

Life History Strategies of two Lemnaceae, *Lemna minor* and *L. trisulca* at
Delta Marsh, Manitoba.

by

Alexander L. McIlraith

A thesis

presented to the University of Manitoba

in partial fulfillment of the

requirements for the degree of

Master of Science

in

The Faculty of Graduate Studies

Winnipeg, Manitoba

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LIFE HISTORY STRATEGIES OF TWO LEMNACEAE, Lemna minor and
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ALEXANDER L. McILRAITH

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ABSTRACT

Lemna minor L. and *L. trisulca* L. flowered abundantly in Delta Marsh, Manitoba. Flowering in *L. trisulca* began in early May, peaked by about June 1 and was finished by early July. The phenology of *L. minor* lagged behind that of *L. trisulca* by about three weeks. Pollen grains and seeds of both species were examined with scanning electron microscopy. Although pollen morphology of the two was similar, *L. trisulca* seed differed from those of *L. minor* in having a longitudinally ribbed surface. Seed-bearing fronds of both species were observed. Seed set varied between years and within sites, and in some sites plants produced no seed. Peak seed densities occurred 3-6 weeks after biomass of flowering plants peaked, indicating that seed may take 3-6 weeks to develop. Seed of both species exhibited dark dormancy, and tolerated drying and freezing. A large *Lemna* seedbank was present at Delta Marsh, but seedlings were not observed in nature even though greater than 95% of seed extracted from sediment was viable. In the laboratory, seeds floated after being dried, and germinated at the water surface. This suggested that drought, followed by rain might liberate seed from sediment and permit it to germinate. It is suggested that the retention of sexuality and tolerance of seed to drought and freezing may function as insurance, allowing some of a clone's genes to survive periods of environmental change.

Replacement series, addition series and 'introduction' experiments were conducted to assess interactions between *L. minor* and *L. trisulca* in the field. In addition, a transplant experiment was conducted to determine whether various sites were capable of supporting a codominant community of *L. minor* and *L. trisulca*. Vegetative biomass trends of natural populations

were monitored in three sites. Results suggested that the two species may compete for light and nutrients. One - way competition for light may give *L. minor* a competitive advantage in eutrophic habitats, while nutrient competition may favor *L. trisulca* in sunny oligotrophic habitats. In a sunny eutrophic habitat, *L. trisulca* dominated in spring and fall, while in summer *L. minor* dominated. Dominance patterns, in time and space, of *L. minor* and *L. trisulca* were explained with a resource competition model (for light and nutrients), and by considering environmental factors and life history.

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Chapter I

LITERATURE REVIEW

1.1 HABITAT, TAXONOMY AND RANGE OF LEMNA

Extensive reference lists for the family Lemnaceae (duckweeds) can be found in Hillman (1961), Landolt (1980) and Kandeler (1985). Duckweeds are floating aquatic plants closely related to the Araceae (Meheshwari and Kapil, 1963), and fossil evidence for the family dates back to at least the Tertiary (Sternberg, 1924). *Lemna* is found mostly in still, slow moving, or stagnant waters, where eutrophic conditions tend to encourage the growth of large populations (Hillman, 1961). In North America, members of the family occur in waters with pH ranging from 6.4 to 10.4, specific conductivities from 17 to 4400 $\mu\text{S}\cdot\text{cm}^{-1}$ (Landolt, 1981), and in both heavy shade and full sun (Hillman, 1961). This study is concerned with *L. minor* and *L. trisulca*. The former floats at the surface, while the latter is submerged.

When attempting to identify Lemnaceae, Landolt's (1983) key is the most useful. Landolt (1975) suggests that *L. minor* s. l. should be divided into *L. minor* L. and *L. turionifera* Landolt s. str. *L. turionifera* tends to have 3-7 papules on its upper surface, to produce turions (see below) and to have red pigmentation on the underside of fronds. *L. minor* s. str. rarely has distinct papules, does not produce turions and is unpigmented. Landolt (1981) indicates that *L. turionifera* occurs in Manitoba while *L. minor* s. str. does not. Clones of *L. minor* s. l. isolated from Delta Marsh, Manitoba (50°

11°N, 98° 23'W) fit the description of *L. turionifera* s. str. while one clone isolated north of Powerview, Manitoba (50° 34'N, 96° 10'W) by Dennis Brown (Technical Services, Manitoba Department of Natural Resources) fits the description of *L. minor* s. str. Dudley (1987) showed that *L. minor* L. clone 6591, collected by Landolt (1957), could produce turions and suggested that observed differences between *L. minor* s. str. and *L. turionifera* may depend on growing conditions. Although clone differences exist, there is doubt that differences are sufficient to justify Landolt's (1975) division of *L. minor* L. For this reason, I use the binomial *L. minor* L. in the sense of *L. minor* L. s. l. There appears to be no such confusion over the naming of *L. trisulca* L.

The Lemnaceae have a world-wide distribution (Landolt, 1984). Both *L. minor* and *L. trisulca* have a circumpolar distribution, with *L. trisulca* having a slightly extended northern limit. Both have been recorded in Africa and Australia, but *L. trisulca* has not been recorded in South America (Landolt, 1975, 1984).

1.2 MORPHOLOGY, CLONAL GROWTH AND ASEXUAL PROPAGATION

Although the Lemnaceae reproduce sexually (see Chapter 2), they are best known for their prolific clonal growth and propagation. Information in this section is from Hillman (1961) unless otherwise specified. The basic structural units in Lemnaceae are 'fronds' which are leaflike but also possess stem characteristics like lateral meristems.

Fronds are iterated functional units or modules (Harper, 1977). New 'daughter' fronds are produced by lateral meristems located in pockets found at the narrow end of the 'mother' frond. The narrow end of a daughter frond is called proximal (close to the mother frond) while the wide end is called distal (far from the mother frond). Often, several generations of daughters remain attached to the mother and thus form 'colonies'. A given clone consistently produces a daughter first from a pocket on one side (+ pocket), then the other (- pocket). When they occur, flowers are in the minus pocket.

Almost the whole plant is chlorenchymatous. In floating forms the upper epidermis is cutinized and contains stomata, while the lower epidermis lacks these characteristics. Rudimentary vascular tissue occurs in both fronds and roots. Roots, which are thought to be adventitious, lack root hairs, have a root cap and contain chloroplasts. Evidently, roots have no significant role in nutrient uptake (Muhonen *et al.*, 1983); the submerged surface of the frond serves this purpose (Hillman, 1961). Roots may, however, function to tangle plants together or to keep them upright.

Growth rate, which is exponential under non-limiting conditions, is thought to be best determined by counting fronds (Hillman, 1961). Datko *et al.* (1980) provide a detailed characterization of growth patterns in *Lemna paucicostata*. During exponential growth, a stable distribution of different frond stages (daughter generations) is attained and is independent of the initial stage distribution. Since a stable stage distribution develops, experiments involving *Lemna* may be started with fronds of a heterogeneous initial stage distribution (Datko *et al.*, 1980).

Although fronds and frond colonies may serve as propagules, specialized fronds may be produced. Many aquatic plants overwinter in the form of dormant buds or 'turions' which serve as propagules (Vintéjoux, 1982). In the Lemnaceae, turions are fronds that have small intercellular spaces, high cellular starch content, roots which are short or lacking, and in the case of *Spirodela polyrrhiza* (and often *L. minor*), much red pigment. They are heavy and sink to the bottom. Turions were first noted in *Spirodela polyrrhiza* and later in *L. minor*, *L. gibba* and *Wolffia* (Hillman, 1961). *L. trisulca* does not appear to produce turions, although it becomes pigmented in the fall.

Most information on turion behavior is based on studies of *Spirodela polyrrhiza* because it is best known, but *L. minor* turions behave similarly. Conditions of short day length, nutrient deficiency and low temperature appear to encourage turion formation (Sibasaki and Oda, 1979; Malek and Oda, 1980; Jungnickel, 1986). Turions are often dormant when produced and may require a period of after-ripening (Jungnickel, 1986) or cold treatment (Jacobs, 1947) before they germinate. They also normally require light to germinate (Newton et al., 1978). Turion germination occurs unevenly in time (Sibasaki and Oda, 1979), but this heterogeneity can be reduced by subjecting turions to mild osmotic stress (Malek, 1981). When turions begin to germinate, each develops a gas bubble which carries it to the surface. Turions break through the surface film, are held at the surface by surface tension, and produce fronds under suitable conditions (Jacobs, 1947).

1.3 ECOLOGICAL STUDIES OF LEMNACEAE

In studying Minnesota Lemnaceae, Jacobs (1947) found that *L. trisulca* was "the most uniformly distributed species", but was easily overlooked when hidden by floating species. Monospecific stands of *L. minor* were found in both heavily shaded and unshaded sites. *L. minor* and *L. trisulca* often coexisted, with *L. trisulca* appearing to dominate in spring before the canopy of *L. minor* closed. Monospecific stands of *L. trisulca* were uncommon. *L. minor* produced turions starting in early August. Jacobs (1947) believed that Lemnaceae were most likely to be dispersed by running water, aquatic mammals and floods. Waterfowl during fall migration were considered potential but poor dispersal vectors. Flowering in both species was observed.

Lawalrée (1961), Den Hartog (1964) and Rejmánková (1975a) reported abundant flowering in *L. minor*, *L. trisulca* and *L. gibba* respectively. The first two authors were mainly interested in pollination mechanisms. No studies have attempted to determine the extent and importance of flowering and seed set in a *Lemna* population.

Landolt (1957) conducted ecophysiological studies on Lemnaceae collected from across North America, including one clone from Delta Marsh (*L. minor* I, 6853). He compared species and clones on the basis of growth response to varying nutrient concentration, light intensity and temperature. He found that some species, including *L. minor*, flowered under conditions of high light intensity and water temperature.

The initial study of competition among free floating aquatics was conducted by Clatworthy and Harper (1962). They found that competition occurred between Lemnaceae, and between Lemnaceae and *Salvinia*. Outcomes of competition between pairs of species could not be predicted from growth parameters determined in monoculture (such as final yield, arithmetic and exponential growth rates) alone. Although not explicitly stated, shading ability was suggested as one important factor involved in determining competitive outcomes.

McLay (1974) examined environmental factors limiting the distribution of *L. perpusilla* in a California lake. Plants did not occur in open water because wind and wave action quickly moved them towards shore. In dense stands of submerged macrophytes, they grew poorly because of the high pH induced by macrophyte photosynthesis. Dense mats of *Lemna* developed in sheltered openings in the emergent macrophyte border of the lake. Densities were low within dense emergent macrophyte stands.

Rejmánková (1973,1975a) studied seasonal dynamics of growth in *L. gibba* relating relative growth rates in the field to light and temperature. Rejmánková (1975b) made one of the first attempts to explain the distribution of *Lemna* (*L. gibba* and *L. minor*) based on considerations of environmental factors (e.g. water nutrient status), plant morphology and interspecific competition. Rejmánková (1975a) suggested that it was *L. gibba*'s ability to overtop *L. minor* that allowed it to dominate in eutrophic waters. Keddy (1976) studied competition for light in *L. minor* and *L. trisulca*, and found that *L. minor* could inhibit its own growth (by shading itself) more than it could limit *L. trisulca*. *L. trisulca* was able to grow when shaded by *L. minor*. He used biogeographical theory to predict that *L. minor*

should occur more frequently in water bodies on the basis of its superior dispersal and establishment ability, and equal or greater competitive ability (for light only).

Landolt and Wildi (1977) examined communities of Lemnaceae in the southwestern U.S.A., using multivariate techniques to establish relationships between water nutrient status and community composition. Dissolved nitrogen and magnesium were correlated with differences in species distribution patterns. Climatic factors (aridity and temperature patterns) and competition were also deemed important in explaining distribution patterns.

Although there is a large amount of literature available on other aspects of *Lemna* biology, such as physiology, embryology and development (Landolt, 1980), this material is beyond the scope of this study.

1.4 JUSTIFICATION AND OBJECTIVES OF RESEARCH

Sexual reproduction of *L. minor* and *L. trisulca* in nature, and the effect of competition between the two species on their dominance patterns is poorly understood. This study was undertaken to: 1) obtain a better understanding of natural sexual reproduction in *L. minor* and *L. trisulca* and 2) develop an understanding of the factors, particularly interspecific competition, which influence dominance patterns of these species in space and time.

Chapter II

THE NATURE AND ROLE OF SEXUAL REPRODUCTION

2.1 INTRODUCTION

Harper (1977) defines reproduction as the development of a new individual from a single cell, and growth as the production of a new individual from a multicellular meristem. For this reason, I use 'clonal growth' to refer to the production of frond colonies, and 'propagation' for the fragmentation of colonies or production of turions from meristems in *Lemna*.

Little is known about sexual reproduction in *Lemna*. It is commonly suggested that flowers rarely occur (Arber, 1920; Hillman, 1961; Keddy, 1976) and that seed set is poor (Caldwell, 1899). At Delta Marsh, Manitoba, however, *Lemna minor* L. and *Lemna trisulca* L. flowered consistently and profusely throughout the period of this study. This chapter describes the sexual life history, and documents flowering and fruiting phenology of *Lemna* at Delta Marsh. The role of the seed habit in *Lemna* has not been previously assessed. To begin to assess this, a field experiment was conducted to determine whether or not seeds survived better than asexual propagules after overwintering at different water depths. The role of the sexual reproduction and the seed habit in the life history of the two species is discussed.

2.2 MATERIALS AND METHODS

Observations were made primarily at the University of Manitoba Field Station (Delta Marsh)(50° 11'N, 98° 23'W) in 1986-87. The mean January temperature at Delta is $-19.8^{\circ}\text{C} \pm 2.9\text{SD}$, and the mean July temperature $19.1^{\circ}\text{C} \pm 1.2\text{SD}$ (Environment Canada, n.d.). The area averages 1600 degree days (above 5.5°C) and 125 frost free days (Weir, 1983). The study was conducted at three sites:

Mixed ditch supported *Lemna minor* and *L. trisulca* in approximately equal proportions. This site is an L-shaped drainage ditch which is constricted at the bend into a north-south arm and an east-west arm. It is 3-4m wide and its depth varies between 0.3m and 1.0m as marsh water flows in and out through a connection with the marsh. Sediment is highly organic silty - clay with some fine sand. The site is bordered by *Salix interior* to the north and by *Typha* spp. and *Phragmites australis* in other directions. Shading is mostly limited to the edges.

Minor pond was dominated by *L. minor* and has no direct connection with the marsh. It is 2m wide, 15m long and its depth varies between 0.1m and 0.8m. Sediment is similar to that described above. This site is heavily shaded in summer by *Acer negundo*, *Salix interior* and *Populus deltoides*.

Trisulca pond was dominated by *L. trisulca*. It is located about 35km from the University of Manitoba Field Station. The surrounding area is marginal farmland and aspen parkland. Surface deposits of calcareous glacial till are evident. Sediments have a high proportion of stone and appear to be much less organic than the other two sites. The dugout is well sheltered by *Salix*

spp. on all sides, is deep (>3m) and has a large area of relatively unshaded water. *Spirodela polyrrhiza* was present but rare.

An overwintering experiment was conducted in 1986 in the Mixed ditch and Minor pond. Seeds were obtained from Mixed ditch sediment collected with an Eckman Grab (sample area=232cm²) in September 1986. Sediment was washed through 1.6mm mesh and 0.3mm mesh sieves, and seeds removed with forceps from organic material caught by the fine mesh. *L. trisulca* fronds and *L. minor* turions were collected one week prior to freeze-up from the Mixed ditch and placed in plastic containers. Fifteen seeds and fronds of *L. trisulca* and 25 seeds and turions of *L. minor* were placed into each of twenty-four 250mL Nalgene bottles filled with wet silica sand (the different number of propagules used for the two species reflects difficulty in obtaining sufficient numbers of *L. trisulca* propagules). An 8mm hole was drilled in bottle caps and covered with 0.3mm nylon mesh to permit water exchange. All material was stored at 4°C until bottles were placed in the field.

In the first week of November, three wooden stakes were placed in the two sites in water 80cm deep. Bottles were assigned randomly to stakes and were attached with stainless steel wire at 0cm, 25cm, 50cm or 75cm above the bottom.

Thermistor probes were attached to a fourth stake at each site (one probe per level). These were encased in 13mm copper pipe (to prevent ice and muskrat damage to cables). Temperatures were taken approximately every 21 days with a YSI telethermometer at each level and at the ice -

snow interface. The overnight low air temperature was obtained from University Field Station weather records.

Bottles were removed in late April, 1987 as the ice thawed, and propagules were extracted from the sand with feather forceps. They were first placed into 125mL Ehrlenmeyer flasks which contained 50mL of Woods Hole MBL growth medium (Nichols, 1973). Flasks were plugged with foam stoppers. Dense algal growth occurred and hindered germination, so propagules were transferred to 50mL distilled water where they subsequently germinated well. Flasks were placed in a controlled environment chamber under continuous illumination (ca. $200\mu\text{E}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ P.A.R) at 25°C. Flasks were checked periodically, and seedlings, germinated turions and living *L. trisulca* fronds counted and removed. Turions and fronds which had no trace of greenness were considered to be dead. Flasks were monitored until late August, at which time only a few ungerminated seeds remained. These were assumed to be either dead or dormant.

Propagule survival was expressed as the ratio of propagules alive after treatment to the total treated. A completely randomized one-factor ANOVA model was used. Data for all variables were normally distributed. Analyses were made using GLM and UNIVARIATE of SAS (SAS Institute, Inc., 1982a,b).

Phenological trends in two of the *Lemna* communities (Minor pond and Mixed ditch) were monitored in 1986 (June to October). In 1987, all sites were sampled for this purpose. Plants were sampled with a circular sieve (area=45.6cm²). Random samples were taken in Mixed ditch (n=12), Trisulca pond (n=12) and Minor pond (n=6) about every 21 days, starting June 24,

1986 Since phenological trends seemed different in the north - south and east - west arms of the Mixed ditch, sampling was stratified (6 samples taken in each arm of the ditch). Sampled material was placed in 9cm diameter plastic petri dishes and stored at 4°C until sorted.

Samples were sorted by placing small amounts of *Lemna* in a white enamel pan (half filled with water), and separating fronds of each species by hand with a small triangular sieve (area=2cm²) and forceps. Flower-bearing fronds were separated from vegetative ones in 1987. Fertile fractions were oven-dried at 110°C and desiccated over silica gel. A Cahn electrobalance used to measure dry weight to ±0.01mg. The number of mature fruits was recorded.

2.3 RESULTS AND DISCUSSION

Flowers of *L. minor* (Fig. 2.1a) and *L. trisulca* (Fig. 2.1b) occurred commonly in Delta Marsh. Casual searches at Morden, Manitoba and Buffalo Point, Manitoba also produced flowering *Lemna* plants. Jacobs (1947) suggests that, in Minnesota, *L. minor* flowers are not rare. Flowers of *L. minor* and *L. trisulca* were protogynous, as Hillman (1961) had suggested for Lemnaceae in general. While the morphology of flowering and vegetative fronds was similar in *L. minor*, flowering fronds in *L. trisulca* did not float beneath the surface as vegetative fronds did, but rather floated at the surface, develops a cuticle on part of their upper surface. This is similar to *Vallisneria* in which male flowers detach from submerged plants and float on the surface (Faegri and Pijl, 1979). Frond tips curl down into the water and appear uncutinized. The surface exposed to air develops stomata (Den Hartog, 1964).

Figure 2.1: Flowering fronds of A) *Lemna minor* and B) *L. trisulca*
(Fr=frond, St-stigma An-anther).