) observed that during the summer season in a mixed vegetation flat plants always produced flat daughter plants, whereas gibbous plants always produced gibbous

daughter plants. Apparently, the assumption that the flat form is a form of *L. gibba* was disregarded by various research workers who described the different forms occurring in mixed vegetations as *L. gibba* and *L. minor* (e.g. WESTHOFF 1949; MEYER & DE WIT 1955; STANIEWSKA-ZATEK 1972; WOLEK 1974; REICHHOFF 1978). It may be presumed, although it was not especially mentioned, that in these cases the gibbous form of *L. gibba* was concerned, but with regard to the flat plants, no experiments were carried out to ascertain whether the differences in gibbosity were consistent.

The potentiality of flat fronds to become gibbous can be tested with gibbosity inducing agents, such as EDDHA (ethylenediamine-di-o-hydroxyphenylacetic acid) (PIETERSE et al. 1970) and ethylene (PIETERSE 1976; ELZENGA et al. 1980), or by translocation experiments (DE LANGE 1974). Using the EDDHA test DE LANGE & PIETERSE (1973, strains 2 and 3) unequivocally showed that a mixed vegetation of gibbous and permanently flat plants occurred in a small pond in The Netherlands. However, these authors considered other *Lemna* samples which were collected in the field and from which clones were derived for cultures in vitro, to be relatively homogeneous. In addition DE LANGE & PIETERSE (1973) showed that certain *Lemna* strains were only able to become slightly gibbous in the presence of EDDHA, which, also because of the environmental impact on gibbosity, prompted these authors to forward the suggestion that the two taxa could be better combined in a species complex.

In the present study flat and gibbous forms from mixed field vegetations of the *L. gibba* – *L. minor* complex were locally collected, separately cultivated in vitro in the absence and presence of EDDHA and subsequently morphologically compared. In addition plants from various uniformly flat *Lemna* vegetations were exposed to EDDHA in order to test their potentiality to become gibbous.

2. MATERIALS AND METHODS

Samples from 35 *Lemna* vegetations were collected in different parts of The Netherlands in the period October – December 1979. The collection sites are presented in *table 1*. In the field it was observed that 23 of these vegetations contained gibbous as well as flat forms, whereas in 12 vegetations all the plants were flat. From each sample different forms with regard to gibbosity or/and frond size were sterilized with 1% sodiumhypochlorite solution and subsequently single specimens of these different forms were grown in 100 ml Erlenmeyer flasks on M-medium (HILLMAN 1961) supplemented with 10 g/l of sucrose and 10 mg/l of EDDHA. One clone of each form which proved to be consistent was used for the experiments and the others (i.e. morphologically similar ones), were discarded. The clones were cultivated for a period of 4 weeks in the absence of EDDHA (after two weeks a few plants were inoculated on a fresh medium and the old cultures were discarded) in order to eliminate all EDDHA-induced effects. Immediately afterwards experimental cultures of each clone were initiated in the absence and presence of EDDHA and after a period of two weeks observations were made on morphology and flowering. From each culture 5–15

Table 1.

Strain	Place of origin	without EDDHA						with EDDHA						
			gibbosity		width		length		gibbosity		width		length		+
		n	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	n	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	
1	Egmond I	5	0.38	0.08	*2.36*	0.13	3.98	0.11	15	0.49	0.16	3.13	0.14	4.39	0.51	0
1′		5	0.50	0.07	*3.22*	0.26	3.98	0.24	15	**3.41**	0.25	4.79	0.31	5.71	0.45	67
2	Egmond II	5	0.38	0.08	*2.22*	0.16	*2.98*	0.08	10	0.36	0.05	1.96	0.11	2.42	0.14	10
2′		5	0.44	0.05	2.96	0.39	3.78	0.26	15	**3.61**	0.30	4.87	0.28	5.63	0.40	52
3	Heiloo I	5	0.40	0.00	*1.56*	0.09	*2.42*	0.18	15	**0.50**	0.07	2.14	0.19	3.01	0.34	0
3′		5	0.44	0.05	2.92	0.08	3.80	0.23	15	**3.36**	0.35	4.73	0.32	5.48	0.54	55
4	Heiloo II	5	0.40	0.07	*2.34*	0.11	*3.14*	0.19	15	0.44	0.07	2.06	0.18	2.57	0.33	0
4′		5	0.48	0.04	*3.30*	0.20	4.30	0.12	15	**2.97**	0.29	4.70	0.25	5.66	0.56	73
5	Egmond III	5	0.32	0.04	*2.08*	0.08	*3.14*	0.18	15	**0.76**	0.11	3.74	0.28	4.83	0.39	28
5′		5	0.42	0.04	2.92	0.16	3.80	0.21	15	**3.66**	0.22	4.81	0.37	5.68	0.36	64
6	Egmond IV	5	0.38	0.04	*2.44*	0.21	3.56	0.34	15	**0.89**	0.06	3.41	0.21	4.66	0.32	44
7	Castricum	5	0.36	0.05	*2.44*	0.21	*3.16*	0.13	15	0.39	0.03	1.80	0.21	2.37	0.27	3
7′		5	0.40	0.07	2.86	0.13	3.80	0.12	15	**3.30**	0.19	4.46	0.26	5.33	0.22	62
8	Assendelft	5	0.36	0.05	*2.28*	0.13	3.66	0.27	15	**0.51**	0.03	3.25	0.31	4.31	0.42	59
8′		5	0.48	0.08	2.80	0.10	3.84	0.15	15	**3.47**	0.29	4.80	0.47	6.06	0.27	58
9	Buitenhuizen I	5	0.32	0.04	*2.46*	0.34	3.64	0.24	15	**0.50**	0.00	3.50	0.23	4.55	0.26	37
10	Buitenhuizen II	5	0.46	0.09	*2.10*	0.20	*2.88*	0.33	15	**0.50**	0.00	3.55	0.33	4.59	0.36	35
10′		5	0.52	0.04	2.48	0.13	*3.28*	0.23	15	**3.68**	0.39	4.56	0.44	5.83	0.40	57
11	Halfweg	5	0.36	0.05	*1.62*	0.11	*2.44*	0.09	10	**0.50**	0.00	1.62	0.19	2.18	0.30	4
11′		5	0.56	0.05	*3.16*	0.09	3.94	0.39	15	**3.61**	0.20	4.65	0.16	5.54	0.22	63
12	Amstelveen I	5	0.44	0.05	*1.88*	0.11	*2.32*	0.22	15	**0.76**	0.10	3.64	0.34	4.96	0.22	50
12′		5	0.50	0.07	2.54	0.23	3.52	0.15	15	**3.21**	0.27	3.21	0.27	6.19	0.19	60
13	Loosdrecht	5	0.30	0.07	*1.74*	0.27	*2.40*	0.12	15	**0.41**	0.03	1.60	0.16	2.18	0.16	34
13′		5	0.46	0.05	2.68	0.11	3.58	0.24	15	**1.99**	0.23	4.03	0.20	5.03	0.23	65
14	Loenen	5	0.46	0.05	*2.04*	0.17	*3.10*	0.14	15	**0.93**	0.07	3.12	0.21	4.23	0.15	32
14′		5	0.42	0.04	*3.14*	0.25	3.70	0.12	15	**3.33**	0.23	5.01	0.23	6.50	0.43	62
15	Nieuwersluis	5	0.36	0.05	*2.04*	0.11	*3.22*	0.27	15	**0.49**	0.16	2.50	0.22	3.70	0.27	0
15′		5	0.50	0.07	2.76	0.09	3.36	0.15	10	**1.79**	0.20	3.52	0.22	4.63	0.21	3
16	Breukelen I	5	0.36	0.05	*2.32*	0.11	3.46	0.30	15	**0.49**	0.06	2.49	0.28	3.59	0.19	0
16′		5	0.52	0.08	*3.70*	0.44	4.66	0.26	15	**2.81**	0.20	4.68	0.25	6.13	0.32	63
17	Breukelen II	5	0.36	0.05	*2.10*	0.17	*3.08*	0.18	15	**0.69**	0.10	3.31	0.24	4.45	0.23	37
18	Stompwijk	5	0.36	0.09	2.66	0.21	4.02	0.04	15	**0.70**	0.11	3.51	0.26	4.67	0.25	13
18′		5	0.44	0.05	2.96	0.18	4.28	0.11	15	**2.83**	0.42	4.61	0.28	6.04	0.32	41
19	Hoofddorp I	5	0.38	0.04	*2.18*	0.16	*3.30*	0.16	15	0.41	0.08	3.63	0.18	4.94	0.19	60
20	Hoofddorp II	5	0.40	0.00	*2.18*	0.08	*3.08*	0.23	15	0.56	0.12	3.52	0.26	4.72	0.24	66
21	Aerdenhout	5	0.32	0.04	*2.26*	0.23	3.22	0.34	15	**0.67**	0.11	3.37	0.19	4.74	0.31	39
21′		5	0.32	0.04	2.70	0.14	3.90	0.20	15	**2.65**	0.27	4.57	0.37	5.67	0.42	68
22	Overveen	5	0.34	0.05	*1.98*	0.11	*2.90*	0.10	15	0.46	0.17	2.79	0.18	4.31	0.43	0
22″		5	0.36	0.05	*2.44*	0.15	3.50	0.24	15	**0.74**	0.20	3.49	0.37	4.69	0.27	63
23	Spaarndam	5	0.30	0.07	*2.10*	0.20	3.44	0.17	15	**0.45**	0.08	3.44	0.18	4.65	0.15	70
23′		5	0.44	0.05	2.66	0.25	3.96	0.09	15	**3.50**	0.22	5.09	0.43	6.10	0.24	75
24	Amstelveen II	5	0.34	0.05	*1.92*	0.11	*3.20*	0.16	15	**0.43**	0.07	2.60	0.19	4.15	0.23	0
24′		5	0.36	0.09	2.54	0.25	3.58	0.34	15	**2.15**	0.21	3.67	0.16	4.63	0.28	0
25	Wageningen	5	0.38	0.04	*2.10*	0.62	*3.34*	0.25	15	**0.45**	0.06	3.05	0.19	4.56	0.24	0
26	Deventer	5	0.32	0.08	*1.90*	0.20	*2.94*	0.33	15	**0.40**	0.05	2.66	0.23	3.99	0.18	0
26′		5	0.34	0.05	2.48	0.19	3.42	0.13	15	**2.13**	0.12	3.61	0.21	4.97	0.18	64

Table 1.(continued)

		without EDDHA						with EDDHA						
			gibbosity		width		length			gibbosity		width		length		+
		n	x̄	s	x̄	s	x̄	s	n	x̄	s	x̄	s	x̄	s	
27	Winderheim	5	0.34	0.05	*1.54*	0.19	*2.44*	0.09	10	**0.54**	0.05	2.73	0.31	4.27	0.20	0
27″		5	0.36	0.05	2.50	0.16	3.98	0.13	15	**0.59**	0.11	3.34	0.18	4.70	0.28	65
28	Zwartsluis I	5	0.56	0.11	2.86	0.62	3.64	0.23	15	**0.72**	0.08	3.28	0.19	4.85	0.18	25
29	Zwartsluis II	5	0.38	0.08	*2.14*	0.28	3.40	0.34	15	**0.56**	0.10	3.29	0.16	4.58	0.17	35
29′		5	0.44	0.05	2.86	0.15	3.92	0.26	15	**2.90**	0.30	4.71	0.23	5.86	0.19	51
30	St. Jansklooster	5	0.48	0.08	*2.20*	0.07	*3.34*	0.35	15	**0.81**	0.13	3.21	0.18	4.68	0.18	3
31	Oldemarkt	5	0.28	0.08	*1.64*	0.40	*2.70*	0.45	15	**0.36**	0.06	2.49	0.14	3.83	0.21	0
31′		5	0.52	0.08	2.60	0.16	3.50	0.14	15	**2.29**	0.22	4.30	0.56	5.58	0.62	81
32	Ossenzijl	5	0.34	0.13	*1.78*	0.39	*2.68*	0.66	15	0.37	0.05	2.44	0.24	3.73	0.29	0
32″		5	0.38	0.08	*2.00*	0.14	*3.18*	0.04	15	**0.49**	0.08	3.28	0.21	4.68	0.18	14
33	N.O. Polder	5	0.42	0.08	*1.90*	0.25	*2.64*	0.30	15	0.47	0.08	3.33	0.11	4.35	0.19	6
34	Kreileroord I	5	0.36	0.05	2.50	0.10	3.74	0.13	15	**0.61**	0.10	3.47	0.21	4.62	0.14	27
34′		5	0.40	0.07	2.52	0.19	3.66	0.11	15	**3.40**	0.23	5.04	0.36	6.39	0.26	53
35	Kreileroord II	5	0.32	0.04	2.62	0.11	3.66	0.26	15	**0.55**	0.06	3.30	0.19	4.65	0.29	38
35′		5	0.44	0.05	*3.22*	0.26	4.26	0.36	15	**2.49**	0.32	4.75	0.26	5.97	0.19	37

Place of collection dimensions (after cultivation in the absence and presence of EDDHA) and flowering % (in the presence of EDDHA) of the various *Lemna*-samples.
n = nr. of duplicates per strain
x̄ = mean of duplicates
s = standard deviation
+ = flowering % (n = 100)
Figures in *italics* and in **bold** *italics* are indicative for *L. minor* and *L. gibba*, respectively, according to DE LANGE & WESTINGA (1979).
Figures in ordinary **bold type** indicate statistically significant increase in gibbosity after EDDHA treatment.

fronds were used for assessing morphological data with the aid of a sliding gauge with vernier scale (accuracy 0.1 mm). If the gibbosity remained under 1 mm in the presence of EDDHA the plants were described as "permanently flat". Flowering was evaluated with the help of a low power dissecting miscroscope by counting in a sample of 100 fronds the number of fronds bearing evidence of flower initiation. Significance of the reaction on EDDHA was evaluated with the student t-test ($P = 0.05$).

3. RESULTS AND DISCUSSION

The results are presented in *table 1*. It is evident, especially after the cultivation in the presence of EDDHA, that two genetically different forms occurred in 26 of the 35 vegetation samples. In 23 samples there was a mixture of gibbous and permanently flat strains, whereas in three samples, i.e. 22, 27 and 32, there were two permanently flat strains which differed markedly in other frond dimensions.

The other 9 flat samples consisted of a single permanently flat strain. In the absence of EDDHA, when all strains were flat and non-flowering, the differentiation was very much reduced.

In the light of the results it may be concluded that gibbous and permanently flat forms of the *L. gibba-L. minor* complex commonly occur in the same habitat. Moreover, it appears that flat modifications of gibbous forms were absent at the various sites during the time of collection, as all the strains which were originally flat remained relatively flat in the presence of EDDHA (gibbosity remaining under 1 mm). The results could imply that the synsystematic status of the species *L. gibba* and *L. minor* should be reconsidered. However, the delimitation of these species remains a problem. The strains which became "markedly" gibbous in the presence of EDDHA (more than the arbitrary value of 1 mm; in the present investigation these values were at least 1.79 mm) undoubtedly belong to the species *L. gibba* (they comprise the strains marked with ′ in *table 1*). However, the gibbosity of most permanently flat strains was not completely unaffected by EDDHA either (a significant increase in 19 of the 23 permanently flat strains which were mixed with gibbous plants and in 10 of the 15 strains in uniformly flat vegetations). Gibbosity values showing a significant increase after EDDHA treatment are indicated in *table 1* in bold type. On the other hand, in the presence of EDDHA there was a gap between the gibbosity values of the permanently flat strains in the presence of EDDHA (mean values varying more or less continuously from 0.36 mm to 0.93 mm) and "markedly" gibbous strains in the presence of EDDHA (mean values varying more or less continuously from 1.79 mm to 3.68 mm). Consequently, the strains in the present investigation might be divided into two groups which can clearly be separated from each other. Even in the absence of EDDHA the two groups could be further delineated with regard to their surface dimensions, i.e. length, width and width/length ratio. According to the parameters of DE LANGE & WESTINGA (1979) it appears that in general the group with the permanently flat strains is "*L. minor*-like" (width < 2.5 mm, length < 3.4 mm, width/length < 0.71) and the group with the potentially ("markedly") gibbous strains is "*L. gibba*-like" (width > 3.0 mm, length > 4.4 mm, width/length > 0.80). Exceptions are strain 12 with a width/length ratio of 0.81 being slightly "too broad" for "*L. minor*-like" and strains 18′, 21′, 23′ and 31′ with ratio's from 0.67 to 0.69 being somewhat "too narrow" for "*L. gibba*-like". In *table 1* (data in the absence of EDDHA) figures in italics refer to "*L. minor*-like" and figures in bold italics to "*L. gibba*-like".

In general, when grown on EDDHA-medium, the two groups also differ in their flowering response, i.e. relatively low flowering percentages in the group of permanently flat strains and relatively high flowering percentages in the group of markedly gibbous strains. However, there are clear exceptions, such as the permanently flat strains 8, 19, 20, 22″ and 27″ with flowering percentages of respectively 59%, 60%, 66%, 63% and 65% and the markedly gibbous strains 15′ and 24′ with flowering percentages of respectively 3% and 0%. The differences in flowering percentages within the groups accentuate the different genotypes.

DE LANGE & PIETERSE (1973) found a *Lemna* strain (strain 10) which was intermediate – gibbosity values after EDDHA treatment ranged from 1.1 to 1.3 mm – which makes it uncertain whether the gap between the gibbosity values can be used for identification. In contradiction to the occurrence in The Netherlands of permanently flat strains with a weak but significant response to EDDHA, PIETERSE (1974) reported that in an area of South Finland, i.e. an area where only *L. minor* has been recorded, the gibbosity of all *Lemna* strains tested was not significantly affected by EDDHA. There were, however, differences in the gibbosity values of these strains and in one strain (no. 1) specimens were observed with gibbosity values of 1.0 and 1.1 mm.

It is questionable, at least as far as the vegetative morphology is concerned, whether permanently flat strains which nevertheless become significantly more inflated under the influence of EDDHA, especially when the gibbosity values approach the arbitrary limit of 1 mm, should be referred to as *L. minor*. In the literature intermediate genotypes have repeatedly been described as separate taxa, e.g. *L. obscura* (Austin) Daubs (DAUBS 1965), *L. disperma* Hegelm. (DAUBS 1965) and *L. symmeter* Giuga (GIUGA 1973).

In spite of the fact that the delimitation of *L. gibba*, *L. minor* and possible other genotypes within the *L. gibba-L. minor* complex occurring in The Netherlands has not been clarified, it may be concluded that the ecological amplitude of "*L. minor*-like" genotypes is wider than often was assumed. It seems that the differentiation within these genotypes is not correlated with the occurrence of "*L. gibba*-like" genotypes within the same vegetation.

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