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ABSTRACT—The growth and reproduction of Vallisneria as seen and photographed below water in Christmas Lake, Hennepin County, Minnesota, is described. The functions of the water surface film, of wave energy, and of the coiled stem of the pistillate flower, in fertilization is discussed. It is found that many of the plants grow in such depths that fertilization is impossible.

Wild celery, *Vallisneria americana michx.*, is an aquatic plant that supplies food for diving ducks and muskrats in the form of a bean-like fruit and a white, crisp, succulent, buried stem. It is also a most interesting plant, one that makes ingenious use of its watery environment.

The leaves of *Vallisneria* are ribbon-like, some ⅜ inch wide and up to 4½ feet long when mature. They grow in a compact tuft from a fibrous root much as celery does. The young plants have 6 to 8 leaves, the mature plants 12 to 18, in the tufts. At the root, the leaves are white, crisp, relatively thick, and relatively narrow. Above the root they quickly turn bright green, broaden slightly, then taper gently to a blunt tip. The color becomes increasingly brown toward the tip, the leaf increasingly fragile, and somewhat ruffled. Taken from the water, the leaves are limp. Below water they float gracefully; in shallow places the upper part of the leaf may be flat on the water surface. The leaf is readily distinguished from those of similar plants by the four zones running its length, symmetrical about a strong midrib (Fassett, 1940: 8-9, 98).

The plant grows in depths of 3 to 15 feet in Christmas Lake. Its best growth is in depths of 5 to 6 feet and the plant usually rises through thick beds of other plants. It is found generally around the shores of the lake, wherever the bottom is loose, somewhat sandy, marly, and not cohesive. It does not grow in the areas with a peat bottom.

Vallisneria is a perennial. Its leaves and fibrous roots normally grow from nodes at 4 to 12 inch intervals along a buried stem. The stem elongates from year to year, and reaches lengths of 10 feet or more. This vegetative mode of propagation accounts, in part, for the fact that the leaf tufts are usually found in patches of a few to many. Isolated plants that have no apparent stem and are sterile are, however, frequent. One suspects that these are from last year's seeds, that they will develop a stem, and will flower the next season.

Vallisneria is diecious, that is, the individual plants are either male (staminate) or female (pistillate). As a consequence of its vegetative mode of reproduction, the plants tend to form groups of one sex that are often quite isolated from the opposite sex. The isolation gives rise to a problem that *Vallisneria* has solved in a manner all its own.

Near the middle of July the pistillate plants begin to produce small flowers — usually one or two — from each mature leaf tuft. These flowers, when there are several, appear in a rather closely spaced time sequence. They are raised to the surface by means of a long scape (stalk) that looks to the diver very much like a white nylon fishline about 1/16 inch in diameter. The flower develops as the scape grows toward the surface. The first flowers reach the surface near the beginning of August. Initially, the flower is completely enclosed in a transparent white spathe—a thin translucent sack formed from a modified leaf. This the flower penetrates before it reaches the air. The mature flower is about 1¼ inches in length. Its enlarged tip (the calyx), about ¼ inch in diameter, has 3 thick, blunt sepals that open to reveal 3 small linear petals and 3 gleaming white divided stigmas —the latter broad, curled, and beautiful. At maturity, these curl outward between the sepals.

To reach the surface, the scape must attain a length at least equal to the depth of water. This is no problem to the plant out to depths of about 6 feet, but in deeper water, although one sees forests of scapes, many and often all of the flowers fail to reach the surface. By the middle of September the flowers that have not yet reached the surface begin to decay.

The scapes grow straight initially, but most of them develop into long spirals before the flowers reach the surface. The spirals catch highlights from the sun, a pretty and intriguing sight for the diver against the dark background of deep water.

While the pistillate flower is growing toward the water surface the pollen bearing flowers of the staminate plants are maturing. These flowers are contained in spathes—in this case arrowhead shaped—each supported on 2- or 3-inch-long scapes at the leaf tuft base. Each spathe contains hundreds of closely packed tiny white flowers. Each flower is tightly closed, a silvery ball about 1/32 inch in diameter, and each ball is attached by a minute stalk to a central stem within the spathe (Fig. 1).

At the appointed time, after the pistillate flowers have reached the surface, the staminate spathe opens at its tip, the minute flower stems break or disintegrate, and male flowers float to the water surface.

The male flowers are not released in a cloud. The spathe peels back and disintegrates slowly, over a period

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FIG. 1. Staminate plants in aquarium, taken from lake one day before this picture. One spathe newly discharged.

of about 36 hours. The flowers are intermittently released during this time.

There are usually six spathes that mature successively at intervals of 2 to 4 days. Thus, male flowers are released over a period of 2 to 3 weeks. The release of functional flowers ceases during the first half of September, although many abortive flower-filled spathes may be found after that time.

The staminate flowers float freely on the water surface and are carried by wind and currents to the pistillate flowers; of the interesting happenings, then, more will be told in a moment.

The fertilized pistillate flower, and the fruit as it develops, float at the water surface. The bean-like fruit often assumes a curled, pretzel-like shape, and in all cases changes color from its initial bright green to orange—brown at maturity. It is solidly packed with a clear, transparent, mucilaginous substance containing numerous neatly arranged, small, spindle-shaped seeds, which are white when immature and brown when ripe. In early Octobter the scapes rot near the root, lose their buoyancy, and their weight pulls the still bouyant fruit to the bottom, or to a suspended position at some intermediate depth. By mid-October the fruits and scapes have disappeared as the scapes by then have disintegrated and the fruits have been lost in the bottom growth or eaten by ducks.

Ducks eat the fruits, stems, and leaves of *Vallisneria*. The buds from which next year's tufts of leaves will rise are a food available in early spring, and perhaps the seeds also. The stems are succulent morsels for the muskrats.

The origin of the name "wild celery" has intrigued me. My inquiries have yielded nothing. It seems probable that the name originated in the celery-like appearance of the plant near its root. I do find that the stem eaten raw is tasty, with a slightly fibrous texture and a faintly spicy, bitter taste. The enlarged nodes have a nutty texture and are very good. A few stems left on an outdoor table were eaten with obvious relish by a gray squirrel, who began at one end and proceeded until there was nothing left.

Vallisneria has developed a unique method of pollination, already touched upon briefly. This takes place at the water surface. First each flower is provided with sufficient gas within its structure to make it buoyant.

When viewed from above while floating on the surface just after release from the spathe the staminate flower has the appearance of a tiny snow-white onion. The flower has three sepals that join the structure at the lower side of the onion, but these now so tightly clasp the flower that their outlines cannot be distinguished, even under relatively high magnification. This onion, which is the male flower, floats motionless on the surface for some 2 to 10 minutes after release, then one sees it stir. In 1 or 2 seconds its sepals snap open, and rotate approximately 120 degrees about their points of attachment. Now the sepals that enclosed and protected the stamens form a three-legged support beneath them. This elevates the stamens above the water surface, and holds them erect.

The stamens in turn support, what appears through the microscope to be a horizontal bunch of gleaming white grapes; but this is the anther and its pollen, relatively large grains some 2-½ thousandths of an inch in diameter. The number of grains is extraordinarily small, about 100.

There are two thick stamens, although one must look closely to separate them. At the base of the stamens, and at right angles to the long axis of the anther, two cylindrical crystal white processes extend to either side. One of these, I assume, is the remnant of the flower's umbilical cord (pedicel), its minute attachment to its parent stem.

The first sepal to unfold is smaller than the other two. When all three have unfolded, the points at which they touch the water form very nearly an equilateral triangle. The sepals retain the curve of the folded flower's surface and so are cupped; the cups face outward and are inclined so that contact with the water surface is near the lip, but not quite at the lip which is somewhat above the water level. The elastic water surface film clings to this lip, thus holding the structure firmly upright. It is nearly impossible to upset the flower, it rides disturbances of the water surface with the greatest of ease and rights itself if forcibly upset. If one pokes it, it simply slips to the side. When the poking instrument is withdrawn the flower clings to its wetted surface; it remains tenaciously upright with respect to this surface, whether the surface is horizontal, vertical, or upside down.

Apparently all parts of the flower are waxy and impossible to wet. Nevertheless the sepals at their lips in contact with the water are wetted and thus are tied to the surface film as though with elastic bands. This does not appear to be entirely an effect of the size and shape of the capillary space beneath the sepal. If it were, the same effect should hold the flower in upset positions. A possible explanation may be found in the observation that after about 48 hours the flower loses its waxiness, is wet completely, and then adheres to the under side of the surface film. It may be that this effect of aging is felt at the sepal tip at the time the flower reaches the surface.

It appears that before the sepals open the flower floats in such a position that the then concealed stamens are upright, for in most cases the sepals unfold to reveal the stamens in the upright position. The folded flower retains this "ready" position persistently, probably because of its shape (it is flattened on the underside), and perhaps also through tension in the surface film pulling on the small wetted portions of the still folded sepal tips. However, in some cases crowding adjacent flowers may hold one in such a position that, before unfolding, the stamens are not upright. This presents more work, but no problem, to this little flower. As the sepals rotate in unfolding they, being waxy, push on the surface film. Here, I think, is the reason for the small sepal that first opens. It positions the plant to assure that one of the large sepals can push advantageously on the water surface film and that the weight of the second large sepal will assist the process of erecting and elevating the stamens. With a couple of jerks and a heave the plant floats upright. Pretty clever design! I might add that this process is not easy to observe because it happens so rapidly.

The next part of the problem is to bring the staminate flower, floating free before a wind of unknown intensity and direction, to the anchored pistillate flower. To this end, the plant first employs statistical methods. As I have described, each male spathe discharges its hundreds of flowers over a period of about 36 hours, and the several spathes mature and discharge at intervals of a few days. Thus, the chance of a wind in the right direction at some time is much improved.

But this does not end the matter. Employing the physics of surface films, the plant makes the target, the anchored pistillate flower, and the projectile, the freely floating staminate flower, each effectively larger than they are, and so again improves the chance of a hit.

Since both flowers are waxy the water cannot wet them. Their weight then depresses the surface film, just as a weight on a stretched rubber sheet would cause a depression in the sheet. The result is a small depression in the water surface around each flower; that around the pistillate flower is much the larger. The depression around the pistillate flower has a minimum size when the water is calm that is determined by the pull on the surface film of the flower's weight. But the depression increases in size when the flower is forcibly pulled deeper into the water. This occurs momentarily when passing ripples or waves cause tugs on the anchoring scape that effectively pull the flower downward and, when there is a surface current, such as occurs with the lightest breeze, causes a pull on the scape. Under these circumstances, the depression extends some ¼ inch from the pistillate flower, which is itself about ¼ inch in diameter, thus total depressed diameter is ¾ inch, more or less. The depression around the staminate flower is relatively tiny, but when its depression touches that of the pistillate flower the two depressions fuse, and the little flower slides down the slope, coming to rest against its larger spouse. Observe that through this use of the surface film the female, for the purpose of capturing the male, has made herself effectively some three times her actual size. (I resist the impulse to pursue this idea further.)

Thus, the statistics are again improved. And, in addition, the pistillate flower has now a device for holding the staminate flower, which is trapped in the depression. It has also found a device to free itself of floating debris, for practically all such debris is wetted and is repelled from the waxy unwetted flower by the surface film!

The most ingenious part is yet to come, however. Now the two flowers are side by side, floating at the bottom of their little depression in the surface film. The staminate flower is firmly upright. Its projecting sepals touch the pistillate plant. But the sepals hold stigma and anther apart (Fig. 2). A mechanism is needed to enable the staminate flower to vault this barrier.

To this end the plant employs wave energy. A passing wave of sufficient size causes the pistillate flower to be drawn below the water surface. Because the pistillate flower is waxy, a little well forms momentarily above it, before it is completely submerged. The walls of this well collapse inward and downward onto the face of the pistillate flower.

The advantage of the staminate flower being able to cling perpendicularly to a water surface whatever the position of that surface becomes evident. For the wall of

FIG. 2. Flower pulled below its floating position. One staminate flower to left of curled, arched, stigma, and the other against left side of sepal in foreground.

the well above the pistillate flower is the surface to which the staminate flower now clings. It is swept relatively upward and inward, rotated as it clings to the collapsing wall, and is flung, anther first, into the stigmas. There it becomes entangled; pollen grains rub on the stigmas; and the union is accomplished.

In the authoritative literature this tale has a lovely close. It is stated that after fertilization of the pistillate flower its long scape coils to pull the flower below the water surface. There in the protecting water the fruit develops.

I have not been able to confirm this event in Christmas Lake. There, during several seasons of observation, the great bulk of the fruits during development and at maturity have floated at the water surface, with a few just below the surface. A conclusion based on these observations is not possible, unfortunately, since in each of the years of my observations the lake has receded, as a result of evaporation, from a few inches to more than a foot, during the latter half of the summer. The recession may have exceeded the ability of the scape to pull the fruit downward.

The observed events do, however, provide a basis for suspecting that coiling of the scape is for purposes other than that of pulling the fruit below the surface, or perhaps in addition to this.

Many *Vallisneria* grow in water 6 to 15 feet deep. The plants develop pistillate scapes with terminal lengths of 6 to 9 feet. Thus, none of the flowers reach the surface beyond a depth of 9 feet, nor do many of those at lesser depths. The flowers that do not reach the surface are not fertilized, and do not develop fruits. Nevertheless, all the scapes are spiraled, some of them very strongly. In numerous cases, where the flower was near the surface, I have pulled the scape taut and straight to convince myself that the flower could not have reached the surface and then been withdrawn. The spiraling appears to be a matter of age.

On the other hand, I have noted frequently that some scapes, during development of the fruit at the surface, coil into rather short-pitched helices. And I have noted that when the flower is broken from the tip of the scape during the period of vigorous growth, the scape retracts into a helix of very short pitch, ½ inch or so. Some sort of a signal is given.

It seems to me that the coiling of the scape has two functions, one of assisting the process of fertilization I have described, and the other of preventing mechanical damage to the scape.

The scape must be longer than the depth of water. If it were not the flower would be submerged by every passing wave, by the lateral pull of wind-induced currents, and by any rise of the water surface as a result of rain or inflow. A long straight scape would overcome these difficulties, but would also permit the flower to lie flat on the water surface and to remain there, tossing up and down without submerging. A coiled scape, on the other hand, holds the flower nearly upright, the best position, and provides the required latitude for changing depth. More important perhaps, the resilient coiled scape tugs gently on the flower so that it is submerged only by waves of larger size, or very strong currents, thus giving the flower maximum time at the surface to capture the staminate flower, together with the means for submerging for the final act of pollination.

Wave action, while a necessary factor in fertilization, jerks repeatedly on the scape. The coils provide protection against breakage from these forces. As the size of the fruit increases, the wave forces on the scape also increase. It is interesting, in this light, to note that the scapes become more coiled as time goes on, in progress with the development of the fruit.

Wylie (1917) has described the use of the surface film by *Vallisneria* to accomplish pollination, although he may not have observed the same plant that I observed in Christmas Lake, for he designated his plant, observed in Iowa, *Vallisneria spiralis*. I have attempted to repeat and to enlarge upon his observations. In general my observations agree with his, but there are interesting differences. He lays considerable stress upon his observation that the sepals of the staminate flower open very slowly after reaching the water surface. I observed them to snap open. He states that the pistillate spathe opens upon reaching the water surface. I have observed that it opens long before. He states it as an accepted fact that the pistillate flower is drawn below the surface by the coiling of the scape. I have not been able to observe this. The plant must have different habits in different habitats.

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