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The Production Biology Of Eurasian Watermilfoil (*Myriophyllum Spicatum* L.): A Review

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INTRODUCTION

Eurasian watermilfoil (*Myriophyllum spicatum* L.) is a submersed aquatic angiosperm currently considered to be a very troublesome weed, particularly throughout the Eastern United States (7, 14, 50, 65, 72). Its rapid and effective dispersal, largely as plant fragments (65), and its ability to displace other macrophyte species through competition (23, 34) are major factors contributing to its success. Problems typically caused by Eurasian watermilfoil result from the large amounts of plant material that it produces near the water's surface. Additionally, detached plant material floats for a period of time and may interfere with water intake structures (23, 65) or simply wash up on shore and decay. Decomposition *in situ* or of transported fragments can lead to marked alterations of physical and chemical properties of the water that can have detrimental effects upon other biota.

Attempts to control Eurasian watermilfoil have met with only partial success and usually are accomplished at considerable expense. Methods of control have included herbicide treatments (5, 58, 68, 69), mechanical harvesting (11, 47, 58), and manipulation of habitats such as by varying water levels (65, 73). Recently, the alternative of biological control has attracted attention in the hope that it will provide a more permanent solution (17, 66).

The purpose of this paper is to review the existing information on physiological aspects that relate to the productivity of Eurasian watermilfoil. Interest in the production biology of this species is manifold:

1) A better understanding of the processes involved in growth and the factors which control these processes may lead to more effective control methods. Many of the problems created by Eurasian watermilfoil result from its abundance rather than simply its presence, and invasions of Eurasian watermilfoil do not always lead to major infestations.

2) Knowledge of the factors controlling productivity may improve our ability to anticipate future problems.

3) The productivity of Eurasian watermilfoil is central to its competitive capabilities since light is often limiting in aquatic environments, and large plants or dense stands are likely to have a competitive advantage over smaller species for light. Also, since dispersion is principally by fragmentation, the number of disseminules increases as more biomass is produced.

4) Since Eurasian watermilfoil is currently a major component of the littoral zone of many lakes and reservoirs, it is of some limnological significance, particularly with regard to energy flow and nutrient cycling.

BIOLOGICAL CHARACTERISTICS OF EURASIAN WATERMILFOIL

Eurasian watermilfoil (*Myriophyllum spicatum* L.) was first described by Linnaeus in 1753 as occurring in Europe and was reported from North America as early as 1814 (op. cit. 5). The distinction between the Eurasian and American populations of watermilfoils has been debated since Fernald named the American watermilfoil *Myriophyllum exalbescens* Fern. The two have since been treated as varieties, subspecies, and even synonomous by different authors (5, 30, 59). Presently there is no general agreement on their taxonomic status, but it is probably best to distinguish between them at this time since there appear to be both morphological and distributional differences (5, 48). Hereafter Eurasian watermilfoil will be referred to simply as milfoil.

Milfoil is a rooted perennial with long, flexible stems and finely dissected leaves (Figure 1). The plant may reach lengths in excess of 4 m (Grace and Tilly, unpubl.) and must emerse its flowering spike for mature fruits to develop (52). Leaves are arranged in whorls of four with 10 to 26 (typically 14-20) pairs of leaf divisions (52) and are covered with a very thin cuticle (63). Stomata, although essentially functionless, are known to occur on the leaf surface (63), as are certain specialized ion absorption sites known as hydropoten (36). Chloroplasts are most abundant in the epidermis but also occur in the mesophyll, where they are larger in appearance and often store starch (61, 63) (Figure 2). The rooting system is adventitious, and most likely possesses abundant root hairs when rooted (as have been found in American watermilfoil, 64) but not when suspended in water (as shown for *Myriophyllum aquaticum*, 77).

As is common among many submersed angiosperms, the vascular system in milfoil is highly reduced in the number of xylem conducting elements and their degree of lignification (63). However, the importance of xylem as a conduction system should not be dismissed since this function may explain the presence of a casparian strip in the endodermis of the root (63). The phloem, on the other hand, is quite similar to that of terrestrial plants. The highly developed system of air spaces (lacunae) in milfoil (Figure 2) is schizogenous in origin (63) and represents an interactive morphological and physiological adaptation to aid the efficiency

Figure 1. Eurasian watermilfoil: A, habit, x ½; B, whorl of leaves, x 2; C, part of flowering spike showing staminate flowers above and pistillate flowers below, x 4; D, immature fruits, x 4; E, mature fruit, x 4. (From Corroll and Corroll, 13, with permission of Stanford University Press).

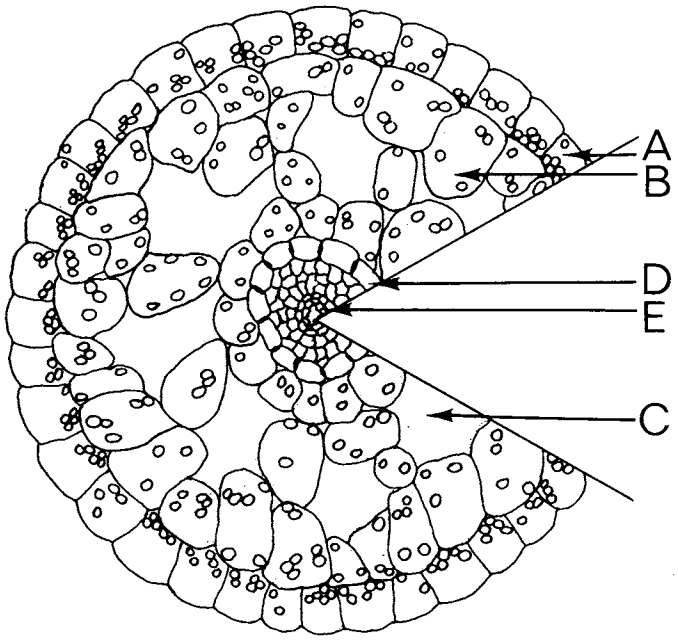

Figure 2. Cross-sectional anatomy of Eurasian watermilfoil leaf, x 100: A, epidermal cell containing chloroplasts; B, mesophyll cell containing large chloroplasts; C, intercellular space (lacuna); D, endodermis cell (darkened area between adjacent endodermal cells is part of the casparian strip); E, vascular strand. [Redrawn after a composite of figures of Sculthorpe (63) and Schenck (61).]

of gas utilization as well as to provide plant buoyancy (91). This lacunal system, although interrupted by thin partitions, acts as an internal gas reservoir capable of allowing diffusive exchange between the roots and shoots (Wetzel, unpublished data for *Myriophyllum heterophyllum*). It has been shown for American watermilfoil that the gas lacunae can account for as much as 43% of total plant volume (25).

Milfoil is able to perpetuate itself by seed, by vegetative fragmentation, and by overwintering in an evergreen condition. The production of viable seeds requires emersion of the typically monoecious flowering spikes (52) with transfer of pollen by wind (anemophily) as the dominant pollination mechanism (30). Seed dispersal is aided by waterfowl and the floating inflorescence. With proper scarification up to 85% of the seeds germinate, but results indicate that under natural conditions seeds may actually have their germination delayed until at least their second spring (24, 53). Seedling establishment appears to be a particularly fragile stage in the life-cycle (54). Fragmentation may be either accidental or the result of abscission. Abscissing fragments often develop roots at the nodes before separation from the parent plant. Fragments float for a period before they sink and thereby are dispersed. Although milfoil is typically herbaceous, it frequently overwinters in an evergreen form and may maintain considerable winter biomass (73). In other cases, overwintering occurs as new, unexpanded shoots attached to rootstocks (Grace and Tilly, unpubl.). The overwintering shoots of milfoil do not usually consist of the compact, abortive leaf tissue generally associated with true turions (30, 63). Although turion formation is common to other species of watermilfoil (*M. exalbescens, M. verticillatum, M. heterophyllum*) and is important to overwintering and propagation (84, 85, 86, 87, Wetzel, unpubl.), we hesitate to assign the term and analogous function to these shoots of *M. spicatum* because of the differing morphology and the need for detailed study.

It is likely that vegetative fragmentation is the most important means of dispersal within a body of water or between nearby bodies of water, while seeds are important both in long distance dispersal and as insurance against local extinction (as evidenced by their delayed germination). Both rootstocks and vegetative fragments commonly serve for overwintering but no data exist as to which is of greater importance in a particular situation.

PHOTOSYNTHESIS AND RESPIRATION

Carbon fixation pathways. The majority of terrestrial plants can be classified as C_3 or C_4 plants based upon specific characteristics which are associated with their photosynthetic pathways (6). Recent studies have led to the general conclusion that the presence of true C_4 plants in the submersed aquatic environment is unlikely, at least for the temperate zone (28), although some C_4 characteristics have been observed for these plants (4, 28).

The first studies conducted to determine if milfoil possessed C_3 or C_4 metabolism were those of Stanley and Naylor (70). Their findings that glycerate-3-phosphate was the first end product of ^{14}C photocarboxylation and that malic acid was not significantly labeled with exposure times less than 30 seconds led them to conclude that the C_3-

pentose phosphate pathway was dominant. This conclusion has been subsequently confirmed by the findings of Van *et al.* (82) who determined that the predominant carboxylation enzyme was ribulose diphosphate (RUDP) carboxylase and that the ratio of phosphoenolpyruvate (PEP) carboxylase to RUDP carboxylase was roughly the same as that found in spinach (C_3 plant).

Another feature of cellular carbon metabolism which is usually associated with photorespiration is glycolate metabolism (31). The production of glycolate from RUDP and oxygen and its subsequent metabolism to CO_2 are typically associated with light-induced CO_2 release in C_3 plants, while in C_4 plants rates of glycolate metabolism are reduced (81). Stanley and Naylor (70) found that glycolate was labeled from $H^{14}CO_3^-$ during photosynthesis of milfoil. Additionally, they later found that glycolate levels were higher in light than in dark and that exogenously supplied glycolate–^{14}C and glyoxylate–^{14}C were incorporated into compounds typical of Calvin Cycle carboxylation. Glycolic acid oxidase was found at levels comparable to those in tobacco (C_3 plant). These observations, plus those of others (82), indicate that although glycolate metabolism is present in milfoil at rates lower than most known C_3 plants, these rates are still higher than typically observed in C_4 plants.

In plants which possess the C_4-type of metabolism there is usually a particular kind of anatomical arrangement (Krantz anatomy) in which bundle-sheath cells containing a few large starch-containing chloroplasts are present (81). Also, in a number of C_4 plants there is a system of tubules (peripheral reticulum) which occurs within the stroma of the chloroplasts (32). In milfoil, the main photosynthetic tissue is the epidermis which has numerous, small chloroplasts (Figure 2). The chloroplasts in the mesophyll cells are much larger than those of the epidermis and contain a large amount of starch (63). Stanley and Naylor (71) hypothesized that these mesophyll cells are functionally similar to the bundle sheath cells of C_4 plants and that, therefore, milfoil has a form of the Krantz anatomy. In addition, Lunney *et al.* (35) described what they believe to be another C_4 characteristics of the anatomy of milfoil: the presence of peripheral reticulum in the chloroplasts. Despite the fact that milfoil possesses some anatomical features usually associated with C_4 plants, low levels of PEP carboxylase and the absence of rapidly formed C_4 acids is evidence that this pathway is not present to a significant degree.

Another aspect of cellular carbon metabolism is the forms of available carbon which can be used in photosynthesis. The original research on this problem with milfoil was that of Steemann Nielsen (74) who found the ratio of affinity for free CO_2 to the affinity for HCO_3^- ions to be 5. This value falls within the range reported by Stanley (67) of 2.8-39.0 (depending on pH). Observations by Van *et al.* (82) agree with the generalization that free CO_2 is the carbon source of preference for milfoil, but they also present evidence that suggests the possible importance of HCO_3^- ions at high pH since they found carbonic anhydrase activity (possibly involved in the ability of plants to use HCO_3^- ions in photosynthesis; 57) in excess of that sufficient to support HCO_3^- utilization as the sole carbon source for photosynthesis. Titus (79) further suggests a preference of free CO_2 by milfoil but the ability to use bicarbonate.

Respiratory pathways. Two distinctively different kinds of "respiration" have been noted in the tissues of higher plants, mitochondrial or "dark" respiration and photorespiration. Mitochondrial respiration is usually measured in the dark as O_2 uptake or CO_2 release while photorespiration is measured in the light (and usually includes mitochondrial respiration).

Stanley (67) found CO_2 evolution in darkness by milfoil to be strongly influenced by temperature, and demonstrated a greater than 2.5-fold increase in dark respiration from 20 to 35 C. Similarly, Van *et al.* (82) reported that at 30 C dark respiration was over 50% of the light saturated net photosynthesis value. As pointed out by Wetzel and Hough (92), there is some evidence to suggest that mitochondrial respiration may be inhibited in the light. However, the intermediate CO_2 compensation point found for milfoil under 1% O_2 levels (9μl/l) suggests that mitochondrial respiration may not be entirely inhibited in the light (82).

Both high glycolate oxidase activity and a high CO_2 compensation point under 21% O_2 suggest an active photorespiratory pathway (31). Glycolate oxidase activity has been reported to be 16.6 μl O_2/gdw/min (70) and 20 μl O_2/mg chl/min (ca. 40 μl O_2/gdw/min) (82). These levels are rather low for C_3 plants but quite high for C_4 plants (82). The typically low light intensities found in the aquatic environment probably combine with the low enzymatic activity to result in rates of photorespiration that are lower than in terrestrial C_3 plants. The conditions most conducive to photorespiration will be dense canopies near the water's surface on calm, clear days when O_2 is supersaturated and when dissolved inoganic carbon is in low concentrations because of reduced water turbulence.

Characteristics of net photosynthesis. Representative values for twelve of the major parameters which characterize the process of net photosynthesis (NPS) in milfoil are presented in Table 1. Included in this characterization are not only the potential rates but also the laboratory responses of NPS to environmental conditions. By itself, Table 1 is only of limited usefulness in predicting the distribution and abundance of milfoil in natural habitats because of the influence of other organisms. However, consideration of certain parameters in Table 1 does indicate the *potential* of milfoil and its preferred conditions.

Both the photosynthetic potential and photosynthetic capacity of milfoil are rather typical of the values reported for submersed macrophytes (82, 89). By themselves these parameters only confirm that milfoil is able to photosynthesize rapidly under optimal conditions for a short period of time.

Milfoil is commonly reported to inhabit the deeper waters of littoral zones (30) as is suggested by its low light compensation point. If full sunlight intensity is assumed to be ca. 2000 μE/m^2/sec PhAR (photosynthetically active radiation) (79), the light compensation point is at 1-2% of surface light. The compensation point is undoubtedly increased when night-time respiration is considered.

The temperature optimum for NPS of milfoil is high

TABLE 1. PHOTOSYNTHETIC CHARACTERISTICS OF EURASIAN WATERMILFOIL AS DETERMINED UNDER LABORATORY CONDITIONS.

Parameter[3]	Representative Values	Sources
Photosynthetic Potential[1]	13 mg C/gdw/hr; 1.6 mg O_2/mg Chl/hr	67;82
Photosynthetic Capacity[2]	4.5 mg C/gdw/hr; 0.15 mg O_2/mg Chl/hr	79;82
Light Saturation of NPS	30 x 10^3 ergs/cm^2/s at 20 C; 600 μE PhAR/m^2/s at 30 C	67;82
Light Compensation of NPS	8 x 10^3 at 20 C, 1.1 x 10^4 at 30 C, 4.6 x 10^4 at 30 C, 4.6 x 10^4 at 35 C (ergs/cm^2/s); 35 μE PhAR/m^2/s at 30 C	67;82
Km (light) of NPS	120 μE PhAR/m^2/s at 30 C; 164 μE/m^2/s at 25 C	82;79
Optimum Temperature for NPS	30 C; 35 C; 35 C	79;70;82
Q_{10} for NPS	1.54; 1.53	70;79
Q_{10} for Dark Respiration	2.28	67
Optimum pH for NPS	6; 8	67;82
Km (DIC) of NPS	0.15 mM at pH 4, 5 mM at pH 8 (30 C); 2.1 mM at pH (25 C)	79;82
CO_2 Compensation Point	ca. 0 at 20 C; 0.4 μM at 25 C (1% O_2), 0.8 μM at 25 C (21% O_2)	70;82
Effect of O_2 on NPS	ca. 5% reduction in NPS from 1% O_2 to 21% O_2 (at 15 μM CO_2)	82

[1] Photosynthetic potential is defined as the maximum attainable rate of net photosynthesis when all external factors are non-limiting (33).
[2] Photosynthetic capacity is defined as the maximum rate of net photosynthesis at levels of dissolved inorganic carbon in equilibrium with the air when all other external factors are optimal (33).
[3] Table abbreviations are gdw = grams dry weight of plant tissue; NPS = net photosynthesis; E = Einsteins; PhAR = photosynthetically active radiation; Km = the value of the independent variable when the dependent variable is at ½ its maximum rate; Q_{10} = the ratio of the response at the optimum temperature to that at 10 C below the optimum temperature; DIC = dissolved inorganic carbon.

compared to terrestrial plants and suggests a preference for warm climates. However, the responsiveness of night-time respiration to temperature is indicated by a high Q_{10} and will likely result in a lower optimum temperature for growth.

The pH of natural waters is considered to be an important variable in the distribution of milfoil (29). Van *et al.* (82) suggest that the pH effect acts principally through its influence on free CO_2 concentration, but some authors believe that pH may have a more direct effect (67). Table 1 shows somewhat variable results by different authors but suggests optimal growth at circumneutral conditions.

Insufficiency of dissolved inorganic carbon (DIC) is apparently capable of severely limiting NPS under nutrient saturated conditions as evidenced by the discrepancy between photosynthetic potential and photosynthetic capacity (Table 1). Nonetheless, the low CO_2 compensation point suggests that milfoil can occur in soft waters of low DIC content, even if limited by DIC.

Since lakes are rarely occupied by only one species of submersed macrophyte, the realized distribution and abundance of milfoil is likely altered by interference from other species. Consideration of the relative success of milfoil in the presence of other macrophyte species requires comparison of photosynthetic characteristics and competition experiments. Few studies of this kind have been done but the existing comparisons are informative. In one study (82), milfoil was compared with coontail (*Ceratophyllum demersum* L.) and hydrilla (*Hydrilla verticillata* (L.F.) Royle) in certain photosynthetic characteristics. This study showed that milfoil possessed a comparatively low CO_2 compensation point and was less affected in its NPS by O_2 concentration than the other species. The difference among the species given the most significance by the authors was the low Km (light) for NPS and low light-compensation point of hydrilla which they believed may have contributed to its ability to dominate over milfoil and coontail in many of Florida's waterways. Another comparative study which emphasized photosynthetic characteristics included milfoil, coontail, and wild celery (*Vallisneria americana*) (79). In this comparison, milfoil was found to have the longest growing season, the most nearly optimal configuration of photosynthetic tissues but the highest Km (light) for NPS. The author hypothesized that despite potentially offsetting factors, milfoil's partial displacement of wild celery in Lake Wingra was primarily the result of a decline in water transparency and a decline in DIC levels.

CARBON METABOLISM AND DRY MATTER PRODUCTION IN NATURAL STANDS

Comparative productivity. Estimates of both "average" and "maximum-site" biomass and the resultant estimates for sustained daily productivity are presented in Table 2. Accumulation of biomass averaged over an entire littoral zone of a lake (or at least all areas sampled) is defined as average biomass, whereas "maximum-site" biomass is that found at the most productive site within a lake. Attempts were made to select values for "maximum site" which are actually representative of a site and not simply deviate samples. However, in all of the examples presented, milfoil is a dominant species.

The seasonal maximum biomass for the littoral zone may serve as an index of the severity of infestation for a particular location. Seasonal maximum biomass is a key parameter since it is this value which is most commonly used to calculate annual net production among herbacious plants (88). The usual procedure is to multiply the seasonal maximum biomass by a ratio of the production to biomass (P/B). This ratio is a measure of the loss of biomass during the period of biomass accumulation (turnover) as well as the production which occurs after the seasonal maximum. Although this P/B ratio is a critical parameter used in the calculation of annual net production, estimates for milfoil are almost completely lacking. Adams and McCracken (1) estimated a P/B value of 3.8 but they failed to subtract nighttime respiration from annual production and, therefore, this value is an overestimate. The P/B ratio for mil-

TABLE 2. ESTIMATES OF BIOMASS AND PRODUCTIVITY OF EURASIAN WATERMILFOIL.[1]

Region	Lake and Year	Seasonal Maximum Biomass, Littoral, g/m²	Maximum Site Biomass, g/m²	Growing Season Mean Productivity g/m²/day	Max. Site Growing Season Mean Productivity g/m²/day	Days to Maximum Biomass	Notes	Source
Wisconsin	Wingra, 1970	264	—	1.72	—	153		1
Wisconsin	Wingra, 1970	ca. 240	1146[4]	1.71	8.11	ca. 140	3	46
Wisconsin	Mendota, 1968	—	389	—	3.89	ca. 100	3	49
Wisconsin	Mendota, 1968	175	223	1.75	2.23	ca. 100	2, 3	34
So. Carolina	Par, 1974	32	288	0.27	2.40	120		22;23
So. Carolina	Par, 1975	47	282	0.39	2.35	120		23
Tennessee	Melton Hill, 1971	184	314	1.14	1.94	162	3	95
Tennessee	Melton Hill, 1972	ca. 360	480	3.00	4.50	80	(120)[5]	73
Tennessee	Gunnersville, 1972	180	—	2.57	—	70	(60)[5]	73

[1] All values are based on a dry weight equivalent assuming that ash weight is 20% of dry (63).
[2] Predominantly milfoil but some other species may be included.
[3] Above-ground biomass only.
[4] Possibly an overestimate because of the small number of samples.
[5] The number in parantheses is the seasonal minimum biomass.

foil will vary depending on the length of the growing season, the degree of leaf sloughing and branch abscission (which may be extensive), self-thinning of shoots, and overwintering of substantial amounts of biomass. Therefore, we feel that calculations of annual net production for milfoil using P/B ratios should be used with caution until further data on these ratios are obtained. The estimates of daily productivity presented in Table 2 are subject to the just-mentioned criticisms but nonetheless are of interest for comparative purposes since these criticisms apply as well to studies for most submersed macrophytes.

A majority of studies of milfoil have simply reported the biomass of above-ground parts or the total plant biomass, but there are some estimates of the proportionality of roots and shoots. Root to shoot ratios have been studied by a few authors (51; Grace and Tilly, unpubl.) and the ratio at the seasonal biomass maximum is 0.01-0.15 depending somewhat on plant size and water depth. These values for milfoil are very low in comparison to those for most submersed macrophytes.

Temporal and spatial variations in biomass. One of the most conspicuous aspects of temporal variation is the seasonal progression of biomass. Milfoil usually overwinters as fragments or established young shoots. However, in some cases considerable biomass persists throughout the winter and its habit is evergreen (73). The beginning of active growth in the spring varies with latitude but typically occurs between March and May when temperatures are rapidly increasing. Seasonal biomass maxima vary considerably over time and space with two maxima frequently occurring during the growing season. The biomass maxima appear to be related to flowering periods (which are also highly variable) and seem to be less predictable in southern locales. Sloughing and autofragmentation of plant parts are common following periods of flowering and are subsequently involved in a decline of standing biomass. Additionally, as the season progresses the individual plant size increases along with the areal biomass, and thinning of shoots caused by intraspecific interference results in an inverse relationship between plant size and plant density (34).

The abundance of milfoil varies horizontally according to water depth with most common distribution in depths of 1.5-4.0 m (23, 46, 73). Several factors are likely to influence the depth of maximum biomass but the range seems to be set by a balance between sufficient depth to accommodate luxuriant shoot growth and enough light to allow for sufficient stem growth. Additionally, in very clear waters hydrostatic pressure may limit the maximum depth (18, 21). Seasonal patterns seem to interact with horizontal variations such that plants at shallow depths mature earliest and those at greatest depths latest (73). Unless taken into account, this interaction may cause significant error in determinations of the seasonal biomass maximum.

Milfoil is capable of growing to heights of greater than 4.0 m and typically reaches the surface of the water from depths of 2.5 m. Therefore, consideration of the vertical biomass distribution of milfoil is important when discussing metabolism and productivity relations in natural stands. Growth in height is often limited by water depth and stem length seldom exceeds the water depth by more than 50 cm. However, after plants reach the surface of the water the process of canopy formation further alters the vertical distribution of biomass. Canopy formation is caused by profuse branching of shoots at the water surface while the lower leaves and branches tend to slough. In some cases, this canopy formation can cause as much as 70% of the total shoot biomass of plants rooted at 2.5 m depths to occur within the upper 0.5 m of water (estimated from data of Adams *et al.*, 2). In addition, selective sloughing of leaves from lower parts can cause a gradient in the leaf to stem ratio from 3.2 at the water's surface to 0.0 at 2 m from the surface (Grace and Tilly, unpubl.). This process of canopy formation appears to be a tactic by which the plant attempts to achieve optimal growth form relative to available light, and although the optimum is approached throughout the growing season, it is apparently never fully reached (80).

Carbon uptake rates. Seasonal variations in carbon fixation by milfoil in one study closely followed biomass accumulation until after the seasonal maximum when biomass declined due to sloughing but carbon fixation was still high

(1). Some insight into this pattern was gained by studies of the seasonal changes in carbon exchange under standard conditions (79). Within the limits of comparison, these studies suggest that the seasonal trend of carbon uptake is determined primarily by the physiological condition of tissues rather than by the immediate environmental conditions.

Diurnal variations in carbon uptake are striking, as would be expected. Although light intensity is the most important regulating factor, evidence shows clearly that other factors are significant. Diurnal profiles of carbon uptake are typically unimodal during early and mid-summer but subject to mid-day depressions in late summer (37). It has been suggested that these depressions might be partially caused by inorganic carbon limitations (37) but work on other submersed macrophytes indicates that diurnal changes in photorespiration and extracellular release of dissolved organic compounds can cause such depressions (26, 27, 90, 93).

As a result of the vertical biomass distribution, rates of carbon fixation are highest near the water's surface. The process of canopy formation amplifies this tendency and in one example caused the majority of carbon uptake to shift from the upper 100 cm of the water column in May to the upper 20 cm in August (2). Some compensation for self-shading occurs by light adaptation of the lower leaves (2) but this shade adaptation only slightly offsets the effects of severe light attenuation. There is some disagreement regarding the potential for photo-inhibition (37, 79) but no examples of *in situ* surface inhibition of carbon fixation have been reported for milfoil.

The need to integrate the component processes and regulating factors is apparent if net production is to be predicted for a given set of conditions. This need has prompted one team of investigators to construct a computer stimulation model of certain aspects of the production biology of milfoil (80). While such models can be useful in suggesting needed research and integrating related processes, they are presently limited by the lack of a strong data base and are not yet sufficiently developed for application in management practices.

THE INFLUENCES OF MINERAL NUTRIENTS ON PRODUCTION

Ion absorption. Many submersed aquatic macrophytes, including milfoil, are characterized by having a rather modest root system, structurally reduced xylem components, and a very thin cuticle on the shoots (63). The shoots are known to be capable of ion uptake and because of their submergence, unable to generate a transpiration pull to transport water and solutes from root to shoot (76). For these reasons, it has long been debated whether submersed aquatic macrophytes absorb mineral ions principally through their roots, their shoots, or both. Recent evidence has demonstrated that for many aquatic macrophytes both roots and shoots are important in ion adsorption (8, 30, 63, 91).

Milfoil has certain anatomical structures associated with both the roots and leaves which may be important in ion absorption. Hydropoten have been described as occurring on the leaves of milfoil and are thought to be the major sites of mineral ion absorption in shoots (36). These specialized areas of epidermal tissue have been noted to be more freely permeable to salts and are stained readily by dyes *in vivo* (36). The production of abundant root hairs has been reported for American watermilfoil (64) and increases greatly the surface area of the root system. Sculthorpe (63) has pointed out that a casparian strip, which in terrestrial plants acts to regulate the inward passage of mineral ions, exists in the endodermis of the roots of milfoil. The presence of this structure suggests that significant root absorption occurs. Finally, some evidence exists to indicate that an acropetal current, analogous to the transpiration stream, occurs in some submersed macrophytes, including milfoil (78). However, at present these results seem unsubstantiated and have led both Sculthorpe (63) and Hutchinson (30) to conclude that sustained directional flow of water in aquatic macrophytes has yet to be conclusively demonstrated.

The importance of roots has been demonstrated in several studies employing American watermilfoil (8, 41, 56). One approach has been to compare growth when plants were rooted in sand to that which occurs when they were rooted in an organic sediment. Another approach has been to compare growth when plants were rooted in sediments to that occurring when they were suspended above sediments. Still another kind of experiment has evaluated the effect of providing a complete mineral nutrient medium to either roots or shoots. Despite the fact that some of these investigations are inconclusive by themselves, when considered as a whole the generalization can be made that roots are not always essential for plant survival; however, both the roots and shoots of plants grow best when rooted in an organic sediment.

Specific functions performed by roots which aid shoot growth have also received attention. The predominant interest has been in mineral nutrition and a summary of some of the findings is presented in Table 3. Although differing methodologies prevent critical comparison of Eurasian and American watermilfoils, the similarity of their uptake and translocation of phosphorus suggest that the qualitative generalization drawn from these data apply to both species.

Since nitrogen and phosphorus are considered by some investigators to be the most likely limiting nutrients for macrophyte growth (30), it is not surprising that these two elements have received the most attention. However, sodium, rubidium (typically considered an analogue of potassium), chlorine, iron, and calcium ions have also been studied. It is clear from Table 3 that the roots of watermilfoil are capable of absorbing phosphorus and nitrogen at rates at least comparable with those of shoots. Furthermore, upward translocation of N and P can occur to a significant extent and, in some cases, very rapidly (less than 15 minutes). Roots and shoots can both absorb Na, Rb, Cl, Fe, and Ca in significant amounts. However, upward translocation of Na appears negligible. Downward translocation has only been demonstrated for N, P, and Rb in watermilfoil.

The observations presented thus far are significant pri-

TABLE 3. ANALYSIS OF NUTRIENT UPTAKE BY WATERMILFOIL UNDER EXPERIMENTAL CONDITIONS.

Element Studied	Type of Experiment	Results	Duration	Watermilfoil Species	Source
P	Supplied ^{32}P to roots	The roots supplied 59% of the P incorporated into new shoots. When roots were removed, upward translocation of P was reduced by 33%. P was not translocated downward.	10 days	American	9
P	Supplied ^{32}P to roots or shoots	Leaf uptake was 72%, and stem uptake 11%, of that demonstrated by roots on a dry-weight basis.	1 hour	American	9
P	Supplied ^{32}P to roots or shoots	Shoot uptake was 62% of root uptake on a dry-weight basis. Roots supplied 8% of shoot P. Shoots supplied 1% of root P.	24 hours	Eurasian	83
P	Supplied ^{32}P to rooted plants *in situ* and in the laboratory	Roots supplied 12% of the shoot P. Downward translocation of P occurred in less than 15 minutes.	8 hours	American	16
N	Field observation	Plant nitrogen correlated better with the sediment N than with the water N.	During two seasons	Eurasian	44
N	Plants supplied with available N only through the roots	Plants grew well and flowered.	Several months	Eurasian	45
N	^{15}N supplied to roots or shoots	Roots supplied 38% of the N for new shoots and 14% for old shoots. New shoot uptake was 97% and old shoot uptake was 117% of root uptake on a dry-weight basis. Shoots supplied 12% of the root nitrogen.	14 days	Eurasian	45
Fe Ca	Supplied ^{59}Fe and ^{45}Ca to roots or shoots	Autoradiograph demonstrated that uptake and significant translocation to shoots occurred.	8 hours	American	16
Na Rb Cl	Supplied isotopes to roots or shoots	Root uptake was 43%, 32%, and 80% of shoot uptake for Na, Rb, and Cl, respectively. Transport from root was 0.3% (Na), 22% (Rb), and 9% (Cl) of shoot uptake. Transport from shoot was $< 0.1\%$ (Na), 19% (Rb), and 1% (Cl) of root uptake.	24-48 hours	Eurasian	83

marily because they indicate the ion absorption capabilities of watermilfoil, largely under laboratory conditions. However, what is most interesting is the relative importance of roots and shoots *under natural conditions*. As suggested for a marine seagrass (38, 55), the relative importance of root versus shoot uptake of nutrients is dependent upon external concentrations. In almost all the cited studies, the root and shoots have been presented with equal concentrations of the various nutrients, a situation not commonly found in nature. For these reasons, the relative importance of root and shoot uptake of minerals will vary among habitats, but for phosphate and combined nitrogen it is likely that the sediments are the predominant source in a majority of cases. However, Nichols and Keeney (45) suggest that when 0.1 mg/l NH_4–N occurs in the water, foliar uptake of N may exceed root uptake in milfoil.

It is generally believed that for most nutrients ion uptake by aquatic macrophyte leaves is an active process which includes absorption into the cytoplasm, translocation through the cytoplasm, and subsequent entry into the vacuole (30, 63). However, these processes have not been confirmed for watermilfoil species. The process of ion uptake in vascular plants is typically composed of both high and low affinity components which predominate at low and high external concentrations respectively (30). This uptake has been confirmed for milfoil using phosphorus (39) and the two components were shown to operate simultaneously.

Mineral nutrition. Higher plants in general require sixteen essential elements to grow and reproduce (33). Three of these elements, C, H, and O are not typically considered as mineral nutrients and have been dealt with in previous sections. The remaining thirteen elements include the macronutrients N, P, K, S, Ca, and Mg, and the micronutrients Cu, Zn, B, Cl, Mo, Mn, and Fe. After the elements have been absorbed and incorporated, they possess varying degrees of mobility by which they may move to sites of active growth. According to Larcher (33), N, P, S, K, and to some degree Mg, are the only essential nutrients with good transportability, which is of course important when considering the topic of nutrient limitation.

Although any of the above-mentioned nutrients are capable of limiting the production of milfoil, they have not all received equal study. Huchinson (30) has generalized that P and N are the most likely nutrients to limit macrophyte production.

There have been several approaches to the problem of determining limiting nutrients in aquatic macrophytes. The two primarily used for watermilfoil in natural habitats are the analysis of ambient water samples and the analysis of plant tissues for nutrient status. Analyses of nutrient contents of natural waters have been used primarily to determine the relationship between nutrient concentrations and plant distributions rather than to detect limiting nutrient levels. Also, water analyses suffer from an inability

to determine the total supply of a nutrient available over time, rates of nutrient regeneration, and neglect the sediments as a nutrient source.

The analysis of plant tissues for nutrient status is based on the determination of a "critical tissue concentration" for a particular nutrient, below which growth is limited by that nutrient and above which growth is independent of nutrient concentration (20). It was originally proposed by Gerloff and Krombholz (20) that the critical concentrations of 1.5% for N and 0.15% for P (on a dry weight basis) were the same for all submersed macrophytes, but later it was found that the values for milfoil were considerably lower (0.75% for N and 0.07% for P) than for the other macrophytes examined (19, 39). Potassium has also been examined in this regard and was found to have a comparatively high critical concentration in milfoil (39). Both the critical concentrations and the tissue concentrations which have been found in natural habitats are presented in Table 4.

In order to interpret these data, two major assumptions must be made. First, nutrient concentrations are assumed to be relatively uniform throughout the plant body and therefore the critical concentration applies to values for entire shoots. This assumption is certainly false but the differences between index segments and entire shoots are not likely to cause major errors (10, 12). Secondly, the established critical concentrations are considered constant regardless of plant condition. If these assumptions are made, then the data presented in Table 4 does not demonstrate any cases of P or N limitation and shows evidence for potassium limitation in only one case. It is advisable to be very cautious in these interpretations since these assumed constant, critical concentrations have not yet been sufficiently confirmed and are contrary to recent findings of some authors (62). In addition, the lakes studied most thoroughly are high in nutrients, therefore giving a somewhat biased view.

It is quite likely that many cases of nutrient limitation in nature involve elements other than nitrogen, phosphorus, or potassium. Unfortunately, the importance of other nutrients to milfoil have received little attention. A notable exception has been calcium which appears to play an important role in the maintenance of proper membrane function (69). This role has been evidenced by calcium induced enhancement of phosphate uptake (67), herbicide uptake (69), and resistance to NaCl toxicity (15). The action of calcium in plant growth is complex, making predictions difficult. Nevertheless, calcium concentrations seem to be of some importance in explaining the distribution of milfoil (29), as has been demonstrated for a number of other submersed macrophytes (40, 90).

Some insight into mineral nutrition can be gained by examining the distribution and abundance of watermilfoil. Although both Eurasian watermilfoil and American watermilfoil occur in a variety of habitats, they are considered to be typical inhabitants of eutrophic (nutrient rich) waters (30, 34). However, Mulligan *et al.* (42) found that the enrichment of artificial ponds with N and P resulted in reduction or elimination of American watermilfoil even though the level of enrichment used was optimal for growth in the laboratory. This result suggests the importance of competition, both with other macrophytes and planktonic as well as epiphytic algae in determining the distribution and abundance of these watermilfoils.

Another approach to the problem of predicting competition at different nutrient levels has been to compare uptake kinetics. Based on results of comparative uptake studies, it has been predicted that milfoil should be outcompeted for P and K by a variety of algae and macrophytes with which it has been compared (19, 39, 79). However, results of actual competition studies deviated somewhat from those predicted (19) and indicate some of the difficulties involved in making such predictions, even when ignoring the roots as a source of nutrients. Further work on the subject with attention being given to root uptake and longer time spans would be useful.

TABLE 4. CRITICAL CONCENTRATIONS AND RANGES OF NUTRIENTS IN TISSUES OF MILFOIL FROM NATURAL AND SEMINATURAL HABITATS.

Species	Critical Concentrations % P	% N	% K	Tissue	Location	Source
Eurasian	0.07	0.75	0.35	Second one-inch segment of tip	—	39; 19
American	0.06-0.08	—	—	Entire shoots	—	94
	Ranges of Tissue Values					
Eurasian	0.14-0.61	1.85-4.30	0.19-0.46	Second one-inch segment of tip	Wisconsin	39
"	0.42	—	1.87	Shoots	Minnesota	43
"	0.18	—	—	Shoots	Minnesota	43
"	—	—	0.62	Shoots	Alabama	30
"	0.31-0.74	2.30-3.76	1.20-2.10	Shoots	New Jersey	60
"	0.74-5.59	—	—	Entire plants	Scotland	10
"	0.11-0.67	—	—	Shoots	Wisconsin	1
"	—	1.72-6.29	—	Growing tips	Wisconsin	44
"	—	—	1.5-1.8[1]	Shoots	Chesapeake	3
"	0.10-0.54	—	1.43-2.23	Shoots	S. Carolina	22
"	0.08-0.50	1.40-3.40	1.6-2.5	Shoots	Wisconsin	12
American	0.26-0.41	2.15-2.99	—	Entire plants	Artificial ponds	41
Watermilfoil sp.	0.35-0.41	2.42-2.77	—	Shoots	Wisconsin	20

[1] Based on the assumption that wet/dry weight = 10/1.

SUMMARY AND CONCLUSIONS

Eurasian watermilfoil is a submersed aquatic angiosperm which is currently a major weed problem in many areas of the North America. This herbaceous perennial is capable of rapid dispersion through vegetative reproduction, principally by fragmentation of plant parts. Metabolic studies of the carbon fixation pathways have shown the Hatch-Slack-Kortschak Pathway to be lacking but anatomical characteristics are similar to the "Krantz" anatomy which is usually associated with C_4 plants. Studies of carbon fixation have demonstrated that free CO_2 is the preferred form of dissolved inorganic carbon but evidence suggests milfoil is able to utilize HCO_3^- ions at elevated pH. Both dark respiration and photorespiration have been shown to occur in milfoil but photorespiration is likely to be of lesser magnitude than that found in either terrestrial C_3 plants or other submersed angiosperms since associated enzymatic activities are low and the effect of high O_2 concentrations is minimal. Comparisons of dry matter production show milfoil to be only average relative to other submersed angiosperms and rather unproductive when compared to emergent and terrestrial vegetation. However, milfoil gives the appearance of being highly productive since it concentrates its biomass in dense canopies near the water's surface, even from depths as great as 4 m. The uptake of nutrients by milfoil occurs through both roots and shoots but in a majority of locations the sediments are probably more important sources of nitrogen and phosphorus than the water. Exceptions to this relationship will certainly occur in nutrient-rich waters since considerably more surface area is provided for absorption by the shoots than by the roots. Only one case of potential limitation by mineral nutrients has been indicated for natural habitats, and that was for potassium. However, much further work is needed before confident statements can be made about the most likely limiting nutrients and their complex interactions.

In conclusion, milfoil seems to be highly successful in colonizing new habitats, replacing other submersed macrophytes and avoiding nutrient limitations. Part of its success is due to a high efficiency in fixing inorganic carbon which may be related to certain anatomical features that aid in refixation of respired CO_2. Although based on metabolic criteria milfoil seems to be at a disadvantage in utilizing available light, its growth form seems to be highly compensatory for any metabolic deficiencies. The existing evidence suggests that the ability of milfoil to avoid nutrient limitations, especially by N and P, is the result of root uptake from the sediments and low requirement for these minerals, rather than because of well-adapted uptake kinetics. Despite excessive growth of milfoil, it is not especially productive when considered by quantitative criteria. Therefore, anatomical features, growth form, low requirements of nitrogen and phosphorus, and high vegetative reproductive capacity of this species are implicated as major factors determining its distributional and competitive success.

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