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FEASIBILITY OF RELATING PHENOLOGY
AND CARBOHYDRATE PARTITIONING TO
IMPROVE AQUATIC PLANT CONTROL

by

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19. ABSTRACT (Continue on reverse if necessary and identify by block number) <p>Phenology and carbohydrate literature for waterhyacinth (<i>Eichhornia crassipes</i> (Mart.) Solms), hydrilla (<i>Hydrilla verticillata</i> L.f. Royle), Eurasian watermilfoil (<i>Myriophyllum spicatum</i> L.), and alligatorweed (<i>Alternanthera philoxeroides</i> (Mart.) Griesb) was surveyed to assess the feasibility of using phenology/carbohydrate relationships for improving control tactics. Many studies have examined phenology of waterhyacinth, hydrilla, and Eurasian watermilfoil, but not alligatorweed. Phenology of monoecious and dioecious biotypes of hydrilla differs in growth pattern and propagule development. The monoecious biotype appears to be better adapted than the dioecious biotype to live at Northern latitudes because of its ability to produce more tubers and turions at lower water temperatures. A few investigations involving Eurasian watermilfoil and alligatorweed suggested that control efforts directed at the low ebb of carbohydrates will decrease biomass production. Little information on carbohydrate partitioning has been</p> <p style="text-align: right;">(Continued)</p>					
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reported for waterhyacinth and hydrilla. Previous studies of these plants have not evaluated the role of starch reserves for plant survival. Environmental factors (e.g., temperature, light, and nutrients) have been shown to influence phenology and, by inference, carbohydrate partitioning. How these factors control carbohydrate partitioning in these plants is unknown. Phenological and carbohydrate relationships have not been fully developed to allow plant control programs to take advantage of weak points in a plant's life cycle.

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Preface

This study was sponsored by the Department of the Army, Office of the Chief of Engineers (OCE), Directorate of Civil Works (DAEN-CW), through the US Army Corps of Engineers Aquatic Plant Control Research Program (APCRP). Funds were provided by DAEN-CW under Department of the Army Appropriation No. 96X3122 Construction General. The APCRP is managed by the US Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss. Technical Monitor for OCE was Mr. E. Carl Brown.

The Principal Investigator for this study was Dr. Howard E. Westerdahl, Environmental Laboratory (EL), WES. The report was prepared by Dr. George J. Pesacreta, with contributions from Dr. Kien T. Luu, both of the EL (currently assigned to WES under the Intergovernment Personnel Act). Mr. Victor Ramey and staff at the Aquatic Plant Information Retrieval Center, University of Florida, provided many of the literature resources cited in this study. Technical reviews of the report were provided by Drs. Kurt Getsinger, R. Michael Smart, John Barko, and Douglas Gunnison of the EL. The report was edited by Ms. Jessica S. Ruff of the WES Information Technology Laboratory.

The investigation was performed under the general supervision of Dr. John Harrison, Chief, EL; Mr. Donald Robey, Chief, Ecosystem Research and Simulation Division; and under the direct supervision of Dr. Thomas Hart, Chief, Aquatic Processes and Effects Group. Mr. J. Lewis Decell was Manager of the APCRP at WES.

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FEASIBILITY OF RELATING PHENOLOGY AND CARBOHYDRATE PARTITIONING
TO IMPROVE AQUATIC PLANT CONTROL

Introduction

1. The relationship between phenology and carbohydrate partitioning is well known for many terrestrial species (Mooney 1972). This knowledge has been used to successfully control nuisance terrestrial plants (Linscott and McCarthy 1962, Klingman 1965, Schirman and Buchholtz 1966, McAllister and Haderlie 1985). For example, it is known that perennial plants store carbohydrates in roots and rhizomes during late summer and autumn for winter survival and initiation of spring growth. As a result of frequent mechanical cutting during summer and fall, translocation of carbohydrates to below-ground storage structures will be dramatically reduced (Klingman, Ashton, and Noordhoff 1975). Without adequate reserves, the plants are more susceptible to winter injury or death, and their spring growth is diminished. Consequently, the time in which stored carbohydrates are depleted is a vulnerable period, or weak point, in the life cycle for applying a control technique and improving efficacy.

2. As with terrestrial vegetation, use of the relationship between phenology and carbohydrate partitioning may have application to the control of aquatic vegetation. Aquatic plants may be more susceptible to control tactics following carbohydrate depletion in early spring and prior to translocation of carbohydrates to storage organs in autumn. Although the growth cycles of many nuisance species are relatively well known, the effects of various control methods directed during specific growth stages are not.

3. In addition, aquatic plant control using carbohydrate and phenological relationships must consider the effects of environmental stress on timing of the phenological event. Carbohydrate reserves allow plants to recover from periods of environmental stress, e.g., temperature extremes, disease, and physical injury from control attempts or grazing. In fact, the use of control techniques without this information, as well as knowledge of competitive relationships among aquatic plants, may result in selection of undesirable plant species.

4. This report is based on a survey of the existing literature on phenology and carbohydrate partitioning in four major nuisance aquatic plants:

waterhyacinth (*Eichhornia crassipes* (Mart.) Solms, hydrilla (*Hydrilla verticillata* L.f. Royle), Eurasian watermilfoil (*Myriophyllum spicatum* L.), and alligatorweed (*Alternanthera philoxeroides* (Mart.) Griesb. The objectives of this study were to: (a) assess the feasibility of coordinating control tactics with plant phenology through identification of susceptible periods (weak points) in the growth cycle, (b) evaluate possible effects of environmental factors on phenology and carbohydrate partitioning, and (c) identify research needed to clarify phenology and carbohydrate relationships.

Phenology

5. Phenological events, e.g., seed germination, flowering, senescence, and dormancy, occur over seasonal cycles. Changes in environmental factors can induce stress and alter phenological events. Environmental factors that can affect the growth of aquatic plants include light, photoperiod, temperature, nutrients, and sediment composition. The quality and quantity of light transmission through water can determine the distribution of submersed plants within an aquatic environment (Spence and Crystal 1970a,b; Sheldon and Boylen 1976; Singer, Roberts, and Boylen 1983). Daylength can influence some aspects of growth, such as carbohydrate content (Grainger 1947), tuber production (Van, Haller, and Garrard 1978), turion formation (Perry 1968, Weber and Nooden 1976), dormancy and germination (Perry 1968), and growth rates (Chapman et al. 1974). Temperature plays an important role in growth and development of aquatic plants. Several studies have concluded that elevated air and water temperatures increase biomass and accelerate development (Young 1973, Haag and Gorham 1977, Grace and Wetzel 1978). Recent evidence suggests that a combination of light and temperature influences morphology, biomass, and metabolism of aquatic plants (Barko and Smart 1981a).

6. Although light and temperature may be the overriding factors in aquatic macrophyte growth, other conditions can influence the growth and development of these plants. These growth responses have been linked to nutrients in the sediment (Carignan and Kalff 1979, Barko and Smart 1980, Barko and Smart 1981b). In addition, sediment density and organic content may dictate the density and distribution of aquatic species (Barko and Smart 1983, 1986).

7. The following is a survey of literature describing the phenology of waterhyacinth, hydrilla, Eurasian watermilfoil, and alligatorweed.

Waterhyacinth

8. Growth in the floating species, waterhyacinth, is primarily by expansion of a clone. Daughter plants (ramets) are produced by axillary buds located near the distal end of the stem (Bock 1966). Once ramets become separated from the parent plant, their buoyant, sail-like leaves allow each to float rapidly from place to place (Holm, Weldon, and Blackburn 1969). This free-floating condition and the rapid rate of production of daughter plants enable waterhyacinth to spread horizontally and cover an entire water body.

9. Waterhyacinth produces leaves of two different forms, and these depend upon both plant density and plant location within the population (Musil and Breen 1977). Large, bulbous petioles are typical when the plant is not crowded. Petioles become longer and thinner as interplant space decreases. The bulbous leaf form predominates at the edge of the mat nearest the open water, or in populations where conditions preclude the development of a closed canopy. The swollen petiole allows the plant to remain upright and float along the water surface (Holm, Weldon, and Blackburn 1969).

10. Studies show that freezing conditions can terminate growth and cause the waterhyacinth mats to turn completely brown (Penfound and Earle 1948). During a mild winter, a population of mostly small leaf plants has been observed (Center and Spencer 1981). The smaller leaves, which lie close to the relatively warm water, are better able to survive frost conditions than the larger, more exposed leaves. New seasonal growth and increase in leaf size can occur by early spring, with the greatest growth occurring in mid-summer (Penfound and Earle 1948, Bock 1969). Center and Spencer (1981) observed small and large leaf plants of waterhyacinth in the spring in Lake Alice, Florida. The authors noted that tall, large leaf plants dominated in summer. By autumn, a second recruitment of smaller plants occurred in the population. During this period, a second increase in biomass production occurred until the first frost. Frost may kill some plants, but the stem bases of mature plants may survive through winter, resulting in a spring population dominated by young plants.

11. Flowering in waterhyacinth varies and has been observed to occur from June to mid-November in California (Bock 1969), April to June and late-September to October (Center and Spencer 1981), or throughout the year in

Florida (Bock 1966). Shoreline plants usually bloom first. It is also common for one population to exhibit mass blooming, while a neighboring population produces few or no flowers (Bock 1966, Watson 1984). Plants that flower profusely produce few ramets, whereas plants that rarely produce flowers have many ramets. Pieterse, Aris, and Butter (1976) and Watson (1984) pointed out that exogenously supplied gibberellic acid induced profuse flowering. Richards (1982) demonstrated that nutrient deficiency stimulated flowering, and Watson (1984) found flowering was inversely correlated with ramet population growth rate. The mechanisms that trigger waterhyacinth flowering have yet to be determined.

12. Pollination and production of ripe seeds in waterhyacinth occur until freezing weather prevents the production of flowers. Both cross-pollination and self-pollination occur in this plant (Djalil 1973). Seed production probably occurs worldwide within its range (Penfound and Earle 1948, Djalil 1973, Tag el Seed and Obeid 1975, Obeid and Tag el Seed 1976).

13. Seed germination in waterhyacinth is low, apparently because germination requires several factors to be present simultaneously: scarification; well-oxygenated, warm, shallow water; and high light intensity (Das 1969, Center and Spencer 1981). Ruptured seed coats result from wetting, drying, and rewetting and give the quickest and most complete germination in laboratory studies (Robertson and Thein 1932, Parija 1934, Penfound and Earle 1948, Obeid and Tag El Seed 1976). Bock (1966) suggested that if parent plants are removed, their seeds would become the primary source for reinfestation. Following a lake drawdown, seeds would be expected to germinate along the shoreline (Haller 1981).

Hydrilla

14. Two biotypes of this submersed species are known in the United States. Monoecious plants, with both staminate and pistillate flowers on the same plant, occur in Delaware, Maryland, Virginia, and North Carolina. The dioecious biotype, with distinct pistillate-flowered plants, is found in Florida, South Carolina, Louisiana, Georgia, Texas, Arizona, Alabama, and California (Senft 1981, Haller 1982).

15. Hydrilla grows from fragments (Langeland and Sutton 1980), vegetative propagules (Haller 1978), and seeds (Cook and Luond 1982). Upon germination, internodes elongate, and shoots grow toward the water surface. As foliage of dioecious hydrilla approaches the surface, profuse branching occurs, resulting

in the formation of a dense canopy that shades out other submersed species (Haller and Sutton 1975; Haller 1980; Swarbrick, Finlayson, and Cauldwell 1982). Varshney and Rzoska (1973) have shown that nearly half of the photosynthetic tissue and biomass of dioecious hydrilla lies within 20 cm of the water surface, and 61 percent of the total biomass lies within 40 cm of the surface. Rather than forming dense canopies, monoecious hydrilla spreads along the bottom, sending shoots toward the surface in scattered patches (Environmental Laboratory 1985). However, canopy formation has been observed in monoecious plants growing in North Carolina (personal observation).

16. Seasonal biomass patterns differ for the two biotypes of hydrilla. A biomass gradient even exists between southern and northern Florida lakes for the dioecious biotype. Hydrilla persists throughout the year in southern Florida lakes, but the canopy collapses in northern Florida lakes during winter (Bowes, Holaday, and Haller 1979). Hydrilla biomass peaks anywhere from July to November (Nall and Schardt 1978; Bowes, Holaday, and Haller 1979). Monoecious plants from the mid-Atlantic states completely senesce, with little viable biomass and few fragments overwintering (Environmental Laboratory 1985; Harlan, Davis, and Pesacreta 1985).

17. Hydrilla forms two asexual reproductive propagules, subterranean tubers and above-sediment turions, which account for the plant's ability to infest new areas and regrow from year to year (Haller 1978). Reports indicate that more tubers are produced than turions (Mitra 1964; Haller 1978; Dhahiyat, et al. 1982; Sastroutomo 1982; Harlan, Davis, and Pesacreta 1985). Maximum tuber production for the dioecious biotype in the United States varies from 400 to 882 tubers per square metre (Miller, Garrard, and Haller 1976; Anderson and Dechoretz 1982; Sutton and Portier 1985). Up to 1,300 tubers per square metre were produced by monoecious hydrilla in North Carolina impoundments (Harlan, Davis, and Pesacreta 1985). Estimates of maximum turion production ranged from 42 turions per square metre for monoecious hydrilla in North Carolina (Harlan, Davis, and Pesacreta 1985) to 273 turions per square metre for dioecious hydrilla in Florida lakes and canals (Sutton and Portier 1985). Why hydrilla produces more tubers than turions has not been determined. Still, the large number of tubers and turions indicates the potential for reinfestation from these propagules.

18. Water temperature and photoperiod play an important role in tuber production of hydrilla. Tuber and turion formation in dioecious hydrilla

occurs from October through April in Florida, with maximum tuber production occurring during the winter months when biomass is lowest (Haller, Miller, and Garrard 1976). Germination of dioecious tubers in Florida lakes occurs from 15° to 35° C. Germination of monoecious tubers was first observed in spring at temperatures of 11° to 13° C in North Carolina (Harlan, Davis, and Pesacreta 1985). Laboratory studies on dioecious tubers show that 100-percent germination occurred between 18° and 33° C for tubers and at 25° C for turions (Haller, Miller, and Garrard 1976). Dioecious hydrilla plants form tubers as daylength decreases, with maximum production during daylengths of less than 13 hr. Dioecious tuber production is inhibited during long days (Van, Haller, and Garrard 1978; Sutton, Littell, and Langeland 1980). Monoecious plants form tubers during short days (Spencer and Anderson 1986), but tubers were occasionally formed during long-day conditions (Harlan, Davis, and Pesacreta 1985). Less is known about turions. Sastroutomo (1980) suggested that the colder water temperature may be the determining factor in turion formation.

19. Monoecious and dioecious tubers were found to respond differently in laboratory tests. Monoecious tubers that were germinated in the laboratory grew at a minimum temperature of 15° C, while dioecious tubers were inhibited at this temperature (Stewart and Van 1984). At higher water temperatures (22° and 30° C), tuber germination occurred in both biotypes. Monoecious tubers are smaller than tubers from dioecious plants (Anderson 1984, Stewart and Van 1984). Also, monoecious tubers grown under short days (10- or 12-hr photoperiod) germinated and produced new tubers by 28 days, while dioecious tubers that germinated and grew for 56 days did not produce new tubers (Spencer and Anderson 1986). Monoecious hydrilla produced turions between 23° and 28° C, while dioecious hydrilla formed turions only at 28° C (Van der Zweerde 1982). Thus, the monoecious biotype is well adapted to live in northern latitudes because of its ability to produce many tubers rapidly under short photoperiod and turions at low water temperatures.

20. Floral initiation varies between the biotypes in this country. Pistillate flowers on the dioecious biotype can occur in the spring or autumn (Haller 1978). Because staminate flowers are absent in Florida, no seeds are produced. The pistillate and staminate flowers of the monoecious biotype are formed from September through early-October (Langeland and Smith 1984). Cook and Luond (1982) suggested that, in tropical climates, flowering can occur throughout the year. Prior to the introduction of the monoecious biotype,

sexual reproduction had not been considered a major means of propagation of hydrilla in the United States. Hydrilla was assumed to be functionally sterile in this country. Seed production from natural populations of monoecious hydrilla has been recorded in North Carolina. These seeds were collected and germinated in the laboratory (Langeland and Smith 1984). Presumably, all plants of the monoecious biotype from the mid-Atlantic states are capable of producing viable seeds. Sexual reproduction may increase the genetic variation in the monoecious biotype; however, any advantages given these plants by this form of propagation are unknown.

Eurasian watermilfoil

21. Following winter, growth in the submersed species, Eurasian watermilfoil, can occur from plants that have overwintered in a dormant evergreen state or as viable plant fragments, root crowns, or seeds (Amundsen and Brenkert 1978; Grace and Wetzel 1978; Aiken, Newroth, and Wile 1979). When propagating root crowns break winter dormancy, they produce new stems and begin spring growth. Biomass development and subsequent canopy formation are rapid (Stocker and Kent 1984). Greater than 50 percent of the photosynthetic production can occur within 20 cm of the water surface (Adams, Titus, and McCracken 1974), and 75 percent of the plant biomass can be concentrated in the top 30 cm of the water column (Titus 1977). Most leaflets underlying the canopy senesce and drop from the plant as the canopy develops.

22. Eurasian watermilfoil has been reported to flower once (Aiken, Newroth, and Wile 1979; Carpenter 1979) or twice (Young 1973) during the year. Flowering occurs in North America anytime from May to November (Warrington 1983, Nichols and Shaw 1986). After a first peak biomass and flowering period in summer, fragmentation occurs. This period is immediately followed by a second flowering and peak biomass period and a subsequent fragmentation and senescence period (Young 1973, Stanley et al. 1976).

23. Phenological variations of Eurasian watermilfoil have been observed in geographically similar water bodies. Warrington (1983) reported that growth and flowering differed in two ponds near Vancouver, British Columbia. Standing vegetation occurred year-round in Centennial Park Pond, with flowering from May to September and fruit production from June to August. In Queen Elizabeth Park Pond, standing vegetation was absent from January to March. Flowering was from May to June, and no fruits were produced. Why these phenological differences occurred in two nearby ponds is unknown. In Melton

Hill Reservoir, Tennessee, flowering occurred 1 month earlier at a station located near the thermal discharge as compared with stations remote from the thermal influence (Young 1973).

24. Seed production and germination may be an important mechanism for the introduction and infestation of Eurasian watermilfoil in new areas. Seeds require cool, dark conditions to germinate (McDougall 1983). The specific conditions needed for germination suggest seed germination would be sporadic under natural conditions. However, seeds, fragments, and the overwintering evergreen plant appear to be important for long-term survival of the species (Grace and Wetzel 1978).

Alligatorweed

25. At least two biotypes of alligatorweed have been reported in this country (Kay and Haller 1982; Wain, Haller, and Martin 1984). Alligatorweed can be separated into plants having narrow stems and short, rounded leaves (NSA) and those having broad stems and narrow leaves (BSA). Both biotypes are similar when growing in water, but distinct differences occur when the plants are grown on land. Specifically, BSA produces significantly greater biomass and shorter stem lengths than NSA when grown on land.

26. Alligatorweed also occurs as two morphotypes: an aquatic form (emergent and free-floating) and a terrestrial form. The emergent aquatic morphotype usually occurs anchored in the sediment near the shoreline. A free-floating variety is commonly found attached to rooted plants along the shoreline. Weldon (1960) reported that alligatorweed could grow as a free-floating mat, though Sculthorpe (1967) suggested that the plant cannot survive for extended periods unless rooted. Alligatorweed can also become completely terrestrial, for example, following drawdown or if established in dredged material (Langeland 1986). Alligatorweed produces a "tough, fleshy, root-like rhizome" when grown out of water (Kay and Haller 1982). Stems in the terrestrial form are smaller in diameter, more lignified, and have smaller internodal cavities and shorter internodes than the aquatic stems. Although the terrestrial form exists, alligatorweed grows primarily as a rooted, emergent, or floating plant with most foliage growing out of the water.

27. Few studies have described the entire growth cycle of alligatorweed. Alligatorweed characteristically undergoes winter dieback to root crowns, or its stems fragment and become loosely attached to the shoreline (Penfound 1940; Penfound, Hall, and Hess 1945). The plant produces few shoots

throughout the winter. In spring, shoot elongation originates from underground stems. Growth and flowering in the spring may be controlled by water and air temperature (Penfound, Hall, and Hess 1945). By early summer, large floating mats are formed (Coulson 1977). By autumn, shoots reach maximum height, and the plant spreads horizontally from the shoreline into the open water. Fragmentation of the stems during senescence in late-autumn or winter usually allows only root crowns and stem fragments to survive.

28. Alligatorweed forms only pistillate flowers in this country (Penfound 1940). The plant is dispersed primarily by the dislodgement of plant mats and their reestablishment in other areas of a water body. If a plant group detaches from the mat, it will continue to grow as a floating aquatic until it anchors again in the sediment or along the shoreline (Weldon 1960).

Carbohydrate Partitioning

29. Carbohydrate partitioning describes how photosynthetically produced sugars are distributed in various tissues of a plant. Knowledge of how carbohydrates partition in plant tissues (during different phenological events) can help identify sink and source energy reserves. Carbohydrates, which are produced by the photosynthetic process, are the principal organic materials stored in plants (Smith 1975). Therefore, their concentrations are important as an energy source for growth, development, and maintenance of plants. Carbohydrates can be divided into two major groups: total structural carbohydrates (TSC) and total nonstructural carbohydrates (TNC). The TSC include permanent structural substances such as cellulose, hemicellulose, and other complex polymers. Structural carbohydrates provide for the physical structure of the plant and usually remain where they are synthesized. In contrast, TNC can be converted to simple sugars and cycled in physiological processes.

30. The TNC can be separated into two fractions: soluble sugars (monosaccharides and disaccharides, e.g., glucose, fructose, maltose, and sucrose) and reserves (polysaccharides, e.g., starch and fructosan). Soluble sugars are readily available for metabolism, and their amounts vary in plant tissues. The reserve carbohydrate components of plants are stored in various organs (e.g., stem bases, tubers, turions, rhizomes, and roots) and later metabolized during respiration and growth. The rate of carbohydrate synthesis (photosynthesis) must exceed the rate of utilization (respiration and growth) for a

plant to accumulate reserve carbohydrates. These reserves are essential if the plant is to survive over winter. Moreover, they are the primary source of energy during periods of growth in early spring (Smith 1975).

31. Light and temperature are two important environmental factors that influence carbohydrate remobilization and subsequent partitioning. Germination of terrestrial grasses in spring, production of overwintering propagules, and storage of carbohydrates in autumn can be linked to measurable changes in the environment, most noticeably, temperature and daylength (Hanson and Juska 1969). These investigators reported that maximum storage of carbohydrates in grasses occurs in autumn at the temperature near the minimum required for shoot growth.

32. Limited information exists regarding the relationship between carbohydrate reserves and growth in aquatic plants. Several studies have shown that TNC and starch reserves of rhizomes decrease during the spring growth period in emergent aquatic plants (Linde, Janisch, and Smith 1976; Graneli, Sytsma, and Weisner 1983; Gallagher, Wolf, and Pfeiffer 1984). Harvesting giant cutgrass in autumn caused reduced carbohydrate levels and decreased plant growth in the following summer (Birch and Cooley 1983). Linde, Janisch, and Smith (1976) were able to recognize the minimum TNC level in cattails based on the phenological expression of the plant. Seasonal trends of starch in the submersed species, coontail (*Ceratophyllum demersum*), elodea (*Elodea canadensis*), and egeria (*Egeria densa*), were higher in winter, with a depletion in spring and an accumulation in autumn (Best 1977; Getsinger 1982; Elly, Best, and Visser 1983).

33. Presented below is a summary of the available information on carbohydrate partitioning in waterhyacinth, hydrilla, Eurasian watermilfoil, and alligatorweed.

Waterhyacinth

34. Little information is available on carbohydrate partitioning in waterhyacinth. Most studies analyzed whole plant carbohydrates to determine the potential of the plant as a source of methane gas production or animal feed (Baldwin, Hentges, and Bagnall 1974; Boyd 1974; Wolverton and McDonald 1975, 1976; Bagnall 1980; Reddy 1983; and others). Tucker (1980) showed that lowest TNC concentrations in waterhyacinth occurred in February (during the period of minimal plant growth), and peak values were observed in May and

July. Tucker and DeBusk (1981) found that crude protein decreased while fiber and TNC increased, as waterhyacinth productivity increased in warm weather.

35. Penfound and Earle (1948) examined the density of starch grains and found that waterhyacinth possessed abundant starch with the greatest amount in the rhizomes, intermediate amounts in the stolons, peduncles, and leaves, and the least amount in the roots. Rhizomes are the main organ of starch storage in waterhyacinth, and starch concentration diminishes with distance from them.

Hydrilla

36. Few investigators have studied the temporal and structural distribution of carbohydrates within hydrilla. Guha (1965) studied diel cycling of carbohydrates in stems and leaves of hydrilla and found increased carbohydrate levels during the day and decreased levels by night. Partitioning of carbohydrates to the stem region appeared to occur during the day. Seasonal cycles of carbohydrates in hydrilla were not examined. Haller (1974) showed that the lower stems and leaves of hydrilla, collected in September and January, contained three times more starch and sucrose than the stems and leaves located on upper portions of the plant.

37. Miller, Garrard, and Haller (1976) investigated the organic composition of hydrilla tubers. Based on dry weight, tuber composition was 46.8 percent starch, 4.47 percent sucrose, 4.0 percent lipids, 5.3 percent crude protein, and 0.39 percent reducing sugars. Structural carbohydrates probably accounted for a majority of the remaining dry weight.

Eurasian watermilfoil

38. Seasonal TNC data for Eurasian watermilfoil have been obtained by several researchers. Titus (1977) found that TNC concentrations in the roots and shoots from Lake Mendota, Wisconsin, were greatest in autumn and under ice cover in winter. During June 1974 and May 1975, minimal amounts of TNC were found in roots and shoots from Lakes Wingra and Mendota (Titus and Adams 1979), while complex carbohydrates were stored by the plant during the fall and winter. Stored complex carbohydrates were then converted during the summer to simple carbohydrates and used for growth. These authors found differences in plant carbohydrates collected at two sites within Lake Wingra and suggest, based on their findings, that multiple sampling sites are necessary to adequately understand the carbohydrate dynamics of this plant in a water body. The decrease of TNC in early winter may be due to loss of

carbohydrates in reproductive fragments with the onset of winter (Titus 1977). These fragments were not recovered for carbohydrate analyses.

39. Kimbel and Carpenter (1981) tested the hypothesis that harvesting disrupted the seasonal pattern of TNC storage in Eurasian watermilfoil. For example, an autumn harvest may have disrupted carbohydrate partitioning from shoots to roots, thereby diminishing the following year's growth. Eleven months posttreatment, TNC concentrations were significantly lower in a harvested plot than in a control plot. Kimbel (1982) has shown that vegetative fragments increased in TNC content prior to winter.

Alligatorweed

40. Weldon and Blackburn (1968) studied the seasonal trends of TNC in alligatorweed for 1 year at two sites. A minimal concentration of TNC was observed in April and July, in Savannah, Ga., and Jacksonville, Fla., respectively. Highest TNC values at the Savannah site were observed from October through the completion of the study in December. The greatest TNC observed at the Jacksonville site occurred in September. Underground stems of alligatorweed were treated with the herbicides Silvex and 2,4-D in March, May, July, September, and November. Greatest efficacy and depletion of TNC were achieved with the herbicide treatments that coincided with the low ebb of carbohydrates found in April at Savannah and in July at Jacksonville. The authors concluded that herbicide applications on alligatorweed prevented replenishment of carbohydrate reserves and resulted in more effective control.

Discussion

41. Perennial aquatic plants rely on stored carbohydrate reserves for survival through winter and for initiation of spring growth. These reserves, primarily nonstructural carbohydrates, are stored in specialized structures such as stem bases, root crowns, roots, rhizomes, tubers, and turions. In addition to winter survival and early growth, carbohydrate reserves allow a plant to recover from periods of stress, e.g., temperature extremes, nutrient depletion, disease, grazing, and control tactics (Mooney 1972). Certain periods in which carbohydrate reserves are minimal represent weak points relative to control techniques in the life cycle of the plant. Theoretically, implementing control tactics at these weak periods would optimize control efficacy.

42. Probable weak points in the life cycle include: (a) the initial spring growth phase; (b) the onset of flowering, or sexual reproduction, and (c) the onset of winter quiescence and dormancy. During the initial spring growth phase, carbohydrate reserves are depleted for growth and development. This depletion process continues until the young plant can produce carbohydrates through photosynthesis. When photosynthesis exceeds usage, carbohydrate storage will commence. At the onset of flowering, carbohydrates normally used for vegetative growth or storage reserves are redirected toward development of sexual reproductive structures. As a result, vegetative growth slows. During fall, plants shunt carbohydrates to storage structures in preparation for winter quiescence or dormancy. These carbohydrate reserves are necessary for winter survival and initiation of spring growth.

43. Several studies have described seasonal changes in the energy reserves of aquatic plants and related these changes to developmental cycles (Elly, Best and Visser 1983; Gallagher, Wolf, and Pfeiffer 1984; Steinmann and Brandle 1984; Best and Dassen 1987). However, few have considered application of this type of information to improve the control of aquatic weed species.

44. Kimbel and Carpenter (1981) mechanically harvested Eurasian watermilfoil in July and reported that TNC concentrations were significantly lower in the harvested plots 11 months posttreatment, compared with unharvested, reference plots. They suggested that a late-summer harvest disrupts TNC allocation in shoots and roots, resulting in a reduction of TNC and biomass the next season. Greatest efficacy in alligatorweed was achieved when herbicide treatment coincided with minimum carbohydrate levels in rhizomes (Weldon and Blackburn 1968). These authors concluded that timing of chemical treatment could prevent replenishment of carbohydrate reserves and result in more effective control of alligatorweed. Neither of these studies supplied sufficient information to draw a reliable conclusion on the relationship between carbohydrates and phenology as related to control.

45. Linde, Janisch, and Smith (1976) developed a relationship between TNC levels and phenological events in cattails (*Typha latifolia*). When the pistillate spike was "lime green" and the staminate spike was "dark green," carbohydrates were at their lowest concentration. These investigators suggested that efficacy would be maximized if control tactics were applied during this period of the life cycle. Birch and Cooley (1983) showed that an autumn harvest of giant cutgrass (*Zizaniopsis miliacea*), prior to carbohydrate

translocation to rhizomes, caused a substantial decrease of regrowth the following year. Getsinger (1982) suggested that control of the submersed species egeria (*E. densa*) could be improved if control techniques were applied during the low point of its carbohydrate reserves.

46. The available information on phenology and carbohydrates varies considerably for waterhyacinth, hydrilla, Eurasian watermilfoil, and alligatorweed. Although phenological studies have been conducted on these four plants, few have related carbohydrate partitioning to life cycle events. For example, most carbohydrate studies on waterhyacinth have been aimed at determining the seasonal trend within whole plants to evaluate the potential of methane gas production or feed quality; therefore, carbohydrate distribution among plant parts at different growth stages has not been evaluated (Boyd 1974, Tucker and DeBusk 1981, Reddy 1983, and others). To our knowledge, no information exists relating phenology and carbohydrate partitioning in hydrilla. Titus and Adams (1979) followed seasonal trends of TNC in roots and shoots of Eurasian watermilfoil. However, they did not relate carbohydrate partitioning to specific phenological events.

47. Effects of environmental factors on phenology and carbohydrate partitioning have been described in the literature. Numerous studies have been conducted to assess the influence of environmental factors, e.g., light, temperature, and nutrients, on the phenology of nuisance aquatic plants (particularly submersed species), as reviewed by Davis and Brinson (1980) and Barko, Adams, and Clesceri (1986). Also, Westerdahl and Hall (1987) observed a differential response of hydrilla and watermilfoil to fluridone treatments when the plants were grown in two different substrate environments, i.e., a sand-peat compared to a natural substrate. Few if any studies have considered the effects of stress, as induced by environmental factors, on carbohydrate partitioning. Periods of stress caused by fluctuations in temperature, drought, nutrient depletion, turbidity, or other parameters may disrupt carbohydrate distribution among plant structures. Moreover, Otto and Svenson (1981) and Otto (1983) suggested that aquatic plants may contain metabolites that would reduce stress imposed by grazing from aquatic herbivores and thereby mitigate the effects of grazing. Whether these metabolites are produced in response to herbivore action or are present throughout the growth cycle is not known. Also, stress may affect the timing and occurrence of specific phenological events, e.g., flowering and tuber formation.

Conclusions

48. Based on results from the literature survey, the effectiveness of control techniques for aquatic plants, e.g., type, timing, and frequency, may be improved by understanding phenology and carbohydrate relationships. Investigators working with alligatorweed and Eurasian watermilfoil suggested that control treatments applied during the low ebb of carbohydrates caused decreased biomass production. Hence, the timing of control techniques to coincide with low carbohydrate concentrations within selected plant structures should enhance efficacy of the control tactic.

49. Most carbohydrate investigations with hydrilla and waterhyacinth have been concerned with whole plant carbohydrate analysis. Studies on alligatorweed and Eurasian watermilfoil have considered TNC in specific plant parts, but not how starch reserves are distributed. Little information exists on carbohydrate partitioning within various sinks and sources for these four aquatic plant species.

50. Environmental factors may influence plant phenology, carbohydrate mobilization, and the effectiveness of selected control tactics, e.g., herbicide efficacy. The importance of these factors with regard to the timing of phenological events and carbohydrate partitioning within the aforementioned target aquatic plants is not known.

51. Based on this literature survey, previous carbohydrate partitioning and phenological studies were inadequate for each species of interest. Previous research has not addressed, specifically, how phenology and carbohydrate partitioning relationships can be applied to improve control of these aquatic plants.

Recommendations

52. The investigation of the following areas will improve our understanding of the relationship between phenology, carbohydrate partitioning, and aquatic plant control. Consequently, recommendations for additional research are directed toward the following areas:

- a. Describe the phenology for waterhyacinth, hydrilla, Eurasian watermilfoil, and alligatorweed in relation to carbohydrate partitioning.

- b. Identify the weak points in the life cycle of each plant, based on carbohydrate partitioning information.
- c. Evaluate, under laboratory and field conditions, selected control tactics, based on carbohydrate partitioning research.

53. Once an understanding of carbohydrate partitioning relative to plant phenology is obtained, implementation of selected control strategies should be conducted at several geographical locations for developing guidance that will assist operational personnel in improving their aquatic plant control program.

References

- Adams, M. S., J. Titus, and M. D. McCracken. 1974. Depth distribution of photosynthetic activity in a *Myriophyllum spicatum* community in Lake Wingra. *Limnology and Oceanography* 19:377-389.
- Aiken, S. G., P. R. Newroth, and I. Wile. 1979. The biology of Canadian weeds; 34. *Myriophyllum spicatum* L. *Canadian Journal of Plant Science* 59:201-215.
- Amundsen, C. C., and A. Brenkert. 1978. Characterization of the growth of *Myriophyllum spicatum* and its influence in the aquatic ecosystem of the Tennessee Valley. Research Report 67, Tennessee Water Resources Research Center, University of Tennessee, Knoxville.
- Anderson, L. W. J. 1984. Preliminary research on monoecious hydrilla. Proceedings of the 19th Annual Meeting, Aquatic Plant Control Research Program, 26-29 November, Galveston, Tex. Miscellaneous Paper A-85-4, US Army Engineer Waterways Experiment Station, Vicksburg, Miss., pp 185-189.
- Anderson, L. W. J., and N. Dechoretz. 1982. Growth, reproduction and control of *Hydrilla verticillata* Royle (L.f.) in an irrigation system in the southwestern United States. Proceedings, EWRS 6th Symposium on Aquatic Weeds, 20-25 September, Novi Sad, Yugoslavia, pp 54-62.
- Bagnall, L. O. 1980. Waterhyacinth energy aquaculture. Paper No. 80-5042, American Society of Agricultural Engineers, St. Joseph, Mich.
- Baldwin, J. A., J. F. Hentges, and L. O. Bagnall. 1974. Preservation and cattle acceptability of waterhyacinth silage. *Hyacinth Control Journal* 12:79.
- Barko, J. W., and R. M. Smart. 1980. Mobilization of sediment phosphorus by submersed freshwater macrophytes. *Freshwater Biology* 10:229-238.
- Barko, J. W., and R. M. Smart. 1981a. Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. *Ecological Monographs* 51:219-235.
- Barko, J. W., and R. M. Smart. 1981b. Sediment-based nutrition of submersed macrophytes. *Aquatic Botany* 10:339-352.
- Barko, J. W., and R. M. Smart. 1983. Effects of organic matter additions to sediment on the growth of aquatic plants. *Journal of Ecology* 71:161-175.

- Barko, J. W., and R. M. Smart. 1986. Effects of sediment composition on growth of submersed vegetation. Technical Report A-86-1, US Army Engineer Waterways Experiment Station, Vicksburg, Miss.
- Barko, J. W., M. S. Adams, and N. L. Clesceri. 1986. Environmental factors and their consideration in the management of submersed aquatic vegetation. *Journal of Aquatic Plant Management* 24:1-10.
- Best, E. P. H. 1977. Seasonal changes in mineral and organic compounds of *Ceratophyllum demersum* and *Elodea canadensis*. *Aquatic Botany* 3:337-348.
- Best, E. P. H., and J. H. A. Dassen. 1987. A seasonal study of growth characteristics and the levels of carbohydrates and proteins in *Elodea nuttallii*, *Polygonum amphibium* and *Phragmites australis*. *Aquatic Botany* 28:353-372.
- Birch, J. B., and J. L. Cooley. 1983. Regrowth of giant cutgrass (*Zizaniopsis miliacea*) following cutting. *Aquatic Botany* 15:105-111.
- Bock, J. H. 1966. An ecological study of *Eichhornia crassipes* with special emphasis on its reproductive biology. Ph.D. dissertation, University of California, Berkeley.
- Bock, J. H. 1969. Productivity of the waterhyacinth *Eichhornia crassipes*. *Ecology* 50:460-464.
- Bowes, G. A., A. S. Holaday, and W. T. Haller. 1979. Seasonal variation in the biomass, tuber density, and photosynthetic metabolism of hydrilla in three Florida lakes. *Journal of Aquatic Plant Management* 17:61-65.
- Boyd, C. E. 1974. Utilization of aquatic plants. *Aquatic Vegetation and Its Use and Control*, D. S. Mitchell, ed., Paris, UNESCO, pp 107-114.
- Carignan, R., and J. Kalff. 1979. Quantification of the sediment phosphorus available to aquatic macrophytes. *Journal of the Fisheries Research Board of Canada* 36:1002-1005.
- Carpenter, S. R. 1979. The invasion and decline of *Myriophyllum spicatum* in a eutrophic Wisconsin lake. *Aquatic Plants, Lake Management and Ecosystem Consequences of Lake Harvesting, Proceedings, Madison, Wis., February 14-16*, J. E. Breck, R. T. Prentki, and O. L. Loucks, eds., pp 11-31.
- Center, T. D., and N. R. Spencer. 1981. The phenology and growth of waterhyacinth (*Eichhornia crassipes* (Mart.) Solms) in a eutrophic north-central Florida lake. *Aquatic Botany* 10:1-32.
- Chapman, V. J., J. M. A. Brown, C. F. Hill, and J. L. Carr. 1974. Biology of excessive weed growth in the hydroelectric lakes of the Waikato River, New Zealand. *Hydrobiologia* 44:349-363.
- Cook, C. D. K., and R. Luond. 1982. A revision of the genus hydrilla (Hydrocharitaceae). *Aquatic Botany* 13:485-504.
- Coulson, J. R. 1977. Biological control of alligatorweed, 1959-1972. A review and evaluation. USDA, ARS, and COE, US Army Technical Bulletin 1547.
- Das, R. R. 1969. A study of reproduction in *Eichhornia crassipes* (Mart.) Solms. *Tropical Ecology* 10:195-198.

- Davis, G. J., and M. M. Brinson. 1980. Responses of submersed vascular plant communities to environmental change. FWS/OBS-79/33, Fish and Wildlife Service, US Department of the Interior.
- Dhahiyat, Y., K. Lankester, A. H. Pieterse, H. Siregar, T. Sutisna, and J. A. C. Vick. 1982. A study on *Hydrilla verticillata* (L.f.) Royle in Lake Curug (Indonesia). Proceedings, EWRS, 6th Symposium on Aquatic Weeds, 20-25 September, Novi Sad, Yugoslavia, pp 63-69.
- Djalil, A. 1973. Notes on seed formation and seed germination of waterhyacinth (*Eichhornia crassipes* (Mart.) Solms. Second Indonesian Weed Science Conference, Yogyakarta, April 2-5, pp 181-188.
- Elly, P., H. Best, and H. W. C. Visser. 1983. The role of storage substances in growth of *Ceratophyllum demersum* L. Proceedings of the International Symposium on Aquatic Macrophytes, 18-23 September, Nijmegen, The Netherlands, pp 25-29.
- Environmental Laboratory. 1985. Monoecious hydrilla in the Potomac River. Miscellaneous Paper A-85-5, US Army Engineer Waterways Experiment station, Vicksburg, Miss.
- Gallagher, J. L., P. L. Wolf, and W. J. Pfeiffer. 1984. Rhizome and root growth rates and cycles in protein and carbohydrate concentrations in Georgia *Spartina alterniflora* Loisel plants. American Journal of Botany 71:165-169.
- Getsinger, K. D. 1982. The life cycle and physiology of the submersed angiosperm *Egeria densa* Planch. in Lake Marion, South Carolina. Ph.D. dissertation, Clemson University, Clemson, S. C.
- Grace, J. B., and R. G. Wetzel. 1978. The production biology of Eurasian watermilfoil (*Myriophyllum spicatum* L.). Journal of Aquatic Plant Management 16:1-11.
- Grainger, J. 1947. Nutrition and flowering of water plants. Journal of Ecology 35:49-64.
- Graneli, W., M. D. Sytsma, and S. Weisner. 1983. Changes in biomass, non-structural carbohydrates, nitrogen and phosphorus content of the rhizomes and shoots of *Phragmites australis* during spring growth. Proceedings of the International Symposium on Aquatic Macrophytes, 18-23 September, Nijmegen, The Netherlands, pp 78-83.
- Guha, J. 1965. Diurnal variation of the carbohydrates and nitrogen content in the leaves and stems of *Hydrilla verticillata* Casp. during its vegetative phase. Bulletin of the Botanical Society of Bengal 19:28-31.
- Haag, R. W., and P. R. Gorman. 1977. Effects of thermal effluent on standing crop and net production of *Elodea canadensis* and other submersed macrophytes in Lake Wabamun, Alberta. Journal of Applied Ecology 14:835-851.
- Haller, W. T. 1974. Photosynthetic characteristics of the submersed aquatic plants hydrilla, southern naiad and vallisneria. Ph.D. dissertation, University of Florida, Gainesville.
- Haller, W. T. 1978. Hydrilla: A new and rapidly spreading aquatic weed problem. University of Florida Agricultural Experiment Station Circular S-245.

- Haller, W. T. 1980. Final project report; Aquatic weed control by sequential herbicide application or drawdown and a continuation of ecological and physiological studies of hydrilla. University of Florida, IFAS, Gainesville.
- Haller, W. T. 1981. Maintenance control of waterhyacinth. *Aquatics* 3(2):6-12.
- Haller, W. T. 1982. Hydrilla goes to Washington. *Aquatics* 4(4):6-7.
- Haller, W. T., J. L. Miller, and L. A. Garrard. 1976. Seasonal production and germination of hydrilla vegetative propagules. *Journal of Aquatic Plant Management* 14:26-29.
- Haller, W. T., and D. L. Sutton. 1975. Community structure and competition between hydrilla and vallisneria. *Hyacinth Control Journal* 13:48-50.
- Hanson, A. A., and F. V. Juska. 1969. *Turfgrass Science*. American Society of Agronomy, Madison, Wis.
- Harlan, S. M., G. J. Davis, and G. J. Pesacreta. 1985. Hydrilla in three North Carolina lakes. *Journal of Aquatic Plant Management* 23:68-71.
- Holm, L. G., L. W. Weldon, and R. D. Blackburn. 1969. Aquatic weeds. *Science* 166:698-709.
- Kay, S. H., and W. T. Haller. 1982. Evidence for the existence of distinct alligatorweed biotype. *Journal of Aquatic Plant Management* 20:37-41.
- Kimbel, J. C. 1982. Factors influencing potential intralake colonization by *Myriophyllum spicatum* L. *Aquatic Botany* 14:295-307.
- Kimbel, J. C., and S. R. Carpenter. 1981. Effects of mechanical harvesting on *Myriophyllum spicatum* L. regrowth and carbohydrate allocation to roots and shoots. *Aquatic Botany* 11:121-127.
- Klingman, G. C. 1965. *Crop Production in the South*. John Wiley and Sons, New York.
- Klingman, G. C., F. M. Ashton, and L. J. Noordhoff. 1975. *Weed Science: Principles and Practices*. John Wiley and Sons, New York, pp 18-20.
- Langeland, K. A. 1986. Management program for alligatorweed in North Carolina. Water Resources Research Report No. 224, University of North Carolina, Raleigh, N. C.
- Langeland, K. A., and C. B. Smith. 1984. Hydrilla produces viable seed in North Carolina lakes; A mechanism for long distance dispersal. *Aquatics* 6(4):20-21.
- Langeland, K. A., and D. L. Sutton. 1980. Regrowth of *Hydrilla verticillata* from axillary buds. *Journal of Aquatic Plant Management* 18:27-29.
- Linde, A. F., T. Janisch, and D. Smith. 1976. Cattail--The significance of its growth, phenology and carbohydrate storage to its control and management. Technical Bulletin No. 94, Department of Natural Resources, Madison, Wis.
- Linscott, D. L., and M. K. McCarthy. 1962. Effect of mowing and 2,4-D on carbohydrate content and amount of ironweed roots. *Weeds* 10:298-303.
- McAllister, R. S., and L. C. Haderlie. 1985. Seasonal variations in Canada thistle (*Cirsium arvense*) root bud growth and root carbohydrate reserves. *Weed Science* 33:44-49.

- McDougall, I. A. 1983. A study of the germination potential in *Myriophyllum spicatum* L. seeds. Studies of Aquatic Macrophytes, Part XXIV, Ministry of Environment, Province of British Columbia.
- Miller, J. L., L. A. Garrard, and W. T. Haller. 1976. Some characteristics of hydrilla tubers taken from Lake Ocklawaha during drawdown. *Journal of Aquatic Plant Management* 14:29-31.
- Mitra, E. 1964. Contributions to our knowledge of Indian freshwater plants; Part 4. On some aspects of the morphology and anatomical studies of turions of *Hydrilla verticillata* (Linn.f.) Royle. *Journal of the Asiatic Society* 6(1)(2):17-27.
- Mooney, H. A. 1972. The carbon balance in plants. *Annual Review of Plant Physiology* 22:337-364.
- Musil, C. F., and C. M. Breen. 1977. The influence of site and position in the plant community on the nutrient distribution in and content of *Eichhornia crassipes* (Mart.) Solms. *Hydrobiologia* 53:67-72.
- Nall, L. E., and J. D. Schardt. 1978. Large-scale operations management test of use of the white amur for control of problem aquatic plants; Report 1, Baseline studies; Vol I: The aquatic macrophytes of Lake Conway, Florida. Technical Report A-78-2, US Army Engineer Waterways Experiment Station, Vicksburg, Miss.
- Nichols, S. A., and B. H. Shaw. 1986. Ecological life history of the three aquatic nuisance plants, *Myriophyllum spicatum*, *Potamogeton crispus* and *Elodea canadensis*. *Hydrobiologia* 131:3-21.
- Obeid, M., and M. Tag el Seed. 1976. Factors affecting dormancy and germination of seeds of *Eichhornia crassipes* from the Nile. *Weed Research* 16:71-80.
- Otto, C. 1983. Adaptations to benthic freshwater herbivory. *Periphyton of Freshwater Ecosystems*, R. G. Wetzel, ed., Dr. W. Junk, The Hague, The Netherlands, pp 199-205.
- Otto, C., and B. S. Svenson. 1981. How do macrophytes growing in or close to water reduce their consumption by aquatic herbivores? *Hydrobiologia* 78:107-112.
- Parija, P. 1934. Physiological investigations on waterhyacinth (*Eichhornia crassipes*) in Orissa with notes on some other aquatic weeds. *Indian Journal of Agricultural Science* 4:399-429.
- Penfound, W. T. 1940. The biology of *Achyranthes philoxeroides* (Mart.) Standley. *Ecology* 20:248-252.
- Penfound, W. T., T. F. Hall, and A. D. Hess. 1945. The spring phenology of plants in and around the reservoirs in north Alabama with particular reference to malaria control. *Ecology* 26:332-352.
- Penfound, W. T., and T. T. Earle. 1948. The biology of the waterhyacinth. *Ecological Monographs* 18:447-472.
- Perry, T. O. 1968. Dormancy, turion formation and germination by different clones of *Spirodella polyrhiza*. *Plant Physiology* 43:1866-1869.
- Pieterse, A. H., J. J. A. M. Aris, and M. E. Butter. 1976. Inhibition of float formation in waterhyacinth by gibberellic acid. *Nature* 260:423-424.

- Reddy, K. R. 1983. Waterhyacinth production systems in nutrient rich waters. The Methane from Biomass and Waste Program; Annual Report for 1982, W. Smith, ed., Institute of Food and Agricultural Science, University of Florida, Gainesville, pp 30-32.
- Richards, J. H. 1982. Developmental potential of axillary buds of waterhyacinth, *Eichhornia crassipes* Solms. (Pontederiaceae). American Journal of Botany 69:615-622.
- Robertson, H. F., and B. A. Thein. 1932. The occurrence of waterhyacinth (*Eichhornia crassipes*) seedlings under natural conditions in Burma. Agriculture and Livestock of India 2:383-390.
- Sastroutomo, S. S. 1980. Dormancy and germination in axillary turions of *Hydrilla verticillata*. Botany Magazine 93:265-273.
- Sastroutomo, S. S. 1982. The role of turions in the re-establishment process of submersed weed vegetation in Japan. Proceedings, EWRS 6th Symposium on Aquatic Weeds, 20-25 September, Novi Sad, Yugoslavia, pp 77-85.
- Schirman, R., and K. P. Buchholtz. 1966. Influence of atrazine on control and rhizome carbohydrate reserves of quackgrass. Weeds 14:233-236.
- Sculthorpe, C. D. 1967. The Biology of Aquatic Vascular Plants. St. Martins Press, New York.
- Senft, D. 1981. Hydrilla--a costly and destructive weed. Agricultural Research 29:4-8.
- Sheldon, R. B., and C. W. Boylen. 1976. Maximum depth inhabited by aquatic vascular plants. American Midland Naturalist 97:248-254.
- Singer, R., D. A. Roberts, and C. W. Boylen. 1983. The macrophyte community of an acidic lake in Adirondack (New York, U.S.A.): A new depth record for aquatic angiosperms. Aquatic Botany 16:49-57.
- Smith, D. 1975. Forest Management in the North, 3rd ed. Kendall/Hunt, Dubuque, Iowa.
- Spence, D. H. N., and J. Crystal. 1970a. Photosynthesis and zonation of freshwater macrophytes; I. Depth distribution and shade tolerance. New Phytology 69:205-215.
- Spence, D. H. N., and J. Crystal. 1970b. Photosynthesis and zonation of freshwater macrophytes; II. Adaptability of species of deep and shallow water. New Phytology 69:217-227.
- Spencer, D. F., and L. W. J. Anderson. 1986. Photoperiod responses in monoecious and dioecious *Hydrilla verticillata*. Weed Science 34:551-557.
- Stanley, R. A., E. Shackelford, D. Wade, and C. Warren. 1976. Effects of seasonal and water depth on Eurasian watermilfoil. Journal of Aquatic Plant Management 14:32-36.
- Steinmann, F., and R. Brandle. 1984. Carbohydrate and protein metabolism in the rhizomes of the bulrush (*Schoenoplectus lacustris* (L.) Palla) in relation to natural development of the whole plant. Aquatic Botany 19:53-63.

- Stewart, K. K., and T. K. Van. 1984. Preliminary laboratory results of monoecious hydrilla. Proceedings of the 19th Annual Meeting, Aquatic Plant Control Research Program, 26-29 November, Galveston, Tex. Miscellaneous Paper A-85-4, US Army Engineer Waterways Experiment Station, Vicksburg Miss., pp 182-184.
- Stocker, E. C., and R. L. Kent. 1984. The distribution, identification, biology and management of Eurasian water milfoil: An Alberta perspective. Alberta Environment, Pollution Control Division, Pesticide Chemicals Branch, Alberta, Canada.
- Sutton, D. L., R. C. Littell, and K. A. Langeland. 1980. Intraspecific competition of *Hydrilla verticillata*. Weed Science 28:425-428.
- Sutton, D. L., and K. M. Portier. 1985. Density of tubers and turions in South Florida. Journal of Aquatic Plant Management 23:64-67.
- Swarbrick, J. T., C. M. Finlayson, and A. J. Cauldwell. 1982. The biology and control of *Hydrilla verticillata* (L.f.) Royle. Special Publication No. 16, BIOTROP SEAMEO Center for Tropical Studies.
- Tag el Seed, M., and M. Obeid. 1975. Sexual reproduction of *Eichhornia crassipes* in the Nile. Weed Research 15:7-12.
- Titus, J. E. 1977. The comparative physiological ecology of three submersed macrophytes. Ph.D. dissertation, University of Wisconsin, Madison.
- Titus, J. E., and M. S. Adams. 1979. Comparative carbohydrate storage and utilization patterns in the submersed macrophytes, *Myriophyllum spicatum* and *Vallisneria americana*. The American Midland Naturalist 102:263-272.
- Tucker, C. S. 1980. Effects of seasonality, nitrogen form and availability and plant stand density on the chemical composition and nutritive value of waterhyacinth (*Eichhornia crassipes*). Cultivation of Macroscopic Marine Algae and Freshwater Aquatic Weeds, J. H. Ryther, ed., Woods Hole Oceanographic Institution, Woods Hole, Mass., pp 35-54.
- Tucker, C. S., and T. A. DeBusk. 1981. Productivity and nutritive value of *Pistia stratiotes* and *Eichhornia crassipes*. Journal of Aquatic Plant Management 19:61-63.
- Van, T. K., W. T. Haller, and L. A. Garrard. 1978. The effect of daylength and temperature on hydrilla growth and tuber production. Journal of Aquatic Plant Management 16:57-59.
- Van der Zwerde, W. 1982. Some introductory experiments on the influence of day-length, light intensity and temperature on turion formation and flowering in two strains of *Hydrilla verticillata* (L.f.) Royle. Proceedings, EWRS 6th Symposium on Aquatic Weeds, Novi Sad, Yugoslavia, pp 71-76.
- Varshney, C. K., and J. Rzoska. 1973. Aquatic weeds in southeast asia. Proceedings of a Regional Seminar on Noxious Aquatic Vegetation, New Delhi, India, 12-17 December.
- Wain, R. P., W. T. Haller, and D. R. Martin. 1984. Genetic relationship among two forms of alligatorweed. Journal of Aquatic Plant Management 22:104-105.

- Warrington, P. D. 1983. An introduction to the life histories of *Myriophyllum* species in southwestern British Columbia. Ministry of Environment, Province of British Columbia.
- Watson, M. A. 1984. Developmental constraints: Effect on population growth and patterns of resource allocation in a clonal plant. *The American Naturalist* 123:411-426.
- Weber, J. A., and L. D. Nooden. 1976. The redistribution of stem sugars in wheat during grain development. *Australian Journal of Biological Science* 20:309-318.
- Weldon, L. W. 1960. A summary review of investigations on alligatorweed and its control. US Department of Agriculture, Agricultural Research Service, Corps Research Division.
- Weldon, L. W., and R. D. Blackburn. 1968. Herbicidal treatment effect on carbohydrate levels of alligatorweed. *Weed Science* 16:66-69.
- Westerdahl, H. E., and J. F. Hall. 1987. Fluridone effects on stressed submersed macrophytes. *Journal of Aquatic Plant Management* 25:26-28.
- Wolverton, B. C., and R. C. McDonald. 1975. Application of vascular aquatic plants for pollution removal, energy and food production in biological systems. NASA Technical Memorandum TM-X-72726.
- Wolverton, B. C., and R. C. McDonald. 1976. Waterhyacinths, *Eichhornia crassipes* (Mart.) Solms; A renewable source of energy. Proceedings, Conference on Capturing the Sun through Bioconversion, Washington, DC, pp 249-252.
- Young, C. A. 1973. Effects of temperature and other environmental factors on standing crop and phenological development of *Myriophyllum spicatum* L. M.S. thesis, University of Tennessee, Knoxville.