Bulletin 41

A GUIDE TO AQUATIC SMARTWEEDS (POLYGONUM) OF THE UNITED STATES

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PREFACE

The object of this research was to establish a better understanding of the aquatic capabilities of smartweeds. These plants are well-known invaders of shallow water, and certain species can cover the entire surface of a reservoir in a period of a few years. The products of the study provide a better basis for understanding our native plants and the processes and capabilities of the amphibious members of the genus for invading aquatic habitats. Such knowledge is essential for planting programs and informed weed control associated with reservoir management programs.

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INTRODUCTION

Aquatic smartweeds are of interest to many people because of their importance as food for waterfowl. In addition, some species are aggressive invaders of lakes, reservoirs, and other wet habitat, and these species are capable of altering the ecological balance of large areas. The foremost intention of the author is to bring specialized knowledge of the plants to persons who might put it to best practical use. Since identification of species in the group has always presented difficulty to the professional as well as the layman, it is hoped that this bulletin will make the task easier. The booklet is divided into two main parts. Part I deals with the plants at the practical and non-technical level, whereas Part II presents more detailed accounts of some of the research conducted in conjunction with an Office of Water Resources Research grant to study the invasion of aquatic habitats by *Polygonum*.

Conscious planting of both native and Eurasian *Polygonum* species by man has produced some very interesting real and potential problems concerning lakes and waterways in the United States. To provide additional food for waterfowl, seeds[1] are made available by federal, state, and private organizations for the purpose of planting. This is an excellent practice, so long as the biological characteristics of the species are understood. Such plantings do, however, break down geographical barriers between species, allowing combinations which would be highly unlikely in nature. If indeed smartweeds hybridize, as has been suggested by Stanford (1925b) and Timson (1964), we are increasing the likelihood of spontaneous production of a new hybrid by growing species in unusual combinations. Such a hybrid might be a better seed producer or have other superior qualities. On the other hand, it might combine characteristics of the parent species which would allow it to invade lakes and reservoirs and ultimately affect fish populations severely.

There is mounting evidence that the amphibious smartweed (*P. amphibium*) arose as an ancient hybrid between semi-aquatic ancestors (Mitchell, 1968). This remarkable plant is capable of spreading floating, vegetative colonies over a water surface in a relatively short time. In 1967 the Pudding Creek

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[1]Nutlets of *Polygonum* are technically not seeds, but single-seeded fruit called achenes.

Reservoir in northern California was found to be covered by mats of this plant, all of which were female (male sterile). With no obvious pollen source the plants had done remarkably well. Local residents never recalled seeing the plant before the dam was built, but claimed that the mats had spread to enormous proportions by the end of the second growing season after the water rose.

Because of the capability of changing in appearance and internal shoot structure with changes in the environment, amphibious *Polygonum* has become one of the most widespread species in the world, with a range extending from Mexico and the United States throughout Canada, Russia, and most of Europe and Asia. The plants can persist for years on a dry lake bed or sand dune, and then produce new vigorous, aquatic shoots when water returns. The adaptations to aquatic life combined in amphibious smartweeds are nearly all found, to some degree, in the non-amphibious species. Gradation between terrestrial and aquatic *Polygonum* species was the subject of a study by the author, conducted for the United States Department of the Interior, Office of Water Resources Research. The recommendations on the planting of native smartweeds, found in Part I of this booklet, are the practical results of a part of this study.

PART I
IDENTIFICATION AND PRACTICAL EVALUATION OF SPECIES

IDENTIFICATION AND PRACTICAL EVALUATION OF SPECIES

The name, *Polygonum*, refers to the characteristic "knees" or swollen nodes of the stems. In addition to these, smartweeds may be distinguished from many plants which resemble them by the unique tube-like sheaths, which arise from each node just below the point of leaf attachment (Figure 1). Each sheath (called an ocrea) surrounds the stem like a collar until it becomes brown and shatters with age. Some "docks" (*Rumex*) have similar structures, but they shatter so early that they are seldom noticed. Willows also frequently have a green stipule just below the leaf on young shoots, but it does not completely surround the twig.

The leaves of smartweeds are simple structures, and are most often lance-shaped with even or slightly wavy margins. Flowers are small (about 1/8 inch in diameter), and are usually borne in dense, elongate spikes. They may be pink to purple or white to green depending upon the species.

A few American smartweeds, such as *Polygonum pensylvanicum*, are annuals with a tap root; however, most species are perennial and spread by horizontal, underground stems. In addition to underground stems (rhizomes) some species have lateral shoots (stolons) which creep over soil surfaces or form mats in the water.

Contact with a moist surface appears to initiate root production at almost any node on a *Polygonum* stem. This so-called adventitious rooting allows each segment to become a potential new plant. Such practices as discing and plowing do not rid a field of *Polygonum*, but aid in its vegetative reproduction.

A taxonomic key appears on pages 24 and 25 of this publication. This is a device which will aid in the identification of smartweeds found in the continental United States. Technical terminology has been purposely kept to a minimum, so that a glossary would not be necessary. Weedy species introduced from Europe and Asia are included in the key. Obscure species and those whose identities are in doubt are omitted, along with a large number of varieties which are presently in need of study. Specimens in dried collections at universities should not necessarily be consulted, since it has been the author's experience that they are frequently up to 50 percent misidentified.

The following list of species, with annotations and recommendations for persons interested in planting *Polygonum*, was prepared both from the author's observations in over 30 states and from a series of experiments documented in Part II of this bulletin. Since the experiments treated only 23 populations in depth, this line of evidence must naturally be accepted with caution; however, experimental results have, so far, substantiated and strengthened field observations in almost every case. Introduced weeds are treated separately, since they were not considered experimentally.

1. *Polygonum punctatum* Ell. Water Smartweed. A common plant in all states of the continental United States. Highly recommended as a shoreline plant; seed production prolific; plants quite variable with many races; rarely floating at water surface, always rooted. Will spread quickly in shallows.

2. *P. hydropiperoides* Michx. Mild Water Pepper. Highly variable species with many races in the United States; excellent species for planting on shorelines, but spreads rapidly in shallows; seed sources from coastal wetland areas are preferable to those from the Piedmont, because they are better adapted to survive inundation and fluctuation of water level.

3. *P. robustius* Fern. A good species for swampy areas; not an aggressive invader in shallow water situations; *P. robustius* should perhaps be regarded only as a variety or race of *P. punctatum*, but plants differ in being larger, more succulent, tending to grow in clumps, producing fewer fruit and having fewer hairs and bristles. Seeds are not readily available, since plants are not common, and are found in coastal swamps.

4. *P. opelousanum* Ridd. A close relative of *P. hydropiperoides*; these plants are good shoreline dwellers which seem to do best on the coastal plain where they are prolific seeders.

5. *P. hirsutum* Walt. This species is found from South Carolina to Florida and the West Indies; it is recommended for planting only with reservation, since it has much vegetative growth, is not a heavy seed producer and requires a climate where there are few heavy freezes.

6. *P. setaceum* Walt. This coastal plain species is also recommended with reservation; it shows little preadaptation to survival during water level fluctuations, and plants are large with average seed production.

7. *P. densiflorum* Meisn. This is a very large relative of *P. punctatum* which produces few seeds per unit of dry weight; it is subtropical or coastal, and is a potential invader of shallow lakes and ponds, being found often in water as well as on shore; it is highest in amphibious capabilities with the exception of *P. amphibium* itself; not recommended for planting.

8. *P. amphibium* L. var. *emersum* Michx. Red Careless, Devil's Shoestring. This non-amphibious plant does not form mats in deep water, but it has become a pest in agricultural areas where soil is moist for months at a time. It forms woody underground stems which propagate new individuals when disced or otherwise broken; a weed of rice fields; not recommended.

9. *P. amphibium* L. var. *stipulaceum* Colem. (including intermediates between this variety and the one previously listed). These plants have unusual capabilities for invading lakes and reservoirs and spreading over the entire surface. Horizontal stems up to 15 feet long can be produced by a single plant, and these may fragment to produce many new plants. Growth chamber studies showed exceptional survival capabilities when plants were submerged, and they thrived when shoots reached the surface. As mentioned earlier, amphibious smartweed can survive on dry lakebeds almost indefinitely and produce aquatic shoots should water return. This variety does not thrive on the coastal plain, but is well established in Piedmont, Montane, and Continental areas, such as the Midwest United States. Its range covers most of the northern hemisphere.

10. *P. pensylvanicum* L. Pinkweed. These are annual, native plants which are prolific seeders; since man's intervention in their native habitats, they have become weedy and spread to cultivated lands and other disturbed situations; they are known for their aggressive invasion of moist, tilled farmland or gardens; if kept under control they may be planted in farm ponds or on marsh borders with success.

11. *P. careyi* Olney. Closely related to *P. pensylvanicum* and like it in its weedy characteristics; this species is restricted to northern states, however. A related species, *P. bicorne* Raf. (*P. longistylum* Small), is doubtfully distinct from *P. pensylvanicum* and probably represents a subspecies at best; however, the group is in need of much study before decisions may be made on such matters.

12. *P. fusiforme* Greene. This rare species from Arizona and California has not been recognized by some floras, but it is a distinct species; it was described incorrectly as a perennial; it behaves as an annual in cultivation in the greenhouse and has been the most prolific seed producer; it is an aggressive weed in the greenhouse, producing seedlings in profusion in all pots surrounding the parent plants; since its potential as a weed outside the greenhouse is not known it is not recommended for planting.

13. Introduced species: the following is a list of annual *Polygonum* species brought into this country from Europe and Asia. They are planted frequently although their weedy nature is widely known. These species are now widespread in moist habitats in both natural and disturbed stiuations: *Polygonum hydropiper* L. Water-pepper; *P. lapathifolium* L. Willow-weed; *P. orientale* L. Prince's Feather; *P. minus; P. persicaria* L. Lady-thumb or Heart's-ease; *P. caespitosum* Blume var. *longisetum* (DeBr.) Stew.

FIGURE 1

A. *Polygonum hydropiperoides* Michx. Mild Water Pepper; B. Silhouettes representing variation in leaf shape of *P. hydropiperoides*; C. Flower of same species enclosing the fruit; D. Flower of *P. opelousanum* Ridd. with protruding fruit; E. Single-seeded fruit (achene) of *P. hydropiperoides* with three sharp angles; F. Sheathing stipule (ocrea) of *P. setaceum* Walt. with spreading hairs characteristic of that species.

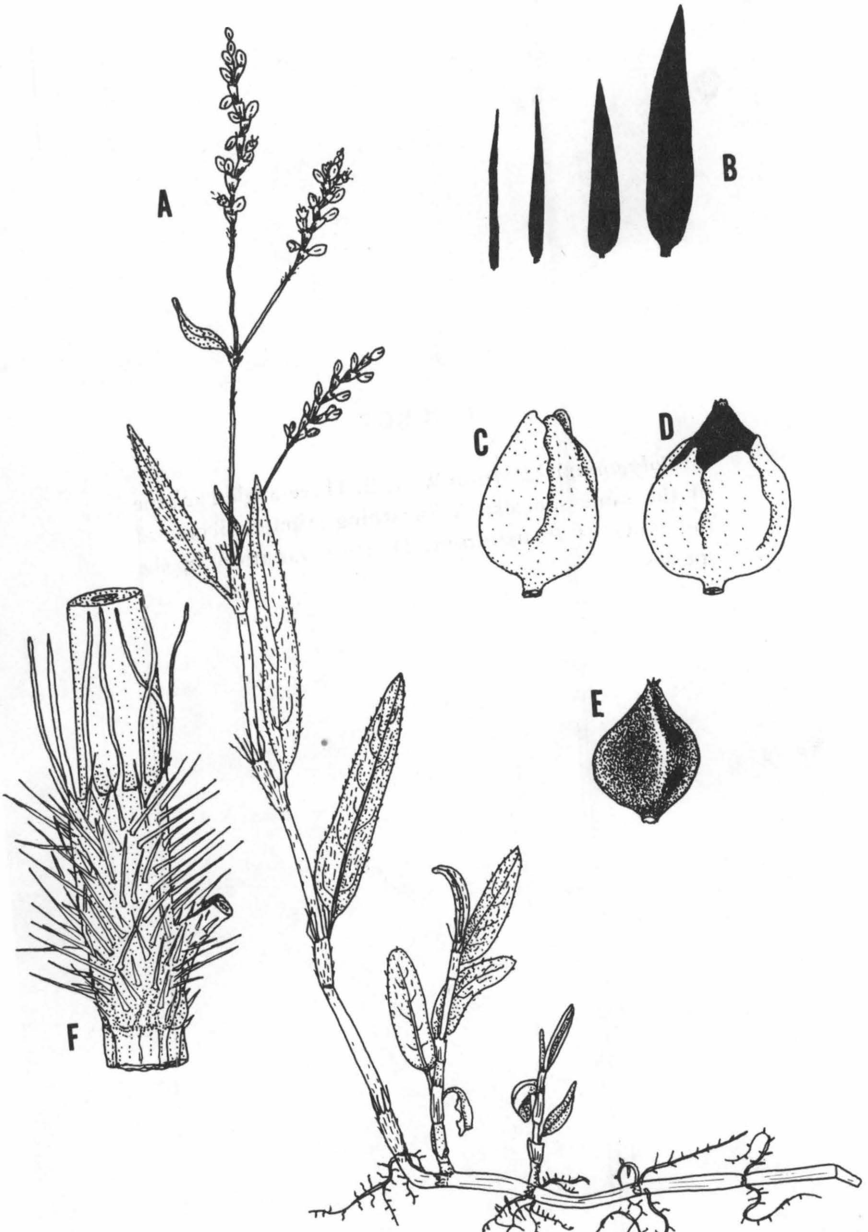
A
B
C
D
E
F
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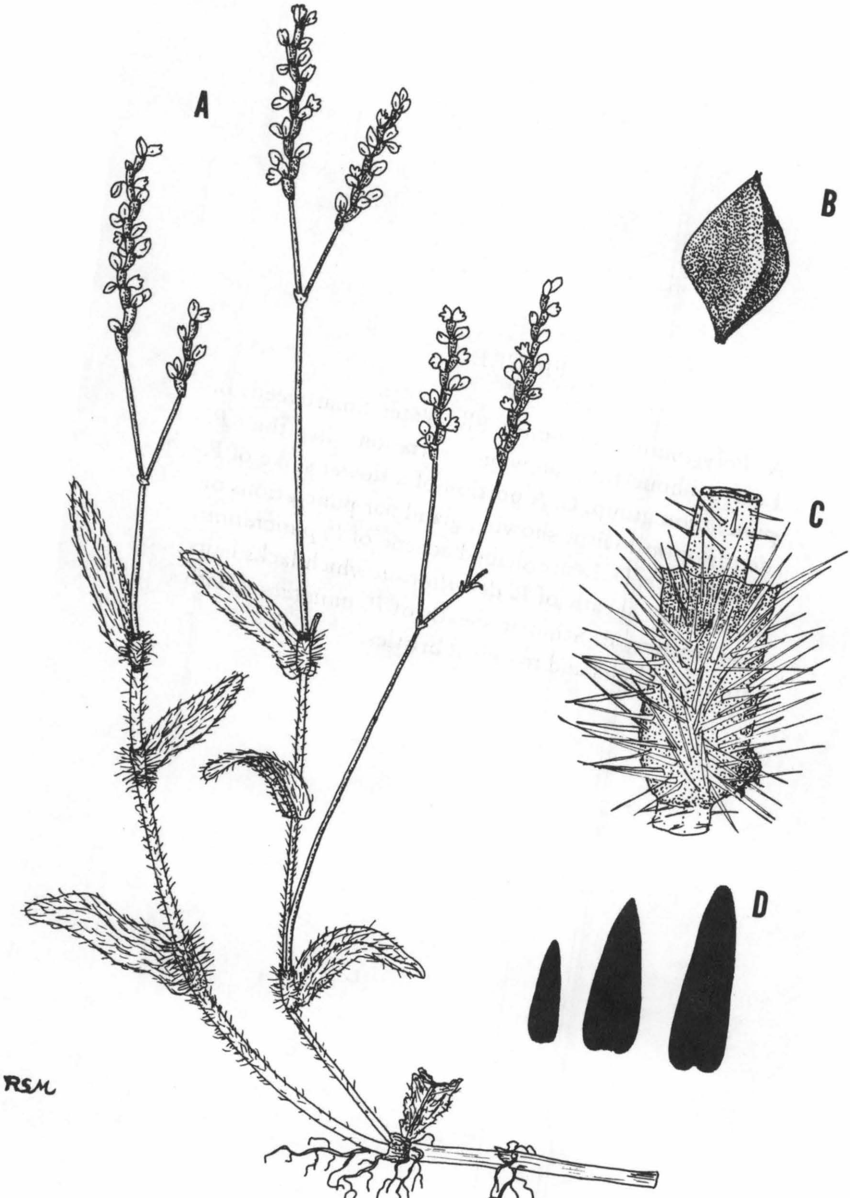
FIGURE 2

A. *Polygonum hirsutum* Walt. B. Three-angled achene of the same species; C. Sheathing stipule (ocrea) at the node of *P. hirsutum*; D. Leaf variation in the species.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B
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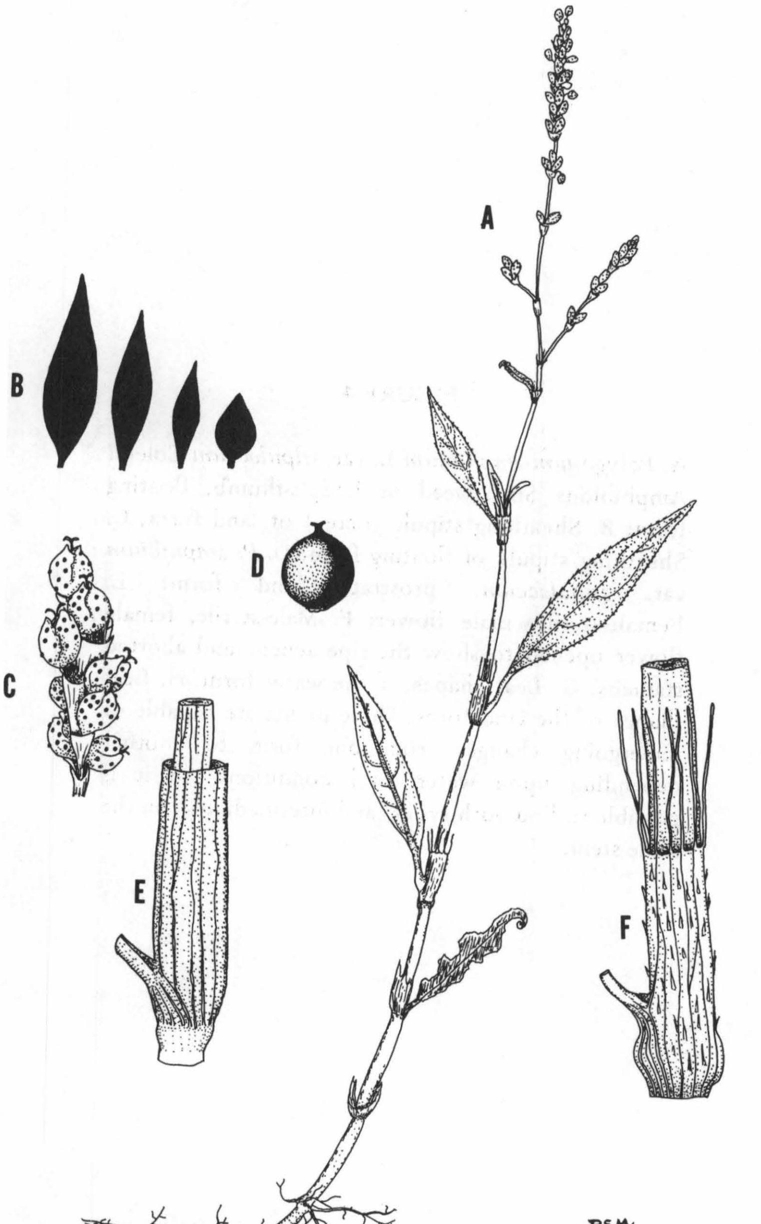
FIGURE 3

A. *Polygonum punctatum* Ell. Water Smartweed; B. Leaf silhouettes showing variation in the *P. punctatum* group; C. A portion of a flower spike of *P. densiflorum* Meisn. showing glandular punctations on the flowers; D. Lense-shaped achene of *P. punctatum*; E. Stipular sheath of *P. densiflorum* which lacks hairs and bristles; F. Stipular sheath of *P. punctatum* with appressed hairs and marginal bristles.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B
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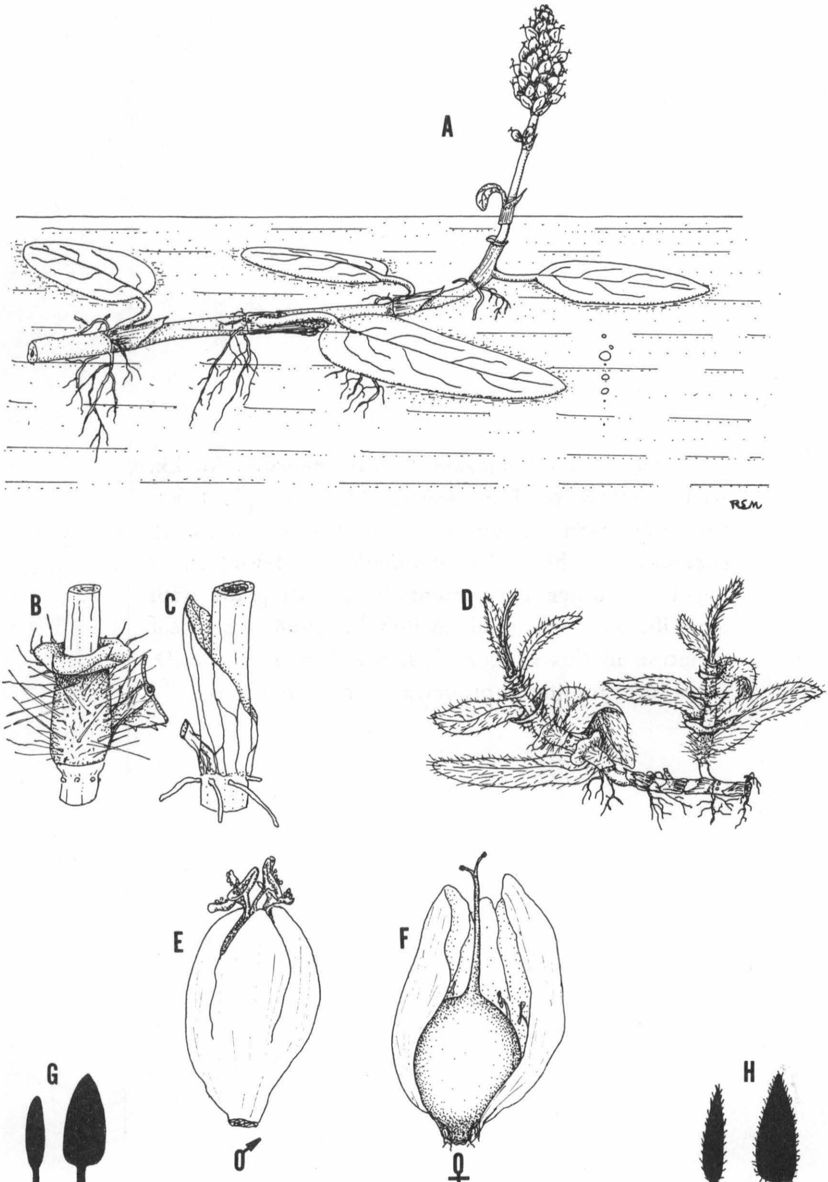
D
E
F
RSM

FIGURE 4

A. *Polygonum amphibium* L. var. *stipulaceum* Colem. Amphibious Smartweed or Lady's-thumb, floating form; B. Sheathing stipule (ocrea) of land form; C. Sheathing stipule of floating form; D. *P. amphibium* var. *stipulaceum*, prostrate land form; E. Female-sterile, male flower; F. Male-sterile, female flower opened to show the ripe achene and aborted stamens; G. Leaf shapes of the water form; H. Leaf shapes of the land form. These plants are capable of undergoing changes from one form to another depending upon water level conditions, so it is possible to find both types (and intermediates) on the same stem.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RSM
B
C
D
E
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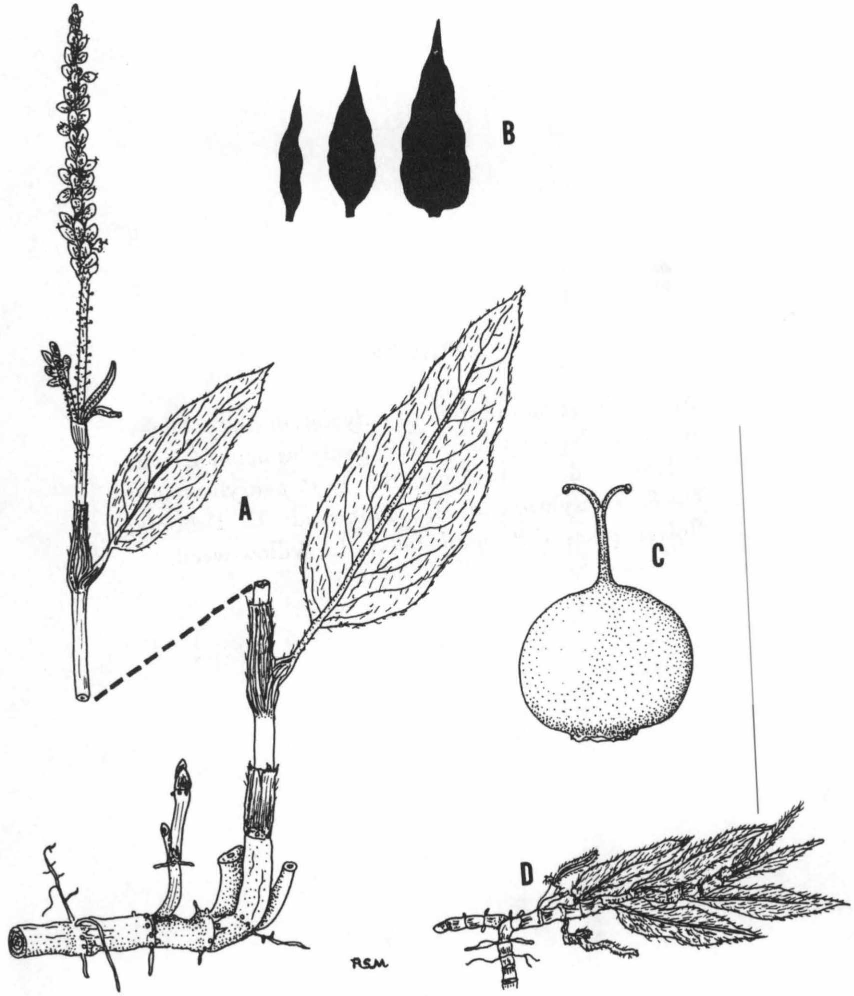
♂
♀
G
H

FIGURE 5

A. *Polygonum amphibium* L. var. *emersum* Michx. Red Careless or Devil's-shoestring; this plant has formerly been known by the species names, *P. coccineum* Muhl. and *P. muhlenbergii* Meisn., but it has been shown experimentally to intergrade with amphibious smartweed (Mitchell, 1968); B. Leaf variation in this variety; C. Lense-shaped achene; D. Land form found in hot, dry areas such as dunes.



A
B
C
D
RSM

FIGURE 6

A. Stiff hairs on the stem of *Polygonum careyi* Olney; B. Lense-shaped achene of *P. pensylvanicum* L. with indented side; C. Leaf variation in *P. pensylvanicum;* D. *P. pensylvanicum* L., Pinkweed; E. Drooping flower spikes of *P. lapathifolium* L., Willow-weed.

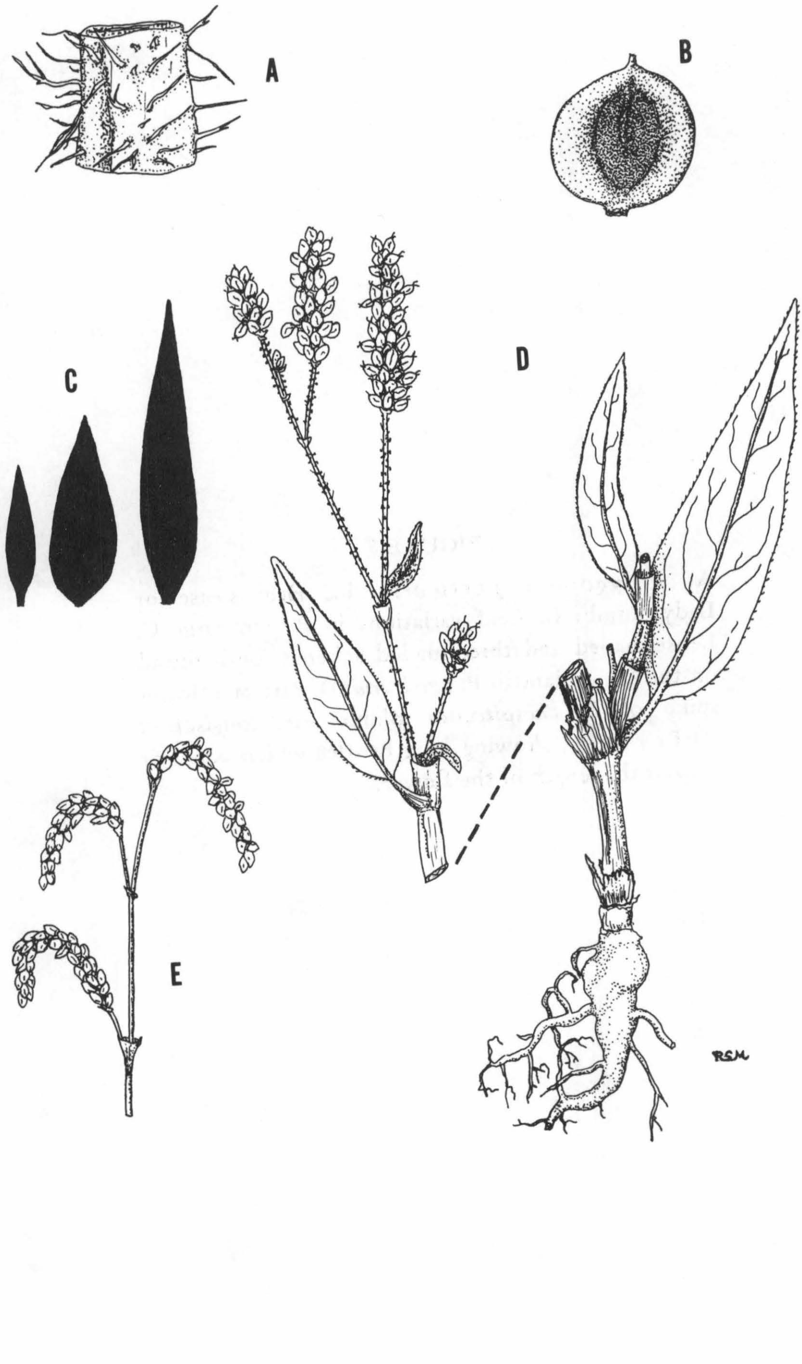
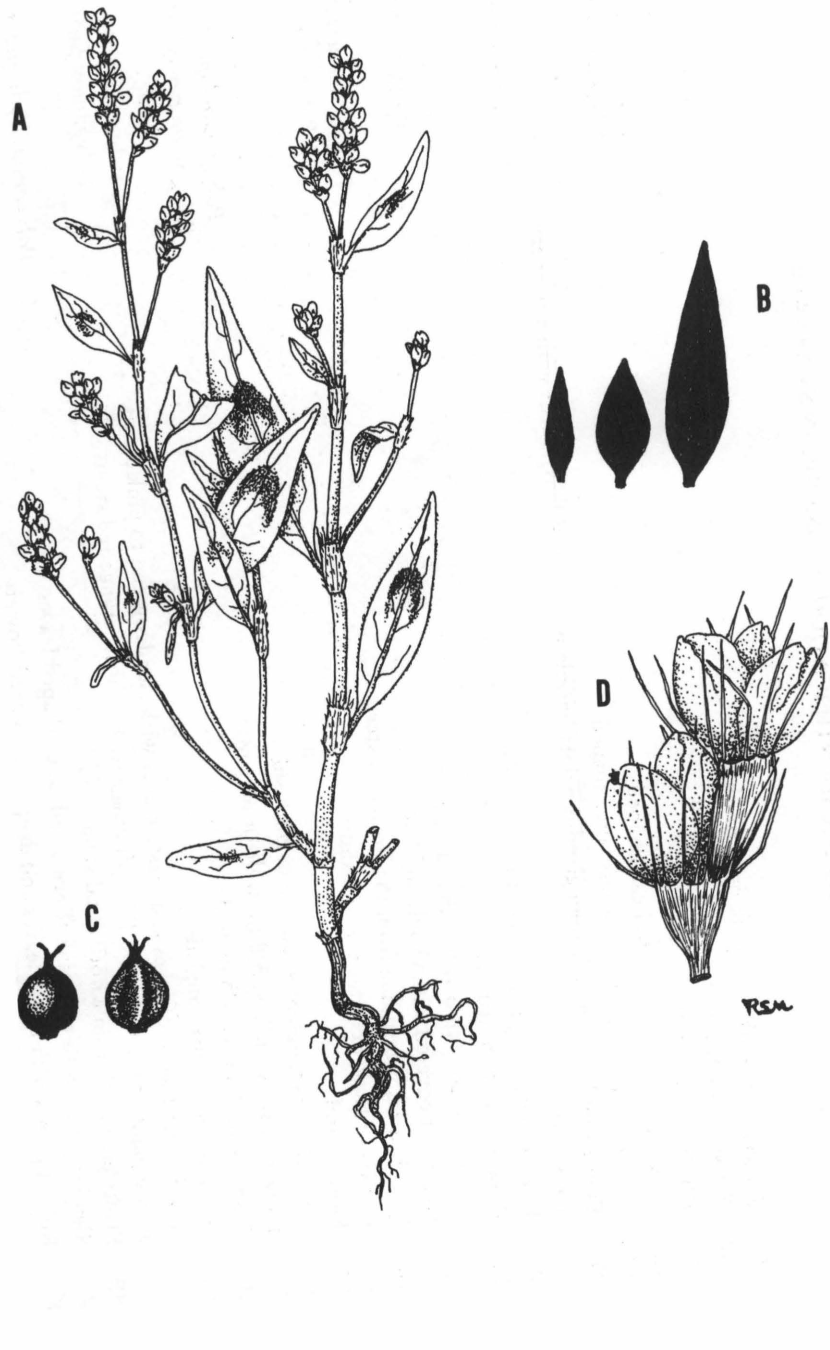

A
B
C
D
E
RSM

FIGURE 7

A. *Polygonum persicaria* L., Heart's-ease or Lady-thumb; B. Leaf variations in P. *persicaria;* C. Lense-shaped and three angled achenes, both found on the same plant in P. *persicaria;* D. Part of a flower spike of P. *caespitosum* Blume var. *longisetum* (DeBr.) Stew., showing long bristles which equal or surpass the length of the flower.


A
B
C
D
RSM

KEY TO THE IDENTIFICATION OF AMERICAN SMARTWEEDS*

A.	Flowers pale pink, rose pink or purplish	(B.)
AA.	Flowers white, cream colored or green	(M.)
B.	Plants annual, from a taproot	(C.)
C.	Leaves broadly rounded to heart-shaped	*Polygonum orientale*
CC.	Leaves not rounded, more or less lance-shaped	(D.)
D.	Flowers with yellow to brown glandular dots (visible with a hand lens); seeds with a peppery, acrid taste	*Polygonum hydropiper*
DD.	Flowers without glands or acrid tasting seeds	(E.)
E.	Flowers purple or dark red	(F.)
F.	Stems covered with bristly hairs and glands	*Polygonum careyi*
FF.	Stems not covered with glands and hairs	(G.)
G.	Long bristles protruding from the flower cluster	*Polygonum cespitosum*
GG.	Bristles of flower cluster few and short	*Polygonum minus*
EE.	Flowers pink	(H.)
H.	Seeds flattened, indented on one or both sides	(I.)
I.	Flower clusters (spikes) 3/8 in. wide or narrower	*Polygonum lapathifolium*
II.	Flower clusters over 3/8 in. wide	*Polygonum pensylvanicum*
HH.	Seeds plump or three-angled	(J.)
J.	A widespread weed of lakes and waste places with slender green to pink stems	*Polygonum persicaria*
JJ.	A rare plant of the Colorado River drainage with robust, orange-red stems	*Polygonum fusiforme*
BB.	Plants perennial from a horizontal stem	(K.)
K.	Slender plants with pale pink flowers and lance-shaped leaves	*Polygonum hydropiperoides*
KK.	Robust plants with broad leaves and deep rose-colored flowers	(L.)

L. Plants flowering while prostrate, usually floating on water; flower cluster 1 1/2 inches long or shorter . . . . *Polygonum amphibium* var. *stipulaceum*

LL. Plants flowering while erect on land or strongly emergent from water; flower cluster 1 3/4 inches long or more . . . . *Polygonum ampnibium* var. *emersum*

M. Plants annual from a taproot, usually with drooping flower clusters . . . . *Polygonum lapathifolium*

MM. Plants perennial from a horizontal, underground stem . . . . (N.)

N. Flowers with yellow to brown glandular dots (visible with a hand lens) . . . . (O.)

O. Ocrea (sheath at node) with bristles on the upper margin . . . . (P.)

P. Robust plants with flowers all adjacent in the cluster . . . . *Polygonum robustius*

PP. More slender plants with interruptions in the cluster . . . . *Polygonum punctatum*

OO. Ocrea with no bristles at the margin . . . . *Polygonum densiflorum*

NN. Flowers without glands, <u>or</u> with only a few pale spots . . . . (Q.)

Q. Mature flowers mostly spherical in outline with the seeds protruding beyond their tips . . *Polygonum opelousanum*

QQ. Mature flowers oblong in outline, always enclosing the seed . . . . (R.)

R. Ocrea covered with long, soft hairs which are not appressed to it, but which stick out like a furry collar . . . . (S.)

S. Leaves with petioles; not clasping the stem . . . . *Polygonum setaceum*

SS. Leaves without petioles; often clasping the stem . . . . *Polygonum hirsutum*

RR. Ocrea hairs appressed or absent . . . . *Polygonum hydropiperoides*

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*Read choices A and AA and determine which of the statements best fits the plant to be identified. Note the letter at the end of the statement selected. Next read the two statements which begin with this letter (they will not always be adjacent), and again determine which best fits the plant. Continue in this manner until the statement chosen ends with the name of the plant instead of a letter.

PART II
EXPERIMENTAL AND DESCRIPTIVE STUDIES OF AQUATIC *POLYGONUM*

EXPERIMENTAL AND DESCRIPTIVE STUDIES OF AQUATIC *POLYGONUM*

Part II deals specifically with experiments and other activities carried out by the author in conjunction with a two-year grant from the U.S. Office of Water Resources Research[1] entitled, "Invasion of the Aquatic Habitat by Amphibious Species of *Polygonum*". In cases where the studies have already been published they are described briefly, and the publication is cited. In the case of submergence experiments a more detailed account is included here, since these experiments are pertinent to recommendations made in Part I of this publication. For persons interested in delving into the literature on aquatic smartweeds, a bibliography is included at the end.

Submergence Experiments

This work was carried out in temperature-programmed environmental chambers (Sherer-CEL 25 HL). An aquarium was placed in each growth chamber and filled with water to a depth of ten inches. In addition to the recording programmer, a dual probe thermograph recorded air and water temperatures simultaneously within each chamber.

In an attempt to simulate natural conditions as nearly as possible, yet maintain a controlled and repeatable scheme, a "summer day" program was designed. This consisted, first, of a light regime based on a 15-hour day, in which the first and last hour of the period were furnished only by incandescent lamps (simulation of dawn and twilight). In simulated full-daylight the incandescent and fluorescent banks produced 6000 ft. candles at a distance of 12 inches from the bulbs. The temperature rose 10°F each hour to reach 92° at noon, where it remained constant until 4 pm. At this time it began to decrease by 5°F increments until midnight when it stabilized at 55°F. This program is shown graphically in Figure 8.

The purpose of the experiments was to test *Polygonum* populations for their amphibious responses upon submergence under controlled conditions. An

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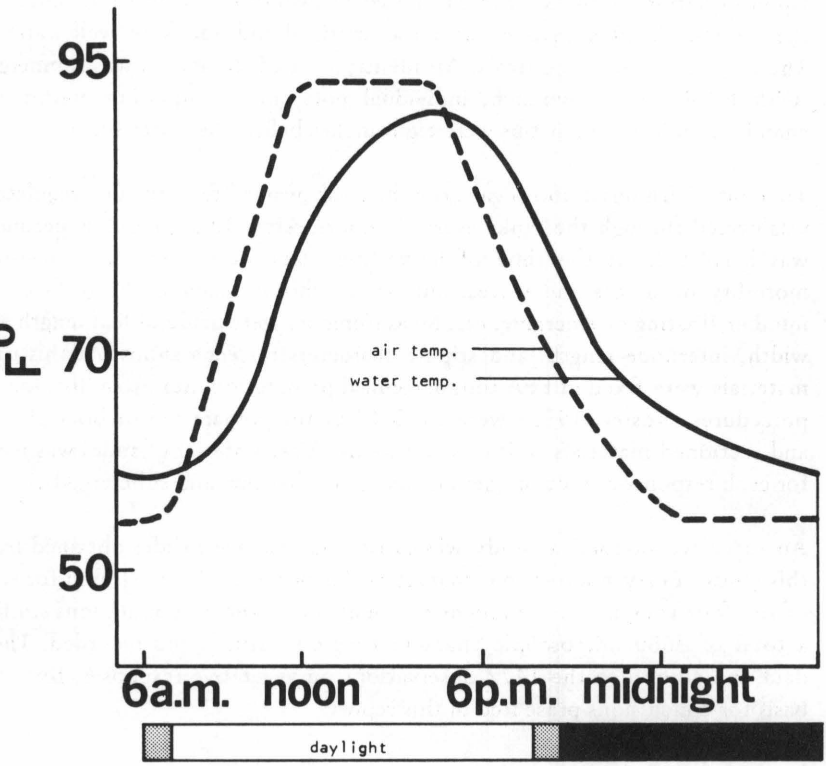
[1]United States Department of the Interior, OWRR project A-028-VA, administered by the Water Resources Research Center at Virginia Polytechnic Institute and State University (1968-1970).

FIGURE 8

"Summer day" temperature and light program under which submergence experiments were carried out in environmental chambers. Air and water temperatures were recorded with a Belfort dual-probe thermograph.


95
70
50
F°
air temp.
water temp.
6a.m.
noon
6p.m.
midnight
daylight

experiment proceeded as follows: twenty shoots per population were separated into sets of two ramets per clone. Soil was then removed from their roots, and they were planted in individual cubes of artificial soil (BR-8, American Can Co.). The substrate was water-saturated, and plants were allowed to grow for six days under Grow-lux lamps in the laboratory. At the end of this equilibration period minor adjustments were made to assure that each shoot tip extended vertically one inch above the surface of the artificial soil.

Upon initiation of an experiment one set of twenty shoots was transferred to the growth chamber in pans with the artificial soil and kept well watered. These served as aerial controls. An identical set of 20 shoots was submerged (with BR-8 soil in two-inch, individual pots) in the aquarium within the chamber, such that their tips were eight inches below the water surface.

To control bacterial and algal growth, fresh water (temperature regulated) was cycled through the tanks every 72 hours. After 30 days each experiment was harvested. At the time of harvesting, data were recorded concerning mortality of shoots and leaves, number of shoots reaching the surface, the number floating or emerging, etc. Measurements were made of leaf length and width, internode length, and stipule characters for each shoot. At this time materials were fixed in FPA for anatomical preparation. Standard histological procedures (Foster, 1955) were carried out for preparation of both cleared and sectioned materials of leaves and stems. A separate set of slides was made for each response-condition (aerial, emergent, floating, and submerged).

An extensive anatomical study was carried out using the slides obtained from this study. Forty microscopic characteristics per leaf were measured for each of the four responses to microenvironment. From the 23 populations studied a total of 3680 microscopic characters were measured and recorded. These data, in addition to the 1472 observations on vegetative responses, form the basis for conclusions presented in this report.

In final data processing, different responses to submergence were compared with and contrasted to the controls. Data were handled in a manner similar to that outlined in a former publication (Mitchell, 1968) with some modifications.

Survival of inundated shoots was unexpectedly high in the growth chambers under the "summer day" program. Even those shoots which never reached the water surface usually remained green and living after 30 days of submergence. Shoot mortality was over 50 percent in only three of the 23 populations, and 17 populations showed no mortality at the end of the experiment. Control populations grown aerially often showed more than 100 percent survival due to vegetative reproduction.

Though survival after inundation was high, shoots showed a considerable range of variation in their success at reaching the water surface. In only one population (M-127, *P. amphibium*) did all shoots break the surface. In the other populations of *P. amphibium* the percentage was in the high 80's except for the two populations of the emergent variety in which only half the shoots reached the surface. Other species ranged from 87 percent in one population of *P. punctatum* to zero in two populations of *P. hydropiperoides*. While the two populations of *P. hydropiperoides* from Virginia were unable to produce shoot growth sufficient to reach the surface, two other populations of the same species from Louisiana and Texas scored 61 percent and 63 percent on surface attainment. The Virginia plants were from stream banks where flooding is sporadic and short-lived, while the Louisiana and Texas plants were from marshy areas subject to longer periods of inundation. Since controls survived equally well in all cases, it may be postulated that high mortality and inability to attain the surface in the Virginia populations was due to lack of preadaptation to submergence. It is not surprising that in a widespread, polymorphic species, such as *P. hydropiperoides*, there may be racial differences of this nature.

In the truly amphibious populations 75 percent or more of the shoots reaching the surface produced only floating leaves, and shoots did not become emergent. Ten of the populations produced at least a few floating shoots. Intercalary growth and petiole elongation proved to be useful indices of amphibiousness, since these responses enhance the chance of survival of inundation. *P. amphibium* var. *stipulaceum* surpassed other taxa by far in these elongation responses.

Through a series of calculations the mean leaf area per shoot was determined for submerged and control populations. This estimate of total green surface area turned out to be a remarkably accurate index of aquatic survival and success capabilities. Amphibious populations produced as much as 183 percent more leaf surface than the controls, while in non-amphibious populations of the same species (*P. amphibium*), submerged shoots produced as little as 11 percent of the leaf area of controls.

An index of vegetative success of submerged shoots (Figure 9) was made using the following ten responses:

1) Response: Survival of inundation (30 days)
Measurement: Direct count
Expression: Percent survival
Amphibious response: Maximum survival

2) Response: Shoots reaching the water surface
Measurement: Direct count
Expression: Percent of inundated population
Amphibious response: Maximum number reaching surface

3) Response: Floating versus emergent shoots
Measurement: Direct count
Expression: Percent of shoots reaching the surface which floated rather than emerging
Amphibious response: Maximum percentage of floating shoots

4) Response: Floating versus emergent leaves
Measurement: A count of emergent leaves and of floating leaves on both emergent and floating shoots
Expression: Percent of the total which were floating
Amphibious response: Maximum percentage floating

5) Response: Leaf survival on submerged shoots
Measurement: Direct count of green leaves
Expression: Percent survival
Amphibious response: Maximum survival

6) Response: Difference in marginal leaf growth between floating and aerial leaves
Measurement: Leaf length and width in cm
Expression: Length/width indices
Amphibious response: Minimum l/w index

7) Response: Change in surface area of floating versus aerial leaves
Measurement: Leaf length and width in cm
Calculation: Floating l x w x 3/,5 divided by aerial l x w x, 3/5
Amphibious response: Maximum area in floating leaves

8) Response: Change in total leaf area per shoot upon submergence
Measurement: Leaf length and width in cm; calculate areas in each treatment
Calculation: Sum of leaf areas of submerged floating and emergent

leaves times leaves per shoot/20 (for submerged treatment); subtract from total area per shoot calculated for aerial control
Amphibious response: Maximum leaf area per shoot in the inundated treatment

9) Response: Petiole elongation in floating versus aerial shoots
Measurement: Petiole lengths in mm
Expression: Floating petiole length minus aerial (control) petiole length
Amphibious response: Maximum elongation of floating petiole

10) Response: Internode elongation upon submergence
Measurement: Internode lengths in cm
Expression: Difference between submerged and aerial internode lengths
Amphibious response: Greatest elongation of submerged internodes

For each of the responses the range of variation was adjusted to a 100 point scale by applying the following formula to each score (X): 100/range(X - lowest X). Each adjusted score could then be read as a percent of the variation range. The ten scores from each population were averaged to give a cumulative score. These were used to produce the histogram called the "cumulative index of quantitative response" (CQR Index, Mitchell, 1968) which places populations in order of their amphibiousness of vegetative response to submergence (Figure 9).

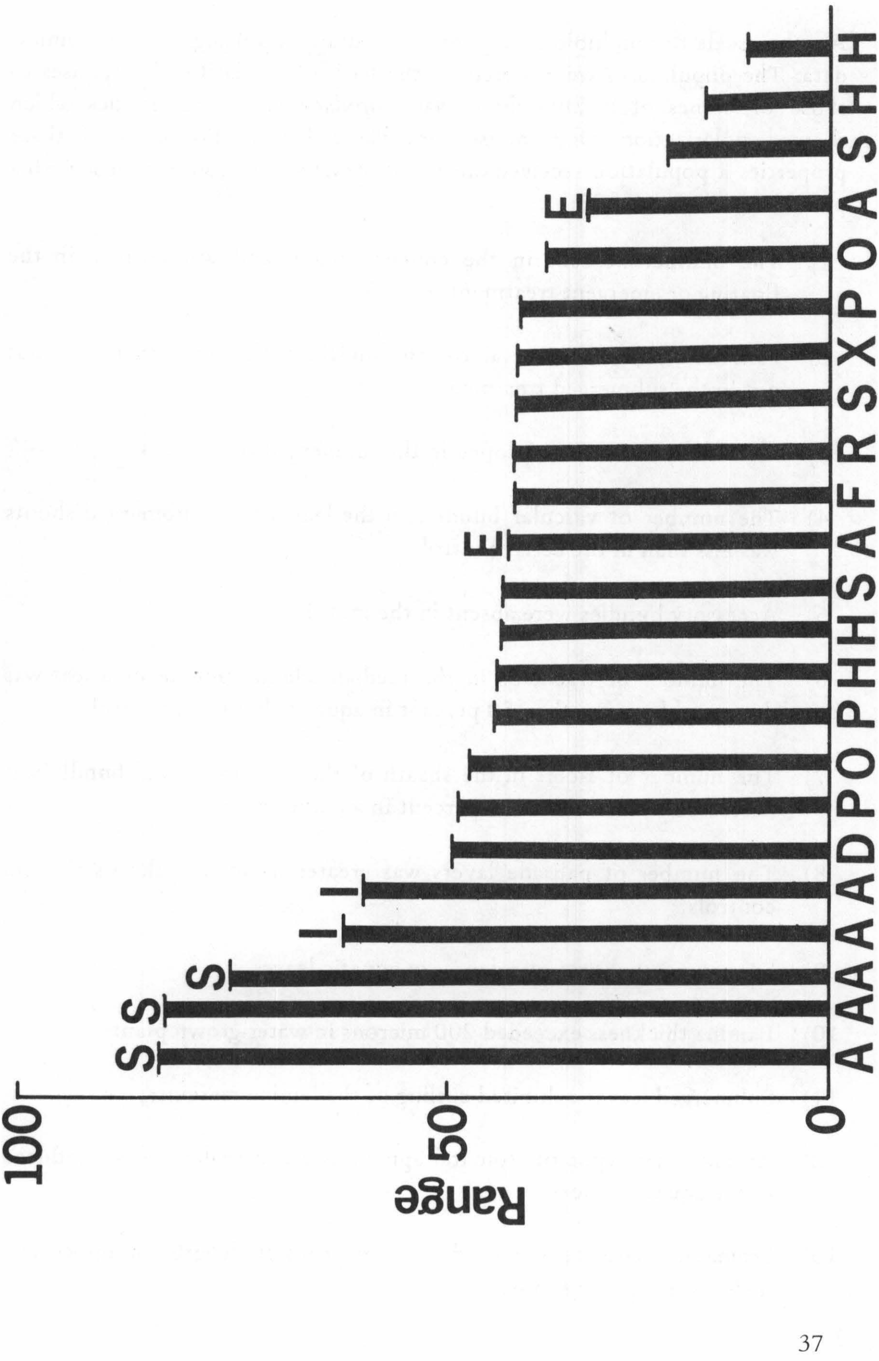
The taxon whose members showed the greatest amphibious response was *P. amphibium* var. *stipulaceum*. The three populations studied scored from 71 percent to 84 percent on the CQR Index. Varietal intermediates of *P. amphibium* scored 58 percent and 62 percent while the two populations of *P. amphibium* var. *emersum* placed thirteenth and twentieth in the order of amphibiousness with scores of 40 percent and 27 percent. This range of amphibious responses supports the notion of a broad cline of phenotypic plasticity within this species (Mitchell, 1968).

Nearly all the other species of *Polygonum* tested had scores between 40 percent and 50 percent. Other than *P. amphibium*, the species showing the best adaptation to survival after inundation was *P. densiflorum*. This is a subtropical and coastal species related to *P. punctatum* and particularly well adapted to life on lake margins where it frequently is found as an emergent. It is a polyploid like *P. amphibium*, and its great size and vigor probably have much to do with its survival and success after submergence. *P. densiflorum* is

FIGURE 9

Cumulative index of vegetative responses of 23 *Polygonum* populations to 30 days submergence in growth chamber experiments. A high cumulative score indicates preadaptation to the aquatic environment. Species names are coded by a letter at the base of each histogram column, and varieties are represented by a letter at the top:

A - *Polygonum amphibium*
Varieties: S - *stipulaceum*; E - *emersum*; I - *intermediate*
D - *P. densiflorum*P. fusiforme; *H - P. hydropiperoides*;
O - *P. opelousanum*; P - *P. punctatum*; R - *P. robustius*;
S - *P. setaceum*; X - *P. hirsutum*


Range
100
50
0
A A A A A D A D P O P H H S A F R S X P O A S H H
S S S I I E E

a strong emergent, exceeding the capabilities of even the emergent variety of *P. amphibium*, and shows little tendency toward the floating habit.

Another scale of amphibious responses was drawn up using only anatomical data. The populations were scored on the basis of similarity of responses to those of clones of *P. amphibium* var. *stipulaceum*. Characteristics which showed polarization of responses are listed below. For each of these properties a population received one point for an amphibious response with a possible total score of 25:

1) The number of cells in the collenchyma strand was greatest in the floating or emergent treatment.

2) Palisade was continuous across the midrib in the aerial treatment but not in the submerged treatments.

3) "Aerenchyma" was developed in the submerged treatments.

4) The number of vascular bundles in the leaves from submerged shoots was less than in the aerial control.

5) Accessory bundles were absent in the midrib.

6) The number of tracheids in the median adaxial bundle of a leaf was decreased by more than 50 percent in aquatic shoots vs. controls.

7) The number of fibers in the sheath of the median adaxial bundle was decreased by more than 50 percent in aquatic shoots.

8) The number of palisade layers was greater in aquatic shoots than in controls.

9) Spongy parenchyma was denser in aquatic leaves.

10) Lamina thickness exceeded 200 microns in water-grown plants.

11) Submerged leaves exhibited curling of the lamina margins.

12) An anisocytic type of stomatal apparatus was prevalent or was induced in the aquatic shoots.

13) Stomatal guard cells exceeded 30 microns in length on upper leaf surfaces in aquatic shoots.

14) Guard cells on the upper leaf surface of aquatic leaves averaged more than one micron larger than those of the control.

15) Guard cells on the lower leaf surface of aquatic leaves decreased in size more than four microns when compared with controls.

16) Epidermal idioblasts were eliminated in aquatic shoots.

17) Epidermal idioblasts were reduced in size in aquatic shoots.

18) Number of epidermal idioblasts/mm^2 was reduced in aquatic shoots.

19) Sclerification of lateral veins was reduced in aquatic shoots.

20) Stomatal ratio more than doubled in floating leaves vs. aerial controls.

21) Epidermal cell size was reduced in aquatic shoots (upper surface of leaf).

22) Epidermal cell size was reduced in aquatic shoots (lower leaf surface).

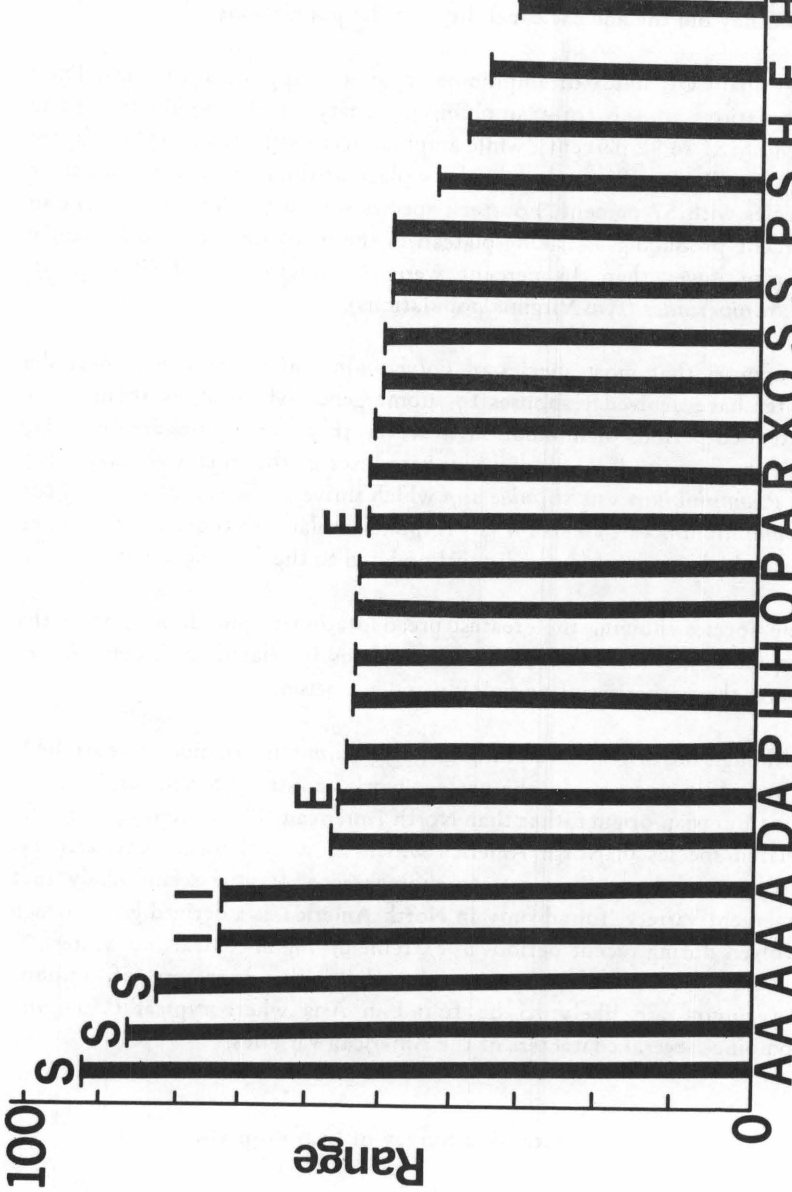
23) Pubescence length was reduced in aquatic shoots (margin, lamina, midrib; three possible points). or 24

24) Pubescence was eliminated from aquatic shoots (margin, lamina, midrib; three possible points).

Scores were corrected for a 100 point scale. One population of *P. amphibium* var. *stipulaceum* scored 100 percent, while the other two had scores of 88 percent and 92 percent. Amphibious intermediates had scores of 80 percent and 84 percent while populations of *P. amphibium* var. *emersum* placed sixth and seventh with scores of 68 percent and 72 percent. All other species tested fell below these percentages with regard to anatomical responses to submergence. The emergent variety of *P. amphibium* showed more similarity to members of its own species in internal anatomical responses and characteristics than it did in its ability to respond vegetatively and survive inundations. The CQR indices for vegetative responses and anatomical responses were combined (given equal weight) to produce a master index of amphibious responses (Figure 10). This actually amounted to a weighting of the vegetative index, since the number of characteristics used to produce the

FIGURE 10

Cumulative index of quantitative response for amphibiousness of 23 populations of *Polygonum* studied in environmental chambers. Both anatomical and vegetative responses were scored, averaged, and corrected for a 100 point scale. This histogram summarizes data comprising over 5,000 measured characteristics. Code letters for species are the same as in Figure 9.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S S S I I E E

anatomical index was 2.5 times greater. This is felt to be justified, however, since anatomical characters tended to emphasize taxonomic similarities more than they did the aquatic capabilities of the populations.

The final CQR index of amphibious responses appears significant. The three populations of the truly amphibious variety of *P. amphibium* (S) scored highest (81 to 92 percent), while amphibious intermediates (I) both scored 71 percent. *P. densiflorum* retained its place as the high scorer from the other species with 57 percent. Fourteen species scored between 46 percent and 57 percent producing a striking plateau in the histogram. The four populations scoring lower than 46 percent were *P. setaceum, P. fusiforme,* and *P. hydropiperoides* (two Virginia populations).

It appears that most species of *Polygonum* which occur in or near shallow water have evolved responses to submergence which allow them to survive extended periods of inundation; however, these capabilities are only of about half the magnitude of amphibious responses of the most well adapted clones of *P. amphibium* var. *stipulaceum* which thrive at the water surface. Plants of *P. amphibium* var. *emersum* (E) respond similarly to those of other emergent taxa which are much more distantly related to the floating aquatics.

The species showing the greatest preadaptation to inundation, other than *P. amphibium,* is *P. densiflorum*. It is not closely related to *P. amphibium*, but shares the properties of polyploidy and gigantism.

Although the origin of amphibious *Polygonum* still remains to be studied over a period of many years, the present work has strengthened suspicions that it is of Eurasian origin rather than North American. There seem to be no closely related species in North America which show both taxonomic affinity and strong amphibious responses to submergence. It now seems likely that the emergent variety, found only in North America, is a derived group which has evolved during recent periods of extreme drying in central and western North America. Present day species related to the ancestors of amphibious *Polygonum* are likely to be found in Asia where typical *P. amphibium* combines several characters of the American varieties.

Anatomical Survey of Leaf Properties

This study was largely of a descriptive nature, resulting in a cataloguing of a mass of anatomical data; however, several findings were of systematic and anatomical importance.

Schotsman (1950) had postulated that leaf glands of *Polygonum* provide consistent characters for species delimitation, and even for the detection of hybrids. This proved not to be the case for North American species, though five specific gland types were found in their leaves. Simple epidermal idioblasts were found in all species with the exception of a few populations of *P. punctatum*. It was later found that they could be induced in this species by inundation. Complex glands with subsidiaries and a four-valved operculum are found in three closely related species; *P. punctatum, P. robustius*, and *P. densiflorum*. It is interesting that these glands may be double in structure and twice the normal size in the polyploid, *P. densiflorum*. It was thought toward the end of this study that *P. opelousanum* could be distinguished by large plate-glands on the abaxial leaf surface. These were later found in plants from populations of *P. hydropiperoides* which had been under the environmental stress of submergence.

Though the example of gland characters just given is typical of the inconsistency with which leaf properties are distributed among species, it is possible, after this study, to identify *Polygonum* species on leaf characters alone.

Some 40 characteristics of leaves of 60 populations (17 taxa) are discussed in detail in a publication resulting from this study (Mitchell, 1971). This research laid the groundwork for experimental studies of anatomical modification.

A Simple Experiment on Prostrateness (Plagiotrophy)

Polygonum amphibium var. *stipulaceum* is an extremely aggressive invader of lakes, and has been of prime interest in this study. One of the most striking features of these plants is the tendency toward a prostrate growth habit, accompanied by shortening of internodes. This is most extreme in the land-form of the plant, found growing on dry soil and sandy banks after the water level recedes. Previously it was shown that prostrateness and internode length were correlated with drier habitats and light colored substrates in a sample of 20 populations in the field (Mitchell, 1968). At that time it was hypothesized that substrate-reflected light might play a role in inducing the "sand dune response."

To test this hypothesis ten clones each of *P. amphibium* (amphibious variety), *P. amphibium* (varietal intermediate) and *P. amphibium* (non-amphibious variety) were tested along with clones of *P. opelousanum* in the following manner: 20 ramets of each clone were divided equally between two treatments. All shoots were placed into trays in a horizontal position with their roots surrounded by moistened artificial soil (BR-8, American Can Company). Half the shoots were placed over filter paper blackened with india ink while the other half were placed over white filter paper. Trays were placed in growth chamber facilities for 48 hours with constant illumination (2000 foot-candles) and constant temperature (70°F). At the end of the period measurements of shoot curvature were made. Each shoot was then rotated such that it was horizontal once more and lights were cut off. After 48 hours of darkness measurements were made again and compared with those from the illuminated treatment. Controls and duplicate experiments were conducted simultaneously.

Results of these experiments may be expressed as follows:

1. The difference of 400 foot-candles reflected from a white substrate and 7 foot-candles reflected from a black substrate produced no significant differences in the curvature of shoots, even though they were oriented horizontally.

2. The mean curvature of shoots under 2000 foot-candles continuous illumination was:

	Angle of upward curvature
P. amphibium (amphibious)	43.5° ± 5.2
P. amphibium (intermediate)	51.4° ± 1.8
P. amphibium (non-amphibious)	90.0° ± 0
P. opelousanum	64.5° ± 4.1

3. In total darkness for 48 hours the responses of the same shoots were evidenced by greater upward curvature, indicating that the curvature is not primarily a photo-response, and that the upward curvature of shoots is inhibited by light. The differences between curvatures in dark versus light treatments match the data above in that amphibious plants are the most sensitive to the inhibitory effect of light upon upward bending:

	Increase in upward curvature in dark treatment versus light
P. amphibium (amphibious)	+21.3° ± 8.1
P. amphibium (intermediate)	+15.0° ± 3.0
P. amphibium (non-amphibious)	0.0° ± 0
P. opelousanum	+ 6.5° ± 1.2

Although much further study is needed before the physiological aspects of this problem can be adequately explained, this study appears to indicate that prostrateness is partly genetically controlled and partly a function of inhibition of negative geotropism by light. This inhibition operates most strongly on amphibious plants, with greater phenotypic plasticity, and does not operate on strongly erect plants of the non-amphibious variety of the same species. Substrate reflected light seems to have played little or no role under the light intensities used in this study.

Rediscovery of *Polygonum meisnerianum* in North America

As a result of the collecting trip sponsored by this project, a species of aquatic *Polygonum* (section Echinocaulon) never before recorded in the manuals and floristic works of this country has come to be recognized as a native of no fewer than four states. *Polygonum meisnerianum* C. and S. var. *beyrichianum* (C. and S.) Schlect. was found by the author in Lake Miccosukee, Florida in 1968. Since it appeared in no floristic manuals of the Southeastern states, a search was begun in herbaria to determine its identity and origin. The answer came in the plant collection of Harvard University where four of the seven known collections from North America are housed. Through a series of inquiries another Florida collection was turned up, and a first collection from South Carolina was found mislabeled. The center of distribution for this interesting species is Brazil, where its nearest relatives occur. Its occurrence in North America is discussed in a publication resulting from this work (Mitchell, 1970). Transplants of this species to the greenhouse assumed a juvenile growth form. This form had been described as a variety of the species, and is reduced to synonymy in the publication.

seeds [illegible] inhibitions [illegible] plants [illegible] greater [illegible] plants [illegible] [illegible] operate in strongly green plants of [illegible] [illegible] species. [illegible] reflected light seems to [illegible] little [illegible] the light intensities used in this study.

Relationship of [illegible] to other [illegible] in North America

A result of the collecting trip [illegible] by [illegible] [illegible] [illegible] [illegible] never before recorded [illegible] and [illegible] [illegible] of [illegible] [illegible] [illegible] [illegible] [illegible] fewer than [illegible] [illegible] [illegible] [illegible] (3) and [illegible] Schlect [illegible] [illegible] Florida in 1964. Since [illegible] [illegible] search was begun in herbaria [illegible] [illegible] [illegible] in the plant collection [illegible] Harvard [illegible] four of the seven known collections from North America [illegible] [illegible] Florida collection [illegible] [illegible] collection from South Carolina was found [illegible] [illegible] for this interesting species [illegible] in North America [illegible] [illegible] work [illegible] [illegible] [illegible] a juvenile growth form. This [illegible] species [illegible] introduced [illegible] [illegible]

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