Chapter 6

ALGAE

6.1 INTRODUCTION

Algae are important components of water quality models for several reasons. For example:

- Algal dynamics and nutrient dynamics are closely linked together since nutrient uptake during algal growth is the main process which removes dissolved nutrients from the water, and algal respiration and decay are major components of nutrient recycling.

- Algal processes can cause diurnal variations in dissolved oxygen due to photosynthetic oxygen production during the daylight combined with oxygen consumption due to algal respiration during the night. Seasonal oxygen dynamics may also be closely tied to algal dynamics, particularly in highly productive stratified systems, since the respiration and decomposition of algae which settles below the photic zone is often a major source of oxygen depletion.

- Algae can affect pH through the uptake of dissolved CO_2 during photosynthesis and the recycling of CO_2 during respiration.

- Algae are the dominant component of the primary producers in many systems, particularly in lakes and estuaries. Since

they form the base of the food chain, they play a major role in the dynamics of all successive trophic levels.

- Suspended algae are often a major component of turbidity.

- Algal blooms can restrict recreational uses of water, sometimes resulting in fish kills under severe conditions.

- Algae can cause taste and odor problems in water supplies, and filter clogging problems at water treatment facilities.

Two general approaches have been used to simulate algae in water quality models: 1) aggregating all algae into a single constituent (for example, total algae or chlorophyll a), or 2) aggregating the algae into a few dominant functional groups (for example, green algae, diatoms, blue-greens, dinoflagellates, etc.).

The first approach is commonly used in river models since the major focus is on short term simulations (days to weeks) where the primary interest is the effects of algae on general water quality parameters such as dissolved oxygen, nutrients, and turbidity. Typical examples include QUAL-II (Roesner et al., 1981; NCASI, 1982, 1983), DOSAG3 (Duke and Masch, 1973), and RECEIV-II (Raytheon, 1974). In contrast, lake and reservior models tend to use the second approach since the focus is on long term simulations (months to years) of eutrophication problems where seasonal variations in different types of algae are important (Bierman, 1976; Bierman et al., 1973, 1980; Canale et al., 1975, 1976; Chen et al., 1975; Tetra Tech, 1979, 1980; Park et al., 1974, 1975, 1979, 1980; Scavia et al., 1976; Scavia, 1980; Lehman et al., 1975). Species-specific differences in nutrient requirements, nutrient uptake rates, growth rates, and temperature preference ranges result in a seasonal succession of dominance by different phytoplankton groups. It is often important to distinguish these differences in order to realistically model both nutrient dynamics and phytoplankton dynamics, and to predict the occurrence of specific problems such as blue-green algal blooms. Multi-group models typically use the same

general model formulations for all groups, but provide different coefficient values to characterize the differences between groups.

6.2 MODELING APPROACHES

Phytoplankton dynamics are governed by the following processes: growth, respiration and excretion, settling, grazing losses, and nonpredatory mortality (or decomposition). A general equation which includes all of these processes and forms the basis for almost all phytoplankton models can be expressed as:

$$\frac{dA}{dt} = (\mu - r - e_x - s - m)\, A - G \qquad (6\text{-}1)$$

where A = phytoplankton biomass or concentration (dry weight biomass, chlorophyll a, or equivalent mass of carbon, nitrogen, or phosphorus), mass or mass/volume

μ = gross growth rate, 1/time

r = respiration rate, 1/time

e_x = excretion rate, 1/time

s = settling rate, 1/time

m = nonpredatory mortality (or decomposition) rate, 1/time

G = loss rate due to grazing, mass/time or mass/volume-time

This equation is appropriate when phytoplankton are modeled in terms of either biomass or nutrient equivalents (carbon, nitrogen, phosphorous, etc.). However, if phytoplankton are expressed in terms of cell numbers, the growth rate is replaced with the cell division rate, and the respiration and excretion terms are omitted since they pertain to changes in biomass rather than cell numbers. The resulting equation is:

$$\frac{dA_n}{dt} = (\mu_n - s - m)\, A_n - G_n \qquad (6\text{-}2)$$

where A_n = phytoplankton cell numbers, numbers or numbers/volume

μ_n = cell division rate, 1/time

G_n = loss rate due to grazing, numbers/time or numbers/volume-time

The cell division rate in Equation (6-2) is assumed to be a continuous process although in reality cell division is a discrete event which is often expressed in terms of the number of divisions per day, n_d. The continuous division rate μ_n is related to the discrete rate n_d by $\mu_n = n_d \ln 2$.

Most models express phytoplankton in terms of biomass (or nutrient or chlorophyll *a* equivalents) rather than cell numbers. This facilitates the modeling of both nutrient cycles and food web dynamics since it allows a more direct linkage between the phytoplankton equations and the mass balance equations for both nutrients and higher trophic levels such as zooplankton and fish. Phytoplankton cell numbers are used in a few models whose focus is restricted to phytoplankton dynamics (e.g., Lehman *et al.*, 1975; Cloern, 1978).

The major differences between different phytoplankton models are: 1) the number of phytoplankton groups modeled, 2) the specific formulations used for each process, and 3) the manner in which the various processes and corresponding terms in Equations (6-1) or (6-2) are combined. Some of the basic features of different phytoplankton models are compared in Table 6-1. The specific process formulations are discussed in later sections.

Many models combine several of the processes in Equation (6-1) into a single term, thereby simplifying the equation. For example, respiration and excretion are usually combined into a single respiration term. Respiration is often combined with growth so that the growth rate μ represents the net growth rate, rather than the gross growth rate as in Equation (6-1). This is consistent with net growth rates typically reported in the literature from laboratory cultures. Some models combine respiration with the other loss terms to give a net loss rate which includes respiration and mortality. Other models combine grazing and nonpredatory mortality into a single mortality term, particularly when algal grazers are not modeled explicitly.

TABLE 6-1. GENERAL COMPARISON OF ALGAL MODELS

Model (Author)	Number of Groups			Processes Computed Separately in Model					Algal Units					Reference
	Phyto-plankton	Attached Algae	Zoo-plankton	Growth	Respir-ation	Settling	Nonpredatory Mortality	Predatory Mortality	Dry Wt. Biomass	Chl a	Carbon	Other Nutrient	Cell Numbers	
AQUA-IV	1		1	X	X	X	X	X			X			Baca & Arnett (1976)
CE-QUAL-R1	2		1	X	X	X		X	X					WES (EWQOS) (1982)
CLEAN	2	1	3	X	X	X	X	X	X					Bloomfield et al. (1973)
CLEANER	3	1	3	X	X	X	X	X	X					Scavia & Park (1976)
MS.CLEANER	4	1	5	X	X	X	X	X	X					Park et al. (1980)
DEM	1			X	X	X				X				Feigner & Harris (1970)
DOSAG3	1			X	X	X				X				Duke & Masch (1973)
EAM	4	1	3	X	X	X		X	X					Tetra Tech (1979, 1980)
ESTECO	2		1	X	X	X		X	X					Brandes & Masch (1977)
EXPLORE-1	1		1	X	X			X			X			Baca et al. (1973)
HSPF	1	1	1	X	X	X	X	X	X					Johanson et al. (1980)
LAKECO	2		1	X	X	X		X	X					Chen & Orlob (1975)
MIT Network	1		1	X	X		X	X				N		Harleman et al. (1977)
QUAL-II	1			X	X	X				X				Roesner et al. (1981)
RECEIV-II	1			X	X		X			X				Raytheon (1974)
SSAM IV	1	1		X			X		X					Grenney & Kraszewski (1981)
WASP	2		2	X	X	X	X	X		X	X			Di Toro et al. (1981)
WQRRS	2	2	1	X	X	X		X	X					Smith (1978)
Bierman	5		2	X	X	X	X	X	X					Bierman et al. (1980)
Canale	4		9	X	X	X		X			X			Canale et al. (1975, 1976)
Jorgensen	1		1	X	X	X	X	X	X					Jorgensen (1976)
Lehman	5			X	X	X	X						X	Lehman et al. (1975)
Nyholm	1			X		X	X		X					Nyholm (1978)
Scavia	5		6	X	X	X	X	X			X			Scavia et al. (1976)

Because of these variations, it is very important to understand the assumptions of a particular model when selecting coefficients. Care must be taken both when extracting values from one model and applying them to another, or when using experimental measurements reported in the literature. For the latter case, the experimental conditions should be checked to make sure they are consistent with the assumptions of the model. If they are different, the appropriate adjustments should be made.

Attached algae (periphyton) and aquatic macrophytes have the same growth requirements as phytoplankton (light and nutrients) and are subject to the same basic processes of growth, respiration and excretion, grazing,and nonpredatory mortality. Therefore, they are usually modeled using the same general approach and process formulations as phytoplankton, although the specific values of the model coefficients will vary. The major differences are: 1) periphyton and macrophytes are associated with the bottom substrate and are expressed in terms of areal densities rather than volumetric densities or concentrations; 2) periphyton and macrophytes do not have settling losses, but instead they have additional losses due to sloughing or scouring from the bottom substrate; 3) periphyton and macrophytes are not subject to hydrodynamic transport; and 4) macrophytes use nutrients from the sediments and interstitial waters rather than nutrients in the water column. The general model equation for attached algae and macrophytes can be expressed as:

$$\frac{dA_b}{dt} = (\mu - r - e_x - s_1 - m)\, A_b - G_b \qquad (6\text{-}3)$$

where A_b = periphyton or macrophyte biomass (dry weight biomass, chlorophyll *a*, or equivalent mass of carbon, nitrogen, or phosphorus), mass or mass/area

S_1 = sloughing or scouring rate, 1/time

G_b = loss rate due to grazing, mass/time or mass/area-time

Benthic algae or macrophytes are included in only a few models such as CLEAN (Park *et al.*, 1974), CLEANER (Park *et al.*, 1975), MS.CLEANER

(Park et al., 1980), EAM (Tetra Tech, 1979, 1980), WQRRS (Smith, 1978), HSPF (Johanson et al., 1980), SSAM IV (Grenney and Kraszewski, 1981), and in Canale and Auer (1982) and Scavia et al. (1975).

6.3 CELL COMPOSITION

The majority of models express algae and other biological constituents as either dry weight biomass (Chen and Orlob, 1972; Chen et al., 1975; Park et al., 1974, 1975, 1979, 1980; Tetra Tech, 1979, 1980; Brandes and Masch, 1977; Smith, 1978; Johanson et al., 1980; Grenney and Kraszewski, 1981; Bierman et al., 1973, 1980; Jorgensen, 1976; Jorgensen et al., 1978; Nyholm, 1977, 1978) or carbon (Baca and Arnett, 1976; Baca et al., 1973, 1974; Canale et al., 1975, 1976; Scavia et al., 1976; Scavia, 1980). Nitrogen or phosphorus have also been used in a few models which focus on a single nutrient cycle and assume that particular nutrient always limits algal growth (Najarian and Harleman, 1975; Harleman et al., 1977). Some models express phytoplankton as chlorophyll a since both field measurements and water quality standards are often reported in these units (Roesner et al., 1981; Duke and Masch, 1973; Raytheon, 1974; Di Toro et al., 1971, 1977; Di Toro and Matystik, 1980; Di Toro and Connolly, 1980; O'Connor et al., 1975; Thomann et al., 1975, 1979).

Dry weight biomass is related to the major nutrients (carbon, nitrogen, and phosphorus) and chlorophyll a through stoichiometric ratios which give the ratios of each nutrient to the total biomass. Typical algal nutrient compositions are summarized in Tables 6-2 to 6-4. Algae expressed as carbon, nitrogen, phosphorus, or chlorophyll a can be converted to dry weight biomass or any of the other units by using the stoichiometric ratios presented in the tables.

Most conventional water quality models assume the nutrient compositions of the cells and the resulting stoichiometric ratios are constant. In reality, cell stoichiometry varies with species, cell size, physiological condition, and recent environmental conditions (external nutrient concentrations, light, and temperature), although it is often assumed

TABLE 6-2. NUTRIENT COMPOSITION OF ALGAL CELLS - PERCENT OF DRY WEIGHT BIOMASS

Algal Type	Percent of Dry Weight Biomass					References
	C	N	P	Si	Chl *a*	
Total Phytoplankton	40.-50.	8.-9.	1.5			Tetra Tech (1976) Chen & Wells (1975, 1976)
	40.	7.2	1.0			Tetra Tech (1980) Bowie *et al.* (1980) Porcella *et al.* (1983)
					2.	Bierman (1976)
	60.					Nyholm (1978)
		6.1	0.88			Jorgensen (1976)
	40.-50.*	7.-9.*	1.-1.2*			Smith (1978)
		8.-9.*	1.2-1.5*		5.-10.*	Roesner *et al.* (1980) Duke & Masch (1973)
	50.*	9.*	1.2*			Brandes (1976)
	42.9-70.2**	0.6-16.**	0.16-5.**			Baca & Arnett (1976)
		1.5-9.3**	0.08-1.17**			Jorgensen (1979)
Diatoms	40.	7.2	1.0	20.-24.		Tetra Tech (1980) Bowie *et al.* (1980) Porcella *et al.* (1983)
				50.		Bierman *et al.* (1976)
	19.-50.**	2.7-5.9**	0.4-2.0**			Di Toro *et al.* (1971)
	20.-53**					Bierman *et al.* (1980)
Green Algae	40.	7.2	1.0			Tetra Tech (1980) Bowie *et al.* (1980) Porcella *et al.* (1983)
	35.-48.**	6.6-9.1**	2.4-3.3**			Di Toro *et al.* (1971)
	15.-74.**					Bierman *et al.* (1980)
Blue-green Algae	40.	7.2	1.0			Tetra Tech (1980) Bowie *et al.* (1980) Porcella *et al.* (1983)
	28.-45.**	4.5-5.8**	0.8-1.4**			Di Toro *et al.* (1971)
	38.-39.**					Bierman *et al.* (1980)
					1.-3.**	Baca & Arnett (1976)
					0.25**	Jorgensen (1979)

TABLE 6-2. (continued)

Algal Type	Percent of Dry Weight Biomass C	N	P	Si	Chl-a	References
Dinoflagellates					275.	O'Connor et al. (1981)
	37.-47**	3.3-5.0**	0.6-1.1**			Di Toro et al. (1971)
	10.-43.**					Bierman et al. (1980)
Flagellates	40.	7.2	1.0			Tetra Tech (1980) Bowie et al. (1980) Porcella et al. (1983)
	29.-67.**					Bierman et al. (1980)
Chrysophytes	35.-45.**	7.8-9.0**	1.2-3.0			Jorgensen (1979)
Benthic Algae	40.	7.2	1.0			Tetra Tech (1980) Bowie et al. (1980) Porcella et al. (1983)
	40.-50.*	7.-9.*	1.-1.2*			Smith (1978)

*Model documentation values.
**Literature values.

constant for modeling purposes. Several of the more recent algal models, however, have included variable cell stoichiometry in their formulations to simulate processes such as luxury uptake and storage of nutrients (Bierman et al., 1973, 1980; Bierman, 1976; Lehman et al., 1975; Jorgensen, 1976; Jorgensen et al., 1978; Nyholm, 1977, 1978; Park et al., 1979, 1980; Canale and Auer, 1982). These models are discussed later with reference to phytoplankton growth and nutrient uptake formulations.

6.4 GROWTH

Algal growth is a function of temperature, light, and nutrients. The major growth limiting nutrients are assumed to be phosphorus, nitrogen, and carbon, with the addition of silicon for diatoms. Other essential micronutrients such as iron, manganese, sulfur, zinc, copper, cobalt,

molybdenum, and vitamin B_{12} may also limit growth under conditions of restricted availability (particularly in oligotrophic systems). However, these effects are generally not included in models since micronutrients are usually not simulated. The algal growth rate formulations used in almost all models can be expressed in general functional form as:

$$\mu = \mu_{max}(T_{ref})\ f(T)\ f(L,P,N,C,Si) \qquad (6\text{-}4)$$

where μ = algal growth rate, 1/time

$\mu_{max}(T_{ref})$ = maximum growth rate at a particular reference temperature T_{ref} under optimal conditions of saturated light intensity and excess nutrients, 1/time

$f(T)$ = temperature function for growth

T = temperature, ^{o}C

$f(L,P,N,C,Si)$ = growth limiting function for light and nutrients

L = light intensity

P = available inorganic phosphorus concentration, mass/volume

TABLE 6-3. NUTRIENT COMPOSITION OF ALGAL CELLS - RATIO TO CARBON

Algal Type	$\frac{N}{C}$	$\frac{P}{C}$	$\frac{Si}{C}$	References
Total Phytoplankton	0.17 - 0.25	0.025		Thomann & Fitzpatrick (1982) Di Toro *et al.* (1971)
	0.18	0.024		Scavia et al. (1976) Scavia (1980)
	0.2			Canale *et al.* (1976)
	0.05 - 0.17**	0.024 - 0.24**		Baca & Arnett (1976)
	0.05 - 0.43**	0.025 - 0.05**		Jorgensen (1979)
Diatoms	0.18	0.024	0.6	Scavia (1980)
	0.067 - 0.21**	0.003 - 0.14**	0.06-0.77**	Jorgensen (1979)

**Literature Values.

TABLE 6-4. NUTRIENT COMPOSITION OF ALGAL CELLS - RATIO TO CHLOROPHYLL a

Algal Type	C / Chl a	N / Chl a	P / Chl a	Si / Chl a	References
Total Phytoplankton	50.-100.	7.-15.	0.5-1.0		Thomann et al. (1975, 1979) O'Connor et al. (1981) Di Toro & Matystik (1980) Di Toro & Connolly (1980) Salas & Thomann (1978)
			0.5		Salisbury et al. (1983)
		7.2	0.63		Larsen et al. (1973)
	25.-112.**	7.-29.**	1.0**		Jorgensen (1979)
	10.-100.**	2.7-9.1**			O'Connor et al. (1981)
Diatoms	100.	10.-15.	0.5-1.0	40.-50.	Di Toro & Connolly (1980) Di Toro & Matystik (1980) Thomann et al. (1979)
			0.5		Salisbury et al. (1983)
	50.-200.*				Baca & Arnett (1976)
	18.-500**	2.2-74.6**	0.27-19.2**	2.4-50.7**	Di Toro et al. (1971)
Green Algae	25.-100.*				Baca & Arnett (1976)
Blue-green Algae	14.-67.*				Baca & Arnett (1976)
Dinoflagellates	275.	19.3			O'Connor et al. (1981)

*Model documentation values.

**Literature values.

N = available inorganic nitrogen concentration, mass/volume

C = available inorganic carbon concentration, mass/volume

Si = available inorganic silicon concentration, mass/volume

Note that the growth limiting function f(L,P,N,C,Si) is simplified in many models by excluding some of the nutrients. For example, silicon is

included only in models which simulate diatoms as a separate algal group (Bierman et al., 1973, 1980; Bierman, 1976; Canale et al., 1975, 1976; Scavia et al., 1976; Scavia, 1980; Chen et al., 1975; Tetra Tech, 1979, 1980; Lehman et al, 1975; Park et al., 1979, 1980; Di Toro and Connolly, 1980). Carbon is frequently omitted since it is often available in excess relative to phosphorus and nitrogen (Bierman et al., 1980; Scavia et al., 1976; Nyholm, 1978; Canale et al., 1975, 1976; Baca and Arnett, 1976; Di Toro and Matystik, 1980). Some models include only one nutrient, phosphorus or nitrogen, and assume that nutrient is limiting at all times for the particular system under consideration (Najarian and Harleman, 1975; Canale and Auer, 1982).

It should also be noted that the nutrient concentrations in the growth limiting function f(L,P,N,C,Si) correspond to the "external" nutrient concentrations in the water for some models, and to the "internal" nutrient concentrations in the algal cells for other models. These distinctions will be discussed in more detail below.

6.4.1 Temperature Effects On Maximum Growth Rates

The quantity $\mu_{max}(T_{ref})$ f(T) in Equation (6-4) represents the effects of temperature variations on maximum algal growth rates under conditions of optimum light and nutrients. The maximum growth rate μ_{max} must be specified at a reference temperature T_{ref} which is consistent with the particular temperature function f(T) used in the model. The reference temperature may correspond to $20^{o}C$, optimum temperature conditions, or some other temperature, depending on the form of the temperature function. Therefore, maximum growth rate coefficients obtained from one model may have to be adjusted before using the coefficients in another model which has a different temperature adjustment function. Maximum growth rates for algae are tabulated in Table 6-5, along with the corresponding reference temperatures.

Although numerous temperature adjustment functions have been used to model algae, most of them fall into one of three major categories

TABLE 6-5. ALGAL MAXIMUM GROWTH RATES

Algal Type	Maximum Growth Rate (1/day)	Reference Temperature (^{o}C)	References
Total Phytoplankton	1.3 - 2.5	20°C	O'Connor et al. (1975, 1981) Thomann et al. (1974, 1975, 1979) Thomann & Fitzpatrick (1982) Di Toro & Connolly (1980) Di Toro & Matystik (1980) Di Toro et al. (1971, 1977) Salas & Thomann (1978) Salisbury et al. (1983)
	1. - 2.5	20°C	Chen (1970) Chen & Orlob (1975) Chen & Wells (1975, 1976) Tetra Tech (1976)
	1. - 2.	20°C	Battelle (1974)
	1.5	20°C	Grenney & Kraszewski (1981)
	1. - 2.7	T_{opt}	Scavia & Park (1976) Youngberg (1977)
	1.5	20°C	Nyholm (1978)
	1.8 - 2.53	T_{opt}	Jorgensen (1976) Jorgensen et al. (1978)
	2.4	T_{opt}	Larsen et al. (1973)
	0.2 - 8.*	20°C	Baca & Arnett (1976)
	1. - 3.*	T_{opt}	Smith (1978)
	1. - 3.*	20°C	Roesner et al. (1980) Duke & Masch (1973)
	0.2 - 8.*	20°C	Grenney & Kraszewski (1981)
	1.5 - 2.*	20°C	Brandes (1976)
	0.58 - 3.**	20°C	Jorgensen (1979)
Diatoms	2.1	20°C	Di Toro & Connolly (1980) Thomann et al. (1979) Salisbury et al. (1983)
	2.0 - 2.5	T_{opt}	Tetra Tech (1980) Bowie et al. (1980) Porcella et al. (1983)
	2.0 - 2.1	20°C	Canale et al. (1976)
	2.1	25°C	Bierman (1976)
	1.6	10° - 14°C	Bierman et al. (1980)
	1.8 - 2.5	T_{opt}	Scavia et al. (1976) Scavia (1980)
	3.0	T_{opt}	Lehman et al. (1975)

TABLE 6-5. (continued)

Algal Type	Maximum Growth Rate (1/day)	Reference Temperature (^{o}C)	References
	1.75**	27°C**	Di Toro et al. (1971)
	0.55 - 3.4**	20°C**	Collins & Wlosinski (1983)
	1.1 - 5.0**	20°C**	Jorgensen (1979)
Green Algae	1.9	25°C	Bierman (1976)
	1.4	20°C	Bierman et al. (1980)
	2.0 - 2.5	T_{opt}	Tetra Tech (1980) Bowie et al. (1980) Porcella et al. (1983)
	1.9	20°C	Canale et al. (1976)
	1.8 - 2.5	T_{opt}	Scavia et al. (1976) Scavia (1980)
	1.6	25°C	DePinto et al. (1976)
	3.0	T_{opt}	Lehman et al. (1975)
	1.5 - 3.9**	25°C**	Di Toro et al. (1971)
	0.7 - 2.1**	20°C	Collins & Wlosinski (1983)
	0.9 - 4.1**	25°C**	
	9.0 - 9.2**	39°C**	
	1.4 - 2.4**	20°C**	Jorgensen (1979)
	1.5 - 3.9**	25°C**	
	1.3 - 4.3**	35°C**	
	5.65**	40°C**	
Blue-green Algae	0.8	25°C	Bierman (1976)
	0.7 - 1.0	20° - 25°C	Bierman et al. (1980)
	1.6	20°C	Canale et al. (1976)
	1.4 - 1.9	T_{opt}	Youngberg (1977)
	1.1 - 2.0	T_{opt}	Scavia & Park (1976) Scavia (1980)
	1.1	25°C	DePinto et al. (1976)
	2.5	T_{opt}	Lehman et al. (1975)
	1.6 - 2.5	T_{opt}	Tetra Tech (1980) Bowie et al. (1980) Porcella et al. (1983)
	0.41 - 0.86**	20°C**	Jorgensen (1979)
	0.2 - 4.9**	25°C**	Collins & Wlosinski (1983)
	2.0 - 3.9**	35°C**	
	0.5 - 11.**	40°C**	

TABLE 6-5. (continued)

Algal Type	Maximum Growth Rate (1/day)	Reference Temperature (^{o}C)	References
Dinoflagellates	0.2 - 0.28	20°C	O'Connor et al. (1981)
	2.16**	20°C	Di Toro et al. (1971)
	0.2 - 2.1**	20°C	Collins & Wlosinski (1983)
Flagellates	1.6	T_{opt}	Tetra Tech (1980) Porcella et al. (1983)
	1.2	20°C	Bierman et al. (1980)
	1.5	T_{opt}	Lehman et al. (1975)
Chrysophytes	1.5	T_{opt}	Lehman et al. (1975)
	0.4 - 2.9**	25°C**	Collins & Wlosinski (1983)
Coccolithophores	1.75 - 2.16**	25°C**	Jorgensen (1979)
Benthic Algae	0.5 - 1.5	T_{opt}	Tetra Tech (1980) Porcella et al. (1983)
	1.08	T_{opt}	Auer and Canale (1982)
	1.5	20°C	Grenney & Kraszewski (1981)
	0.2 - 0.8*	20°C	Grenney & Kraszewski (1981)
	0.5 - 1.5*	T_{opt}	Smith (1978)

*Model documentation values.

**Literature values.

(Figure 6-1): 1) linear increases in growth rate with temperature, 2) exponential increases in growth rate with temperature, and 3) temperature optimum curves in which the growth rate increases with temperature up to the optimum temperature and then decreases with higher temperatures.

The simplest type of temperature adjustment function assumes a linear temperature response curve above some minimum temperature T_{min}. This relationship can be expressed in general form as:

$$f(T) = \frac{T - T_{min}}{T_{ref} - T_{min}} \qquad (6\text{-}5)$$

$$= \left(\frac{1}{T_{ref} - T_{min}}\right) T - \left(\frac{T_{min}}{T_{ref} - T_{min}}\right)$$

$$= \gamma T + \beta$$

where T_{min} = lower temperature limit at which the growth rate is zero, ^{o}C

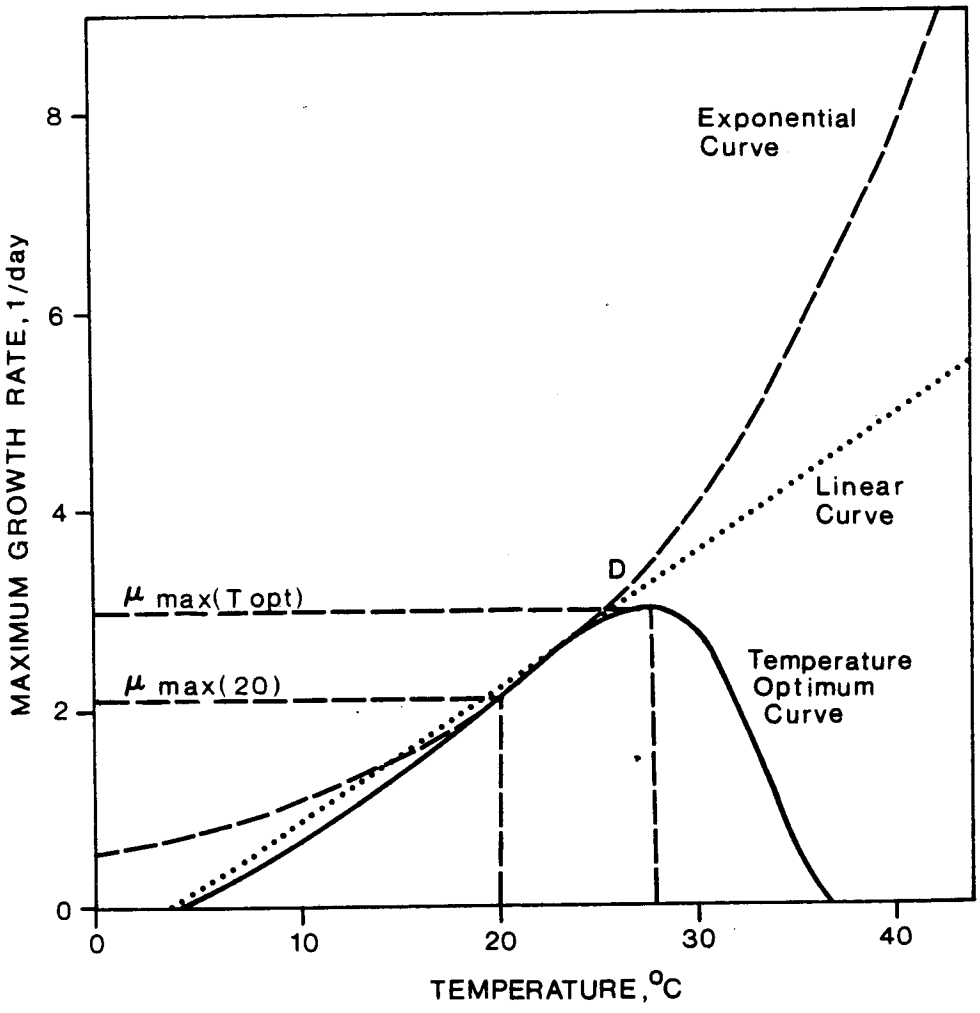

Figure 6-1. Major types of temperature response curves for algal growth.

T_{ref} = reference temperature corresponding to the value of the maximum growth rate $\mu_{max}(T_{ref})$, ^{o}C

$$\gamma = \frac{1}{(T_{ref} - T_{min})} = \text{slope of growth vs. temperature curve}$$

$$\beta = \frac{T_{min}}{T_{ref} - T_{min}} = \text{y-intercept of growth vs. temperature curve}$$

This equation is typically used in simplified form by choosing a lower temperature limit T_{min} equal to zero so that Equation (6-5) becomes:

$$f(T) = \frac{T}{T_{ref}} \tag{6-6}$$

Reference temperatures of either $20^{o}C$ or $1^{o}C$ are usually used which results in:

$$f(T) = \frac{T}{20} \tag{6-7}$$

or

$$f(T) = T \tag{6-8}$$

This approach is used in EXPLORE-I (Baca et al., 1973) and RECEIV-II (Raytheon, 1974) and by Di Toro et al. (1971) in an early version of WASP.

Some models use piecewise linear functions for algal growth with different slopes over different temperature ranges (Bierman et al., 1980; Canale et al., 1975, 1976). HSPF (Johanson et al., 1980) uses Equation (6-5) over the temperature range between T_{min} and the optimum temperature for maximum growth T_{opt}, followed by a constant temperature function above T_{opt}:

$$f(T) = \left(\frac{1}{T_{opt} - T_{min}}\right) T - \left(\frac{T_{min}}{T_{opt} - T_{min}}\right) \quad \text{for } T \leq T_{opt} \tag{6-9a}$$

$$f(T) = 1 \quad \text{for } T > T_{opt} \tag{6-9b}$$

with $$\mu_{max}(T_{ref}) = \mu_{max}(T_{opt}) \quad (6\text{-}9c)$$

where T_{opt} = optimum temperature at which the growth rate is maximum, ^{o}C

This assumes growth increases linearly with temperature until the maximum growth rate is attained, and then remains at the maximum rate as temperature increases further.

The most commonly used exponential temperature adjustment functions are based on the Arrhenius or van't Hoff equation:

$$Q_{10} = \left(\frac{K_2}{K_1}\right)^{\left(\frac{10}{T_2-T_1}\right)} \quad (6\text{-}10)$$

where K_1 = reaction rate at temperature T_1
K_2 = reaction rate at temperature T_2
Q_{10} = ratio of reaction rates at $10^{o}C$ temperature increments

This equation can be rearranged into a more useful form as:

$$K_2 = K_1\ Q_{10}^{\left(\frac{T_2-T_1}{10}\right)} \quad (6\text{-}11)$$

or
$$K(T) = K(T_{ref})\ Q_{10}^{\left(\frac{T-T_{ref}}{10}\right)} \quad (6\text{-}12)$$
$$= K(T_{ref})\ f(T)$$

where f(T) is the temperature adjustment function:

$$f(T) = Q_{10}^{\left(\frac{T-T_{ref}}{10}\right)} \quad (6\text{-}13)$$

The temperature adjustment function (Equation (6-13)) is generally expressed in a more simplified form as:

$$f(T) = Q_{10}^{(1/10)(T-T_{ref})} \qquad (6\text{-}14)$$

$$= \theta^{(T-T_{ref})}$$

where $\theta = Q_{10}^{(1/10)}$ = temperature adjustment coefficient

The temperature adjustment coefficient θ typically has a value between 1.01 and 1.2, with a value of 1.072 corresponding to a doubling of the growth rate for every $10^{o}C$ increase in temperature. Eppley (1972) found that θ equals 1.066 for an exponential envelope curve of growth rate versus temperature data compiled from a large number of studies involving many different species (Figure 6-2).

Most models which use exponential temperature functions assume a reference temperature of $20^{o}C$ which gives the familiar equation (Chen and Orlob, 1975; Baca and Arnett, 1976; Roesner et al., 1981; Brandes and Masch, 1977; Duke and Masch, 1973; Thomann et al., 1979; Thomann and Fitzpatrick, 1982; Di Toro and Matystik, 1980; Di Toro and Connolly, 1980; O'Connor et al., 1981):

$$f(T) = \theta^{(T-20^{o}C)} \qquad (6\text{-}15a)$$

with $$\mu_{max}(T_{ref}) = \mu_{max}(20^{o}C) \qquad (6\text{-}15b)$$

However, Thomann et al. (1975) and Eppley (1972) use a reference temperature of $0^{o}C$ which results in:

$$f(T) = \theta^{T} \qquad (6\text{-}16a)$$

with $$\mu_{max}(T_{ref}) = \mu_{max}(0^{o}C) \qquad (6\text{-}16b)$$

The above equations assume that the temperature adjustment coefficient θ has the same value regardless of the reference temperature. However, a few models have applied Equation (6-14) in a piecewise manner assuming that the value of θ varies over different temperature intervals.

Many formulations have been used to generate temperature optimum curves for algal growth. The reference temperature is generally set at the optimum temperature for maximum growth, and the temperature adjustment function is normalized so it has a maximum value of 1.0 at the optimum temperature and smaller values elsewhere. Most curves begin with a zero value at the lower temperature tolerance limit, increase to a maximum value of 1.0 at the optimum temperature, and then decrease back to a value of zero at the upper temperature tolerance limit. These types of curves are typically based on growth vs. temperature data for a single species. These data generally show no growth at very low temperatures followed by an exponential increase in

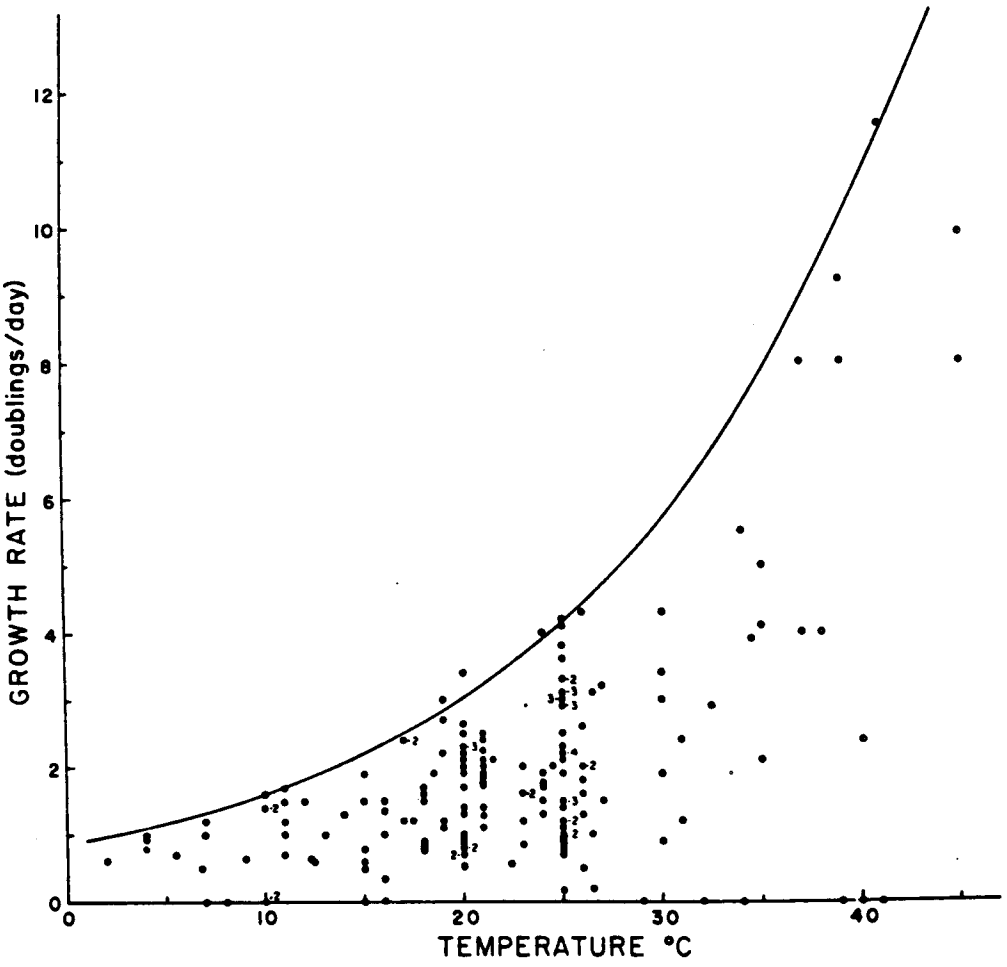

Figure 6-2. Envelope curve of algal growth rate versus temperature for data compiled from many studies involving many different species (adapted from Eppley, 1972; Goldman, 1981).

growth with temperature over a large part of the temperature range. However, the growth rate eventually levels off to some maximum value at the optimum temperature, and then begins to decline at very high temperatures until growth finally ceases at some upper temperature limit.

Lehman et al. (1975) use a skewed normal distribution as a temperature optimum curve for phytoplankton growth. The equation is:

$$f(T) = \exp\left[-2.3\left(\frac{T - T_{opt}}{T_x - T_{opt}}\right)^2\right] \tag{6-17a}$$

with $$\mu_{max}(T_{ref}) = \mu_{max}(T_{opt}) \tag{6-17b}$$

where T_{opt} = optimum temperature at which the growth rate is maximum, ^oC

T_x = T_{min} for $T \leq T_{opt}$
= T_{max} for $T > T_{opt}$

T_{min} = lower temperature limit at which the growth rate is zero, ^oC

T_{max} = upper temperature tolerance limit at which growth ceases, ^oC

Jorgensen (1976) and Jorgensen et al. (1978) use a modified form of Equation (6-17a) which is expressed as:

$$f(T) = \exp\left(-2.3\left|\frac{T - T_{opt}}{T_{opt} - T_{min}}\right|\right) \tag{6-18}$$

Several models including CLEAN (Bloomfield et al., 1973), CLEANER (Scavia and Park, 1976), MS.CLEANER (Park et al, 1979, 1980), and Scavia et al. (1976) use a temperature optimum function originally developed by Shugart et al. (1974). This formulation can be expressed as:

$$f(T) = V^x e^{x(1-V)} \tag{6-19a}$$

$$V = \frac{T_{max} - T}{T_{max} - T_{opt}} \qquad (6\text{-}19b)$$

$$x = \left[\frac{W\,(1 + \sqrt{1 + 40/W})}{20} \right]^2 \qquad (6\text{-}19c)$$

$$W = (\ln Q_{10})\,(T_{max} - T_{opt}) \qquad (6\text{-}19d)$$

with $$\mu_{max}(T_{ref}) = \mu_{max}(T_{opt}) \qquad (6\text{-}19e)$$

where Q_{10} is defined as in Equations (6-10) through (6-14).

The temperature function in Equations (6-19a) through (6-19e) has been modified in the ecosystem model MS.CLEANER by adding a temperature adaption formulation which essentially shifts the whole curve by varying the values of T_{opt} and T_{max} to account for acclimation to different temperatures (Park et al., 1980). This formulation was originally developed by O'Neill (1972), and can be expressed as:

$$T_{shift} = T_{smax}\left[1 - e^{-K_{ac}|T_{avg} - T_{opt}|}\right] \qquad (6\text{-}20)$$

where T_{shift} = magnitude of acclimation (translation of T_{opt} and T_{max}), ^{o}C

T_{smax} = maximum magnitude of acclimation, ^{o}C

K_{ac} = acclimation rate coefficient

T_{avg} = average temperature for previous 2 weeks, ^{o}C

Lassiter and Kearns (1973) and Lassiter (1975) developed a temperature optimum equation of the form:

$$f(T) = \left(e^{K_a(T-T_{opt})}\right)\left(\frac{T_{max} - T}{T_{max} - T_{opt}}\right)^{K_a(T_{max}-T_{opt})} \qquad (6\text{-}21a)$$

with $$\mu_{max}(T_{ref}) = \mu_{max}(T_{opt}) \qquad (6\text{-}21b)$$

where K_a = a scaling constant used in the original equation from which Equation (6-21a) was derived,

$$\frac{df(T)}{dt} = K_a \left(\frac{T_{max} - T}{T_{max} - T_{opt}} \right) \tag{6-21c}$$

These equations result in a temperature optimum curve which is always skewed to the right.

Thornton and Lessem (1978) developed a temperature optimum curve by combining two logistic equations, one describing the rising limb of the curve below the optimum temperature and one describing the falling limb of the curve above the optimum temperature. The second curve is rotated about the y-axis and shifted to the right along the x-axis until the approximate peaks of both curves coincide. The left side of the temperature curve is expressed as:

$$K_A(T) = \frac{K_1 \, e^{\gamma_1 (T - T_{min})}}{1 + K_1 \left[e^{\gamma_1 (T - T_{min})} - 1 \right]} \tag{6-22a}$$

$$\gamma_1 = \frac{1}{(T_{opt(1)} - T_{min})} \ln \left[\frac{K_2 \, (1 - K_1)}{K_1 \, (1 - K_2)} \right] \tag{6-22b}$$

and the right side is expressed as:

$$K_B(T) = \frac{K_4 \, e^{\gamma_2 (T_{max} - T)}}{1 + K_4 \left[e^{\gamma_2 (T_{max} - T)} - 1 \right]} \tag{6-23a}$$

$$\gamma_2 = \frac{1}{(T_{max} - T_{opt(2)})} \ln \left[\frac{K_3 \, (1 - K_4)}{K_4 \, (1 - K_3)} \right] \tag{6-23b}$$

where $T_{opt(1)}$ = lower limit of optimum temperature range, ^{o}C
$T_{opt(2)}$ = upper limit of optimum temperature range, ^{o}C
γ_1 = rate coefficient for left side of curve
γ_2 = rate coefficient for right side of curve
K_1 = rate multiplier near the lower temperature limit T_{min}
K_4 = rate multiplier near the upper temperature limit T_{max}
K_2 = 0.98
K_3 = 0.98

The temperature curve is defined as the product of Equations (6-22a) and (6-23a):

$$f(T) = K_A(T)\ K_B(T) \qquad (6\text{-}24a)$$

with

$$\mu_{max}(T_{ref}) = \mu_{max}(T_{opt}) \qquad (6\text{-}24b)$$

By using different values of the logistic equation parameters for each side, an assymmetric growth curve can be generated. The values of K_2 and K_3 are set equal to 0.98 rather than 1.0 so that the peak of the combined logistic equation is close to 1.0 (since the logistic equation would otherwise only approach 1.0 assymptotically). Two values of the optimum temperature, $T_{opt(1)}$ and $T_{opt(2)}$, are used to allow an optimum temperature range, rather than a single optimum temperature value. This formulation is used in CE-QUAL-R1 (WES, 1982), WQRRS (Smith, 1978), and EAM (Tetra Tech, 1979, 1980). The left side of the curve (the basic logistic equation, Equation (6-22a)) is also used as a temperature adjustment curve in SSAM IV (Grenney and Kraszewski, 1981).

The MIT one-dimensional network model (Najarian and Harleman, 1975; Harleman et al., 1977) uses a temperature optimum curve which is defined as:

$$f(T) = \left(\frac{T}{T_{opt}}\right)^n \exp\left[1 - \left(\frac{T}{T_{opt}}\right)^n\right] \qquad \text{for } T < T_{opt} \qquad (6\text{-}25a)$$

and $$f(T) = 1 - \left(\frac{T - T_{opt}}{T_{max} - T_{opt}}\right)^m \quad \text{for } T > T_{opt} \qquad (6\text{-}25b)$$

with $$\mu_{max}(T_{ref}) = \mu_{max}(T_{opt}) \qquad (6\text{-}25c)$$

The values of the exponents n and m are 2.5 and 2.0, respectively (Najarian and Harleman, 1975).

Some type of temperature optimum curve is generally more appropriate than a linear or exponential formulation when considering a single algal species or functional group, since growth usually slows down and eventually ceases above some upper temperature limit for any given species. This approach is used in most models which simulate several algal groups (e.g., Chen et al., 1975; Tetra Tech, 1979, 1980; Park et al., 1979, 1980; Canale et al., 1975, 1976; Scavia et al., 1976; Lehman et al., 1975; Smith, 1978; WES, 1982), since seasonal variation in temperature is one of the major factors causing seasonal succession in the dominance of different groups (diatoms, greens, blue-greens, etc.). However, since many species are lumped into a few functional groups, the temperature optimum curves and maximum growth rates should be defined so that they encompass the temperature-growth curves of all dominant species in the defined groups. Canale and Vogel (1974) developed a set of temperature-growth curves for diatoms, green algae, blue-green algae, and flagellates based on a literature review of growth data for many species (Figure 6-3).

Since the temperature function includes both the effects of increasing temperature on the growth rates of many individual species as well as shifts in the species composition toward dominance by warmer water species, some modelers have preferred to use exponential or linear formulations over the whole temperature range, particularly when only one or two groups are simulated (Chen and Orlob, 1975; Thomann et al., 1979; Di Toro and Matystik, 1980; Di Toro and Connolly, 1980; Nyholm, 1978). This assumes that as temperature increases, the species composition changes so that species with optimum temperatures near the ambient temperature (and with

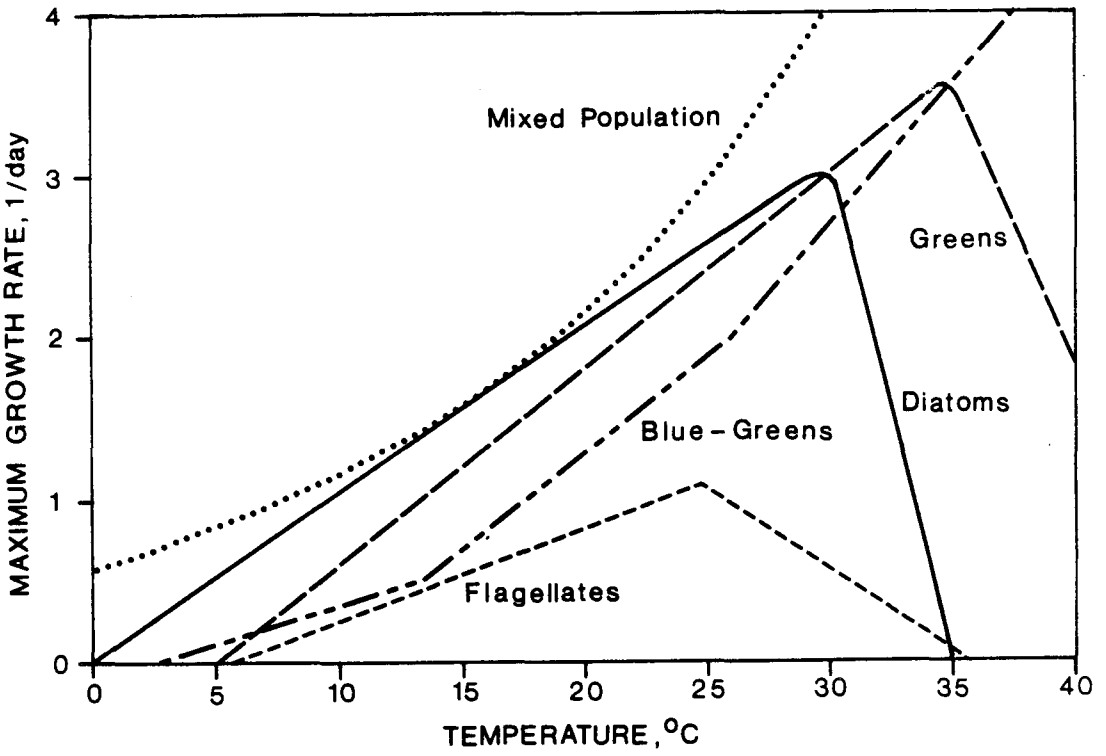

Figure 6-3. Temperature-growth curves for major algal groups (from Canale and Vogel, 1974).

higher maximum growth rates) tend to dominate the phytoplankton assemblage. Eppley (1972) showed that an exponential relationship describes the envelope curve of growth rate versus temperature data from a large number of studies with many different species (Figure 6-2). However, this approach may overestimate the net growth of the assemblage if the growth rates are based on the maximum growth rate of the species assumed to be dominant at any given instant, since much of the biomass will include species which predominated earlier under different temperature conditions (Swartzman and Bentley, 1979). Exponential or linear functions which increase indefinitely with temperature can also be justified in situations where the maximum water temperatures are always below the optimum temperatures for the species present. For example, Canale and Vogel (1974) assumed a linear relationship below the temperature optimum for each algal group in Figure 6-3.

The temperature formulations used in different models are compared in Table 6-6.

TABLE 6-6. COMPARISON OF TEMPERATURE ADJUSTMENT FUNCTIONS FOR ALGAL GROWTH

Model (Author)	Temperature Formulation (Equation No.)				Reference Temperature	Reference
	Linear	Exponential	Optimum Curve	Other Curve		
AQUA-IV		6-14			20°C	Baca & Arnett (1976)
CE-QUAL-R1			6-24		T_{opt}	WES (EWQOS) (1982)
CLEAN			6-19		T_{opt}	Bloomfield et al. (1973)
CLEANER			6-19		T_{opt}	Scavia & Park (1976)
MS.CLEANER			6-19		T_{opt}	Park et al. (1980)
DEM		6-14			20°C	Feigner & Harris (1970)
DOSAG3		6-14			20°C	Duke & Masch (1973)
EAM			6-24		T_{opt}	Tetra Tech (1979, 1980)
ESTECO		6-14			20°C	Brandes & Masch (1977)
EXPLORE-1	6-6				1°C	Baca et al. (1973)
HSPF				piecewise linear saturation		Johanson et al. (1980)
LAKECO		6-14			20°C	Chen & Orlob (1975)
MIT Network			6-25		T_{opt}	Harleman et al. (1977)
QUAL-II		6-14			20°C	Roesner et al. (1981)
RECEIV-II	6-6				1°C	Raytheon (1974)
SSAM IV				logistic equation	20°C	Grenney & Kraszewski (1981)
WASP		6-14			20°C	Di Toro et al. (1981)
WQRRS			6-24		T_{opt}	Smith (1978)
Bierman	piecewise linear			piecewise linear saturation		Bierman et al. (1980)
Canale	piecewise linear				1°C	Canale et al. (1975, 1976)
Jorgensen			6-18		T_{opt}	Jorgensen (1976)
Lehman			6-17		T_{opt}	Lehman et al. (1975)
Nyholm		6-14			20°C	Nyholm (1978)
Scavia			6-19		T_{opt}	Scavia et al. (1976)

6.4.2 Algal Growth Limitation

In addition to temperature effects, algal growth rates are limited by both light and nutrient availability. As mentioned above, only macronutrients (phosphorous, nitrogen, carbon, and silicon) are generally included in models. Growth limitation was expressed previously as the factor f(L,P,N,C,Si) in the algal growth equation:

$$\mu = \mu_{max}(T_{ref})\ f(T)\ f(L,P,N,C,Si) \qquad (6\text{-}4)$$

Separate growth limiting factors are typically computed for light and each potentially limiting nutrient. The number of nutrients considered will vary between models depending on the particular system under consideration. Each growth limitation factor can range from a value of 0 to 1. A value of 1 means the factor does not limit growth (i.e., light is at optimum intensity, nutrients are available in excess, etc.) and a value of 0 means the factor is so severely limiting that growth is stopped entirely.

Four major approaches have been used to combine the limiting factors for light and each limiting nutrient:

1) a multiplicative formulation in which all factors are multiplied together:

$$f(L,P,N,C,Si) = f(L)\ f(P)\ f(N)\ f(C)\ f(Si) \qquad (6\text{-}26)$$

where f(L) = light limitation factor
f(P) = nutrient limitation factor for phosphorous
f(N) = nutrient limitation factor for nitrogen
f(C) = nutrient limitation factor for carbon
f(Si) = nutrient limitation factor for silicon (for diatoms)

2) a minimum formulation in which the most severely limiting factor alone is assumed to limit growth:

$$f(L,P,N,C,Si) = \min \left[f(L), f(P), f(N), f(C), f(Si) \right] \qquad (6\text{-}27)$$

where $\min \left[x_1, x_2, x_3, \ldots \right]$ = minimum of each factor x_i

3) a harmonic mean formulation which combines the reciprocal of each limiting factor in the following manner:

$$f(L,P,N,C,Si) = \frac{n}{\frac{1}{f(L)} + \frac{1}{f(P)} + \frac{1}{f(N)} + \frac{1}{f(C)} + \frac{1}{f(Si)}} \qquad (6\text{-}28)$$

where n = number of limiting factors (5 in this case)

4) an arithmetic mean formulation which uses the average of each limiting factor:

$$f(L,P,N,C,Si) = \frac{f(L) + f(P) + f(N) + f(C) + f(Si)}{n} \qquad (6\text{-}29)$$

The multiplicative formulation has been used in many models (Chen and Orlob, 1972, 1975; Di Toro et al., 1971, 1977; Di Toro and Matystik, 1980; Di Toro and Connolly, 1980; Thomann et al., 1975, 1979; O'Connor et al., 1975; Jorgensen, 1976; Jorgensen et al., 1978; Canale et al., 1975, 1976; Lehman et al., 1975; Roesner et al., 1981; Baca et al., 1973; Duke and Masch, 1973; Brandes and Masch, 1977). This approach assumes that several nutrients in short supply will more severely limit growth than a single nutrient in short supply. The major criticism of this approach is that the computed growth rates may be excessively low when several nutrients are limiting. Also, the severity of the reduction increases with the number of limiting nutrients considered in the model, making comparison between models difficult. Many models assume that light limitation is multiplicative, but use one of the other approaches for nutrient limitation (e.g., Bierman et al., 1980; Bierman, 1976; Baca and Arnett, 1976; Nyholm, 1978; Raytheon, 1974).

The minimum formulation is based on "Liebig's law of the minimum" which states that the factor in shortest supply will control the growth of algae.

This approach has been popular in many recent algal models (Bierman et al., 1980; Park et al., 1979, 1980; Scavia, 1980; Smith 1978; Tetra Tech, 1979, 1980; WES, 1982; Johanson et al., 1980; Grenney and Kraszewski, 1981; Chen et al., 1975; Baca and Arnett, 1976). The minimum formulation is often used only for nutrient limitation, with a multiplicative formulation for the light limitation factor.

The harmonic mean formulation is based on an electronic analogy of several resistors in series. The rationale for this formulation is that it includes some interaction between multiple limiting nutrients, but it is not as severely limiting as the multiplicative formulation. This approach has been used in only a few models, for example, the original CLEAN (Bloomfield et al., 1973) and CLEANER (Scavia and Park, 1976) models and Nyholm (1978). The current version of MS.CLEANER (Park et al., 1980) has abandoned this formulation in favor of the minimum formulation. In fact, the harmonic mean formulation and minimum formulation produce similar growth response curves under a wide range of conditions (Swartzman and Bentley, 1979).

The rationale for the arithmetic mean formulation is the same as for the harmonic mean formulation (i.e., it considers the effects of multiple nutrient limitation, but is not as severely limiting as the multiplicative formulation). However, this formulation (e.g., Patten, 1975; Patten et al., 1975) is rarely used since it does not restrict growth enough. For example, the arithmetic mean formulation allows growth even if a critical nutrient such as phosphorus is totally absent, as long as other nutrients are available.

These and other formulations for combining multiple growth limitation factors are reviewed in De Groot (1983).

6.4.3 Light Limitation

Light limitation formulations consist of two components: 1) a relationship describing the attenuation of light with depth and the effect

of algae on light attenuation, and 2) a relationship defining the effect of the resulting light levels on algal growth and photosynthesis.

The attenuation of light with depth is defined in essentially all models by the Beer-Lambert law:

$$I(z) = I_0 \, e^{-\gamma z} \tag{6-30}$$

where $I(z)$ = light intensity at depth z below the surface
z = depth, length
I_0 = light intensity at the surface
γ = light extinction coefficient, 1/length

The light intensity at the surface I_0 is a function of location, time of year, time of day, meterological conditions, and shading from topographic features or riparian vegetation. The surface light intensity used in the algal growth formulations corresponds only to the visible range, which is typically about 50 percent of the total surface solar radiation used in the heat budget computations. Almost all radiation outside of the visible range is absorbed within the first meter below the surface (Orlob, 1977). In addition, some models (for example, MS. CLEANER) assume that only a portion of the visible radiation (about 50%) is available for photosynthesis (Park et al., 1980; Strickland, 1958).

Light attenuation in models differs primarily in the way the light extinction coefficient γ is formulated. The simplest approach is to assume a constant value of γ. This approach is reasonable for short term simulations or over periods when turbidity does not change significantly. However, in long term simulations, γ should be computed dynamically to account for seasonal variations in turbidity due to algal shading or variations in suspended solids loads.

The light extinction coefficient is most commonly defined as the linear sum of several extinction coefficients representing each component of light absorption. The components include all suspended particulates

(phytoplankton, zooplankton, organic and inorganic particulates) as well as dissolved organic matter. The general equation is:

$$\gamma = \gamma_0 + \sum_{i=1}^{n} \gamma_i \tag{6-31}$$

$$= \gamma_0 + \sum_{i=1}^{n} a_i C_i \tag{6-32}$$

where γ_0 = base light extinction coefficient for water without particulates or dissolved organic matter, 1/length

γ_i = light extinction coefficient corresponding to each component of light absorption i, 1/length

n = total number of absorption components considered in the formulation

C_i = concentration of absorption component i, mass/volume

a_i = coefficient for absorption component i relating the concentration C_i to the light extinction coefficient γ_i

Many models include the effects of all components except phytoplankton in the base extinction coefficient γ_0 (by assigning a higher value), and then compute the temporal variations in γ as a function of the algal densities only. This assumes phytoplankton blooms are the major cause of turbidity changes. Equation (6-32) then becomes:

$$\gamma = \gamma_0 + a_1 A \tag{6-33}$$

where γ_0 = light extinction coefficient for all absorption components but phytoplankton, 1/length

a_1 = coefficient relating the phytoplankton concentration A to the corresponding light extinction coefficient for phytoplankton (also called the self-shading factor), 1/(length-mass/volume)

A = phytoplankton concentration, mass/volume

This provides a way of incorporating self-shading effects in the light limitation portion of the algal growth formulation. Some models which use this approach use a nonlinear formulation to describe the relationship between the phytoplankton concentration and the light extinction coefficient. The general expression is:

$$\gamma = \gamma_0 + a_1 A + a_2 A^{b_2} \qquad (6\text{-}34)$$

where a_1, a_2 = coefficients of the equation relating phytoplankton concentrations to the light extinction coefficient

b_2 = exponent of the equation relating phytoplankton concentrations to the light extinction coefficient

The second component of the light limitation formulation represents the light limitation factor f(L) in Equations (6-26) through (6-29). f(L) defines the relationship between ambient light levels and algal growth rates or rates of photosynthesis. Essentially all formulations fall into one of two major categories (Figure 6-4): 1) saturation type relationships in which the growth rate increases linearly with light at low intensities, but gradually levels off at high intensities to reach a maximum value at the optimum (or saturating) light intensity, or 2) photoinhibition relationships which are similar to the above curves below the optimum light intensity, but which predict decreases in growth rates above the optimum intensity due to photoinhibition effects.

Saturation type responses are typically described by either a Michaelis-Menten (1913) type relationship (Chen and Orlob, 1975; Jorgensen, 1976; Duke and Masch, 1973; Tetra Tech, 1979; Roesner et al., 1981; Johanson et al., 1980; Smith, 1978; WES, 1982):

$$f(L) = \frac{I}{K_L + I} \qquad (6\text{-}35)$$

where f(L) = light limitation function for algal growth

I = light intensity

K_L = half-saturation constant defining the light level at which growth is one-half the maximum rate

or a Smith (1936) formulation (Park et al., 1980):

$$f(L) = \frac{a_1 I}{\sqrt{1 + (a_1 I)^2}} \qquad (6\text{-}36)$$

where a_1 = constant in the Smith formulation ($1/a_1$ is the slope of the linear portion of the photosynthesis vs. light curve), 1/light

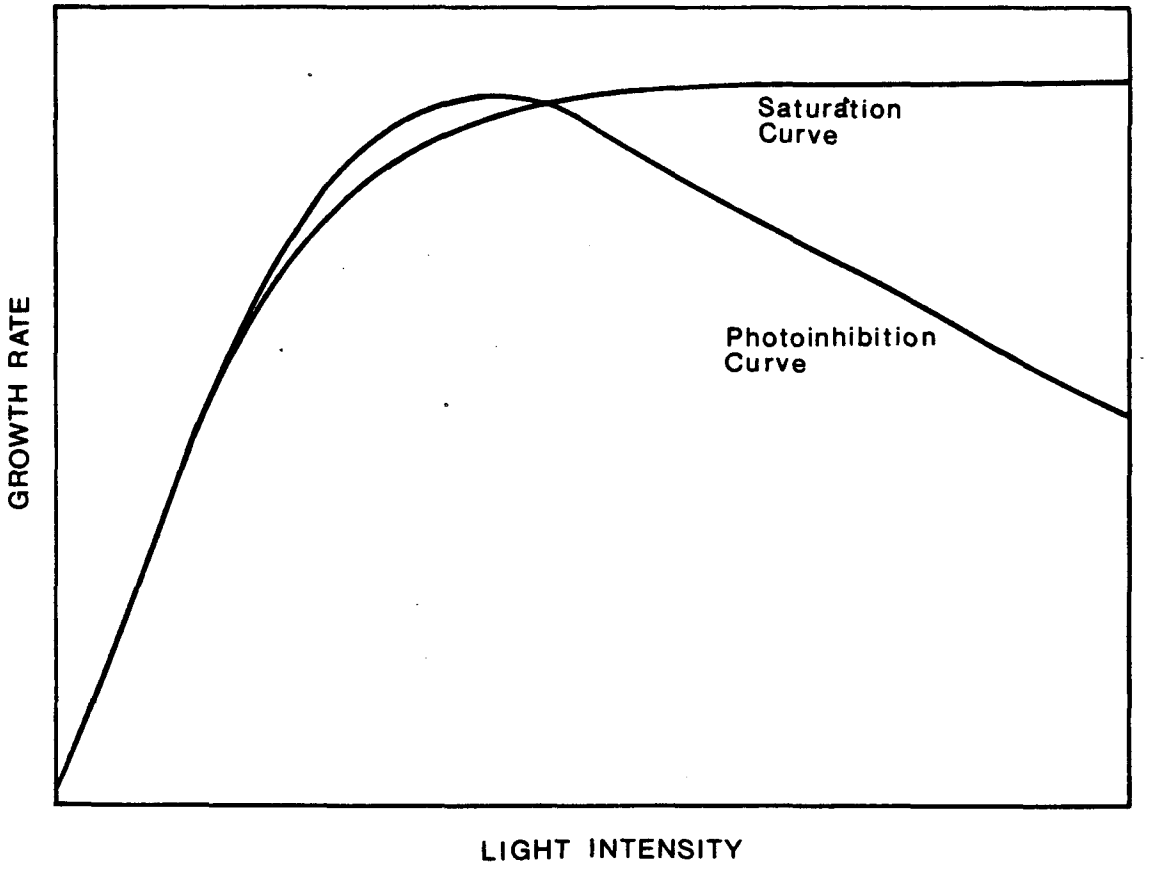

Figure 6-4. Comparison of light response curves for algal growth.

Vollenweider (1965) modified the Smith formulation to give a more general relationship of which the Smith equation is a special case. The Vollenweider form includes photoinhibition effects, and is expressed as:

$$f(L) = \left(\frac{a_1 I}{\sqrt{1 + (a_1 I)^2}}\right)\left(\frac{1}{\sqrt{(1 + (a_2 I)^2)^n}}\right) \qquad (6\text{-}37)$$

where a_2 = photoinhibition factor, 1/light
n = exponent

Baca and Arnett (1976) use this formulation in AQUA-IV with the exponent n equal to 1.

The most commonly used photoinhibition relationship is the Steele (1965) formulation:

$$f(L) = \frac{I}{I_s} e^{\left(1 - \frac{I}{I_s}\right)} \qquad (6\text{-}38)$$

where I_s = optimum (saturating) light intensity

This formulation is used in many models including Di Toro et al. (1971, 1977), Di Toro and Matystik (1980), Di Toro and Connolly (1980), Thomann et al. (1975, 1979), Thomann and Fitzpatrick (1982), O'Connor et al. (1981), Bloomfield et al. (1973), Park et al. (1974, 1975, 1979, 1980), Scavia et al. (1976), Najarian and Harleman (1975), Bierman et al. (1980), Canale et al. (1975, 1976), Lehman et al. (1975), and Baca et al. (1973).

Park et al. (1980) use the Steele formulation above the saturating light intensity I_s and the Smith formulation below I_s. They feel that the Steele formulation is not accurate below the inhibition threshold since the predicted photosynthesis response is partially dependent on the response above the threshold (Park et al., 1979). Under non-inhibiting light

conditions, this may result in a light limitation factor which is too low (Groden, 1977).

Walker (1975) found that the Steele formulation underpredicts photosynthesis rates at high light intensities (above saturation) for some algae, so he modified it by adding an additional parameter n:

$$f(L) = \left(\frac{I}{I_s}\right)^n e^{\left[1 - \left(\frac{I}{I_s}\right)^n\right]} \qquad (6\text{-}39)$$

where n = parameter for modified Steele formulation

This parameter adjusts the rate of decline of the photosynthesis vs. light curve for light intensities above and below the optimum. The original Steele formulation assumes n=1, while Walker used n values of 0.67, 0.80, and 1.0 for three different algal groups.

A few models include light adaptation algorithms in their light limitation formulations to account for the fact that algae adapted to low light levels have a more rapid response to changing light conditions (steeper slope of photosynthesis vs. light curve) than algae adapted to high light levels. Algae adapt to changing light conditions by varying the chlorophyll content of their cells, with algae adapted to lower light intensities having more chlorophyll.

Nyholm (1978) simulates this effect by varying the value of the saturating light intensity at different times of the year to shift the peak of the light limitation function f(L). The I_s values are maximum during summer and minimum during winter. This shifts the slope of the light response curve so it is steepest during the winter when the algae are adapted to low light levels.

Groden (1977) developed a more complicated formulation for the MS.CLEANER model which dynamically computes the slope of the photosynthesis

vs. light curve as a function of light intensity, and then uses this information to compute the saturating light intensity as a function of both light and temperature. The equation for the slope of the photosynthesis vs. light curve in the light inhibited range is:

$$\alpha = K_1 \ln(I) - K_2 \tag{6-40}$$

where α = slope of photosynthesis vs. light curve

K_1, K_2 = constants

This is based on the assumptions that 1) the slope α is a linear function of the chlorophyll content of the cells and 2) chlorophyll decreases exponentially with light intensity until it reaches some minimum value (Groden, 1977). The values of K_1 and K_2 used in MS.CLEANER are 0.1088 and 0.0704, respectively (Groden, 1977; Park et al., 1980). The equation for the saturating light intensity is:

$$I_s = \frac{\mu_{max}(T_{ref})\ f(T)\ e}{\alpha} \tag{6-41}$$

$$= \frac{\mu_{max}(T_{ref})\ f(T)\ e}{K_1 \ln(I) - K_2}$$

Smith (1980) developed a formulation for computing the saturating light intensity as a function of the maximum photosynthetic quantum yield, maximum growth rate, temperature, light extinction coefficient per unit chlorophyll, and the carbon to chlorophyll ratio of the algae. The equation is:

$$I_s = \frac{\mu_{max}(T_{ref})\ f(T)\ C_r\ e}{\phi_{max}\ a_c} \tag{6-42}$$

where C_r = carbon to chlorophyll ratio

ϕ_{max} = maximum photosynthetic quantum yield, moles carbon fixed/mole photons absorbed

a_c = coefficient for light extintion per unit chlorophyll, 1/(length-mass chlorophyll/volume)

The effects of light adaptation are included in the carbon to chlorophyll ratio C_r. This ratio typically ranges from 20 to 100, with 20 corresponding to low-light, high-temperature conditions, and 100 corresponding to high-light, low-temperature conditions (Smith, 1980; Eppley, 1972). Based on observations that the maximum photosynthesis rate typically occurs at the depth where the light intensity is about 30 percent of the surface value ($I_s = 0.3\ I_0$), Smith (1980) suggested the following relationship for estimating C_r as a function of the ambient light levels:

$$C_r = \frac{0.3\ \bar{I}_0\ \phi_{max}\ a_c}{\mu_{max}(T_{ref})\ f(T)\ e} \qquad (6\text{-}43)$$

$$= \frac{0.11\ \bar{I}_0\ \phi_{max}\ a_c}{\mu_{max}(T_{ref})\ f(T)}$$

where $\bar{I}_0$ = daily average light intensity at the surface

These formulations are used by Thomann and Fitzpatrick (1982) in the Potomac Estuary version of WASP. One advantage of this approach is that I_s and C_r are defined in terms of parameters which are well documented in the literature (ϕ_{max}, μ_{max}, a_c), and which have a fairly narrow range of values over a wide range of environmental conditions.

All of the above relationships for the light limitation factor f(L) have been used to fit experimental measurements of the effects of light on photosynthesis under laboratory conditions. However, in water quality models, these expressions are generally integrated over the depth of each model segment or layer since light varies with depth due to attenuation. The light attenuation formulations (Equations (6-30) through (6-34)) are substituted for the light intensity I in the light limitation formulations (Equations (6-35) through (6-39)), and the light limitation functions are integrated and depth averaged.

Since light also varies continuously with time, most models integrate the light limitation function f(L) over 24 hours to get a daily average value for a given time of the year and set of meteorological conditions. This is generally approximated by multiplying the light limitation function by the photoperiod (expressed as the fraction of the day in which the sun is out) and by using the average light intensity during the daylight hours as I_o in the formulation. This approach is used in steady-state models and dynamic models which use daily time steps. The alternative approach when short time steps (minutes to hours) are used is to compute the light limitation and algal growth formulations dynamically throughout the day using instantaneous values of I_o. The latter method simulates the diurnal variations in algal photosynthesis.

The depth and time integrated Michaelis-Menten formulation for light limitation (Equation (6-35)) is expressed as:

$$f(L) = \frac{f_p}{\gamma d} \ln\left(\frac{K_L + I_o}{K_L + I_o e^{-\gamma d}}\right) \qquad (6\text{-}44)$$

where f_p = photoperiod (expressed as a fraction of the day)
d = water depth, length
I_o = average light intensity at the surface during the daylight hours

when averaged over the whole water depth or as:

$$f(L) = \frac{f_p}{\gamma (z_2 - z_1)} \ln\left(\frac{K_L + I_o e^{-\gamma z_1}}{K_L + I_o e^{-\gamma z_2}}\right) \qquad (6\text{-}45)$$

where z_1 = depth at top of layer, length
z_2 = depth at bottom of layer, length

when averaged over a single layer (for example, in a vertically segmented lake model).

The analogous expressions for the Smith formulation (Equation (6-36)) are:

$$f(L) = \frac{f_p}{\gamma d} \ln \left[\frac{a_1 I_o + \sqrt{1 + (a_1 I_o)^2}}{a_1 I_o e^{-\gamma d} + \sqrt{1 + (a_1 I_o e^{-\gamma d})^2}} \right] \quad (6\text{-}46)$$

and

$$f(L) = \frac{f_p}{\gamma (z_2 - z_1)} \ln \left[\frac{a_1 I_o e^{-\gamma z_1} + \sqrt{1 + (a_1 I_o e^{-\gamma z_1})^2}}{a_1 I_o e^{-\gamma z_2} + \sqrt{1 + (a_1 I_o e^{-\gamma z_2})^2}} \right] \quad (6\text{-}47)$$

For the Steele formulation (Equation (6-38)), the depth and time integrated expressions are:

$$f(L) = \frac{2.718\, f_p}{\gamma d} \left(e^{-\frac{I_o}{I_s} e^{-\gamma d}} - e^{-\frac{I_o}{I_s}} \right) \quad (6\text{-}48)$$

and

$$f(L) = \frac{2.718\, f_p}{\gamma (z_2 - z_1)} \left(e^{-\frac{I_o}{I_s} e^{-\gamma z_2}} - e^{-\frac{I_o}{I_s} e^{-\gamma z_1}} \right) \quad (6\text{-}49)$$

Light limitation factors are compared for several models in Table 6-7. Saturating light intensities and half-saturation constants for light limitation are presented in Tables 6-8 and 6-9.

6.4.4 Nutrient Limitation

Two major approaches have been used to compute nutrient limitation factors in algal models. The first approach is based on Monod (1949) or Michaelis-Menten (1913) kinetics and assumes that the growth rates are determined by the external concentrations of available nutrients. External here refers to the nutrient concentrations in the water column as opposed to the internal concentrations in the algal cells. This approach assumes the nutrient composition of the algal cells remains constant, and is generally referred to as fixed stoichiometry models.

TABLE 6-7. COMPARISON OF LIGHT LIMITATION FORMULATIONS

Model (Author)	Light Limitation Formulation					Reference
	Steele	Smith	Michaelis-Menten	Vollenweider	Other	
AQUA-IV				X		Baca & Arnett (1976)
CE-QUAL-R1			X			WES (EWQOS) (1982)
CLEAN	X					Bloomfield et al. (1973)
CLEANER	X					Scavia & Park (1976)
MS.CLEANER	X*	X*				Park et al. (1980)
DEM			X			Feigner & Harris (1970)
DOSAG3			X			Duke & Masch (1973)
EAM			X			Tetra Tech (1979, 1980)
ESTECO			X			Brandes & Masch (1977)
EXPLORE-1	X					Baca et al. (1973)
HSPF			X			Johanson et al. (1980)
LAKECO			X			Chen & Orlob (1975)
MIT Network	X					Harleman et al. (1977)
QUAL-II			X			Roesner et al. (1981)
RECEIV-II	X					Raytheon (1974)
SSAM IV					none	Grenney & Kraszewski (1981)
WASP	X					Di Toro et al. (1981)
WQRRS			X			Smith (1978)
Bierman	X					Bierman et al. (1980)
Canale	X					Canale et al. (1975, 1976)
Jorgensen			X			Jorgensen (1976)
Lehman	X					Lehman et al. (1975)
Nyholm					piecewise linear saturation	Nyholm (1978)
Scavia	X					Scavia et al. (1976)

*Smith formulation used below light saturation, Steele formulation used above light saturation.

TABLE 6-8. ALGAL SATURATING LIGHT INTENSITIES

Algal Type	Saturating Light Intensity (langleys/day)	References
Total Phytoplankton	300 - 350	Thomann et al. (1975, 1979) Salas & Thomann (1978) Di Toro et al. (1971) Di Toro & Connolly (1980) Di Toro & Matystik (1980) O'Connor et al. (1975)
	250 - 350	Scavia et al. (1976) Scavia & Park (1976) Scavia (1980)
	200 - 300	Youngberg (1977)
	216	Desormeau (1978)
	288	Larsen et al. (1973)
Diatoms	225	Thomann et al. (1979) Di Toro & Connolly (1980)
	300	Scavia et al. (1976) Scavia (1980)
	88 - 100	Bierman (1976) Bierman et al. (1980)
	225	Canale et al. (1976)
	144	Lehman et al. (1975)
Green Algae	88 - 100	Bierman (1976) Bierman et al. (1980)
	160	Canale et al. (1976)
	65	Lehman et al. (1975)
Blue-green Algae	44 - 50	Bierman (1976) Bierman et al. (1980)
	43	Lehman et al. (1975)
	600	Canale et al. (1976)
	300 - 350	Youngberg (1977)
	250	Scavia (1980)
Flagellates	288	Lehman et al. (1975)
	100	Bierman et al. (1980)
Chrysophytes	86	Lehman et al. (1975)

TABLE 6-9. HALF-SATURATION CONSTANTS FOR LIGHT LIMITATION

Algal Type	Half-Saturation Constant ($Kcal/m^2/sec$)	References
Total Phytoplankton	0.002 - 0.006	Chen (1970) Chen & Orlob (1975) Chen & Wells (1975, 1976) U.S. Army Corps of Engineers (1974) Tetra Tech (1976)
	0.0046	Jorgensen (1976) Jorgensen et al. (1978)
	0.002 - 0.006*	Smith (1978)
	0.005*	Roesner et al. (1980) Duke & Masch (1973)
	0.003 - 0.005*	Brandes (1976)
	0.004 - 0.006**	Jorgensen (1979)
	0.0044**	Collins & Wlosinski (1983)
Diatoms	0.003	Tetra Tech (1980) Bowie et al. (1980) Porcella et al. (1983)
	0.002*	Tetra Tech (1979)
	0.00005 - 0.0012**	Jorgensen (1979)
	0.00005 - 0.0026**	Collins & Wlosinski (1983)
Green Algae	0.002 - 0.004	Tetra Tech (1980) Bowie et al. (1980) Porcella et al. (1983)
	0.002*	Tetra Tech (1979)
	0.0003 - 0.0011**	Jorgensen (1979)
	0.0003 - 0.0106**	Collins & Wlosinski (1983)
Blue-green Algae	0.002 - 0.004	Tetra Tech (1980) Bowie et al.(1980) Porcella et al. (1983)
	0.002*	Tetra Tech (1979)
Dinoflagellates	0.002*	Tetra Tech (1979)
	0.0043 - 0.0053**	Collins & Wlosinski (1983)

(continued)

TABLE 6-9. (continued)

Algal Type	Half-Saturation Constant ($Kcal/m^2/sec$)	References
Flagellates	0.002 - 0.004	Tetra Tech (1980) Porcella et al. (1983)
	0.0044**	Collins & Wlosinski (1983)
Chrysophytes	0.002*	Tetra Tech (1979)
	0.0014 - 0.0017**	Collins & Wlosinski (1983)
Coccolithophores	0.0003 - 0.0016**	Collins & Wlosinski (1983)
Benthic Algae	0.01 - 0.005	Tetra Tech (1980) Bowie et al. (1980) Porcella et al (1983)
	0.002 - 0.006*	Smith (1978)

*Model documentation values.

**Literature values.

The second approach assumes that algal growth is a two-step process, the first step being nutrient uptake and the second step being cell growth or division. Cell growth depends on the internal concentrations of nutrients within the cells, rather than external concentrations in the water. The uptake rates are dependent on both the external and internal concentrations. Since uptake and growth are modeled separately, the nutrient composition of the cell may change with time, resulting in variable stoichiometry or internal pool models. These models simulate processes such as luxury uptake of nutrients which allows growth even when external nutrients are depleted.

6.4.4.1 Nutrient Limitation in Fixed Stoichiometry Models

The majority of water quality models are of the fixed stoichiometry type. These models are generally based on conventional Monod or Michaelis-Menten kinetics. The algal growth equation for a single limiting nutrient under conditions of optimum temperature and light can be expressed as:

$$\mu = \mu_{max}\left(\frac{s}{K_s + s}\right) \qquad (6\text{-}50)$$

$$= \mu_{max}\ f(s)$$

where s = concentration of the limiting nutrient in the water, mass/volume

K_s = half-saturation constant for the limiting nutrient, mass/volume

The quantity $f(s) = (\frac{s}{K_s + s})$ is the growth limitation factor for the nutrient s. The half-saturation constant refers to the concentration of the nutrient at which the growth rate is one half of its maximum value. The above equation results in a hyperbolic growth curve (Figure 6-5) in which growth increases approximately linearly with nutrients at very low nutrient concentrations, but gradually levels off to a maximum growth rate at high nutrient levels (growth saturation). At this point, the nutrient is no longer limiting, so further increases in the external nutrient supply do not affect growth.

Fixed stoichiometry models typically compute a separate growth limitation factor f(s) for each nutrient modeled, and then combine the factors using any one of the four methods discussed above in Equations (6-26) to (6-29) (i.e., multiplicative formulation, minimum formulation, harmonic mean formulation, or arithmetic mean formulation). The specific nutrient limitation factors are:

$$f(P) = \frac{PO_4}{K_P + PO_4} \qquad (6\text{-}51)$$

$$f(N) = \frac{(NH_3 + NO_3)}{K_N + (NH_3 + NO_3)} \qquad (6\text{-}52)$$

$$f(C) = \frac{CO_2}{K_C + CO_2} \qquad (6\text{-}53)$$

$$f(Si) = \frac{Si}{K_{Si} + Si} \qquad (6\text{-}54)$$

where PO_4 = available dissolved inorganic phosphorus concentration (orthophosphate), mass/volume

(NH_3+NO_3) = available dissolved inorganic nitrogen concentration (ammonia plus nitrate), mass/volume

CO_2 = available dissolved inorganic carbon concentration (carbon dioxide), mass/volume

Si = available dissolved silicon concentration, mass/volume

K_P = half-saturation constant for phosphorus, mass/volume

K_N = half-saturation constant for nitrogen, mass/volume

K_C = half-saturation constant for carbon, mass/volume

K_{Si} = half-saturation constant for silicon, mass/volume

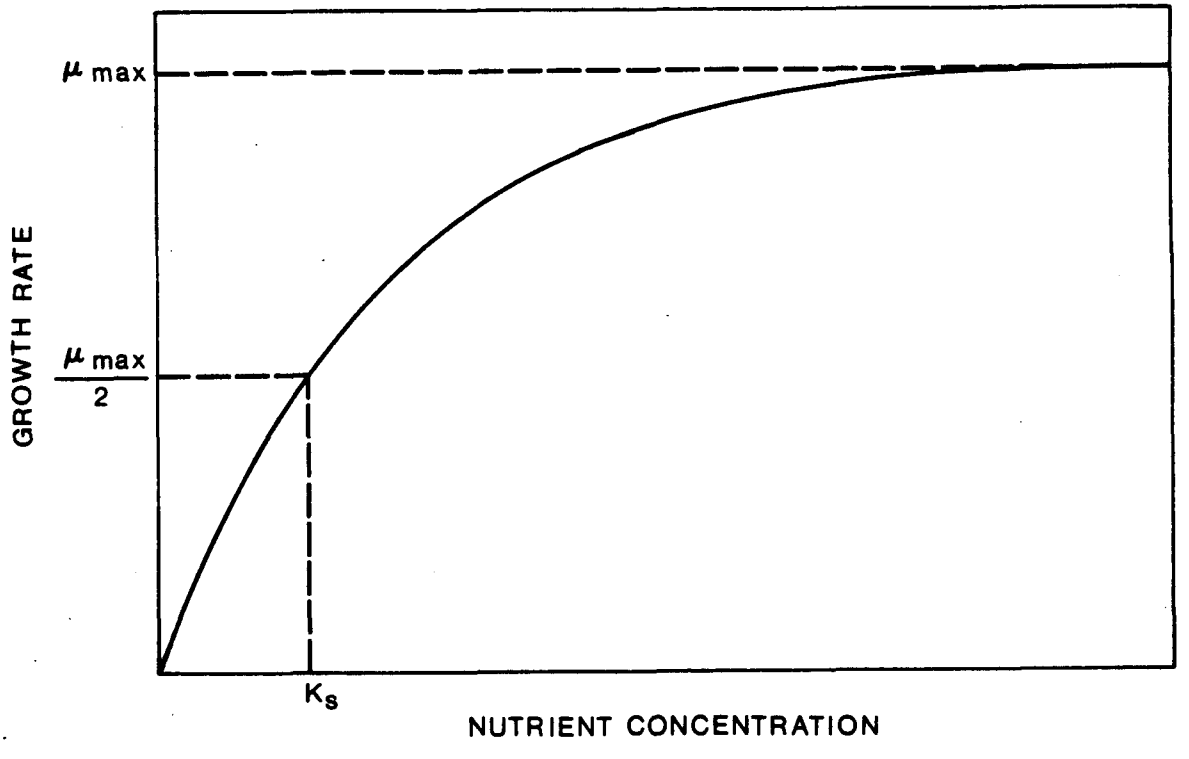

Figure 6-5. Michaelis-Menten saturation kinetics for algal growth limitation by a single nutrient.

The number of growth limiting factors included in a given model depends on both the particular algal species present and the chemistry of the water body under consideration. For example, silicon limitation is only appropriate for diatoms. Nitrogen limitation can generally be omitted for nitrogen-fixing blue-green algae (although nitrogen kinetics for blue-greens must still be included to correctly describe the nitrogen cycle). Carbon limitation is frequently excluded from algal models since carbon is often assumed to be available in excess and is therefore not modeled as a state variable. Lake models often assume phosphorus is the only limiting nutrient, while estuary models often assume nitrogen is limiting at all times.

The way in which nitrogen limitation is computed also varies from model to model. For example, some models simulate available nitrogen as a single constituent (Bierman et al., 1980; Jorgensen et al., 1978; Nyholm, 1978; Thomann et al., 1979), while other models simulate ammonia, nitrite, and nitrate separately and assume both ammonia and nitrate are available for algal growth (Chen and Orlob, 1975; Baca and Arnett, 1976; Baca et al., 1973; Smith, 1978; Najarian and Harleman, 1975; Duke and Masch, 1973). QUAL-II simulates the various forms of nitrogen, but assumes algal growth is only limited by nitrate (Roesner et al., 1981). Some models include factors to account for ammonia preference by algae in their nutrient uptake formulations (Scavia et al., 1976; Canale et al., 1976; Grenney and Kraszewski, 1981; Thomann and Fitzpatrick, 1982; O'Connor et al., 1981; JRB, 1983). Ammonia preference factors are discussed in Chapter 5.

Values of the Michaelis-Menten half-saturation constants for each limiting nutrient are available from many sources, including both the modeling literature and the experimental literature. However, care must be taken when using this information since the values reported will depend on the particular model formulations used for the modeling literature, and on the experimental conditions for the scientific literature. For example, if a multiplicative formulation is used to compute algal growth (Equation(6-26)), the half-saturation constants should be smaller than the corresponding constants where a minimum formulation is used (Equation

(6-27)). In general, the more limiting nutrients that are considered with a multiplicative formulation, the smaller the value of each half-saturation constant. This is necessary in order to get the same growth response with both formulations when more than one nutrient is limiting simultaneously. This is true of both the modeling literature and the experimental literature. When the harmonic mean formulation is used (Equation (6-28)), the half-saturation constants should generally be somewhere between the values of the minimum and multiplicative formulations. Half-saturation constants for each limiting nutrient are tabulated in Table 6-10.

Table 6-11 compares the algal growth formulations used in several models, including the growth limiting factors used, the specific formulations for nutrient limitation, and the methods for combining multiple limiting factors.

6.4.4.2 Nutrient Limitation In Variable Stoichiometry Models

Variable stoichiometry models assume that the growth limiting factor for nutrients, f(P,N,C,Si) in Equation (6-4), is a function of the internal levels of the nutrients in the algal cells rather than the external concentrations in the water column. The internal concentrations are generally defined as:

$$q = \frac{\text{internal mass of nutrient in cells}}{\text{dry weight biomass of cells}} \qquad (6\text{-}55)$$

where q = internal nutrient concentration, mass nutrient/biomass algae

Internal nutrient levels depend on the relative magnitudes of the nutrient uptake rates and the algal growth rates. The uptake rates are functions of both the internal and external nutrient concentrations, while the growth rates depend primarily on the internal concentrations.

Variable stoichiometry models differ in 1) the specific process formulations used to simulate uptake and growth, 2) the number of nutrients considered, and 3) the ways in which multiple limiting factors are combined.

TABLE 6-10. HALF-SATURATION CONSTANTS FOR MICHAELIS-MENTEN GROWTH FORMULATIONS

Algal Type	Half-Saturation Constant				References
	Nitrogen (mg/l)	Phosphorus (mg/l)	Carbon (mg/l)	Silicon (mg/l)	
Total Phytoplankton	0.025	0.0005 - 0.03			O'Connor et al. (1975, 1985) Thomann et al. (1974, 1975, 1979) Thomann & Fitzpatrick (1982) Di Toro & Matystik (1980) Di Toro & Connolly (1980) Di Toro et al. (1971, 1977) Salas & Thomann (1978) Salisbury et al. (1983)
	0.01 - 0.4	0.004 - 0.08	0.03 - 0.8		Chen (1970) Chen & Orlob (1975) Chen & Wells (1975, 1976) U.S. Army Corps of Engineers (1974) Tetra Tech (1976)
	0.2	0.02 - 0.03	0.5		Jorgensen (1976) Jorgensen et al. (1978)
	0.025	0.006 - 0.025			Battelle (1974)
	0.06 - 0.08	0.02			Grenney & Kraszewski (1981)
	0.015	0.0025			Canale et al. (1976)
	0.014	0.001			Larsen et al. (1973)
	0.025 - 0.3*	0.006 - 0.03*			Baca & Arnett (1976)
	0.04 - 0.10*	0.02 - 0.05*	0.02 - 0.04*		Smith (1978)
	0.2 - 0.4*	0.03 - 0.05*			Roesner et al. (1980) Duke & Masch (1973)
	0.015 - 0.3*	0.0025 - 0.08*			Grenney & Kraszewski (1981)
	0.10 - 0.4*	0.03 - 0.05*	0.15*		Brandes (1976)
	0.0014 - 0.018	0.006**			Di Toro et al. (1971)
	0.025 - 0.2**	0.002 - 0.08**			Jorgensen (1979)
	0.0015 - 0.15**				O'Connor et al. (1981)
		0.02 - 0.075**			Collins & Wlosinski (1983)
Diatoms	0.015 - 0.03	0.002	0.03	0.08	Tetra Tech (1980) Bowie et al. (1980) Porcella et al. (1983)
	0.025	0.001 - 0.002		0.030 - 0.1	Thomann et al. (1979) Di Toro & Connolly (1980) Salisbury et al. (1983)
	0.025 - 0.030	0.004 - 0.009		0.03	Scavia et al. (1976) Scavia (1980)
	0.015	0.0025		0.03	Canale et al. (1976)
				0.1	Bierman (1976)
	0.015*	0.03*	0.03*	0.08*	Tetra Tech (1979)
	0.0063 - 0.12**	0.01 - 0.025**			Di Toro et al. (1971)
		0.025**			Jorgensen (1979)
	0.003 - 0.923**	0.001 - 0.163**			Collins & Wlosinski (1983)

TABLE 6-10. (continued)

Algal Type	Half-Saturation Constant: Nitrogen (mg/l)	Phosphorus (mg/l)	Carbon (mg/l)	Silicon (mg/l)	References
Green Algae	0.03 - 0.035	0.004	0.03		Tetra Tech (1980) Bowie et al. (1980) Porcella et al. (1983)
	0.15	0.01			Di Toro et al. (1971)
	0.001 - 0.035	0.005 - 0.024			Scavia et al. (1976) Scavia & Park (1976) Scavia (1980)
	0.15	0.0025			Canale et al. (1976)
	0.03*	0.03*	0.03*		Tetra Tech (1979)
	0.005 - 0.15**	0.01**			Jorgensen (1979)
	0.006 - 1.236**	0.002 - 0.475**	0.068 - 1.5**		Collins & Wlosinski (1983)
Blue-green Algae	0.	0.010 - 0.02	0.03		Tetra Tech (1980) Bowie et al. (1980) Porcella et al. (1983)
	0.001	0.01 - 0.015			Scavia & Park (1976) Scavia (1980)
		0.01			Di Toro et al. (1971)
	0.015	0.0025			Canale et al. (1976)
	0.*	0.06*	0.03*		Tetra Tech (1979)
	0.062 - 4.34**	0.006**	0.031 - 0.088**		Collins & Wlosinski (1983)
Dinoflagellates	0.005				O'Connor et al. (1981)
	0.08*	0.06*	0.03*		Tetra Tech (1979)
	0.007 - 0.13**				Di Toro et al. (1971)
	0.019 - 0.589**				Collins & Wlosinski (1983)
Flagellates	0.08	0.012	0.03		Tetra Tech (1980) Porcella et al. (1983)
	0.0084 - 0.13**				Jorgensen (1979)
	0.001 - 0.052**				Collins & Wlosinski (1983)
Chrysophytes	0.015	0.02*	0.03*		Tetra Tech (1979)
	0.006**	0.047 - 0.076**			Collins & Wlosinski (1983)
Coccolithophores	0.006 - 0.019**				Collins & Wlosinski (1983)
Benthic Algae	0.05 - 0.1	0.004 - 0.008	0.03 - 0.1		Tetra Tech (1980) Bowie et al. (1980) Porcella et al. (1983)
	0.06 - 0.08	0.02			Grenney & Kraszewski (1981)
	0.04 - 0.10*	0.02 - 0.05*	0.02 - 0.04*		Smith (1978)
	0.015 - 0.3*	0.0025 - 0.08*			Grenney & Kraszewski (1981)

*Model documentation values.

**Literature values.

TABLE 6-11. COMPARISON OF ALGAL GROWTH FORMULATIONS

Model (Author)	Growth Limiting Factors						Stoichiometry		Nutrient Limitation Formulation		Method for Combining Factors			Reference
	Light	PO_4	NO_3	NH_3	CO_2	Si	Fixed	Variable	Michaelis-Menten	Other	Multiplicative	Minimum	Harmonic Mean	
AQUA-IV	X	X	X	X			X		X		light	nutrients		Baca & Arnett (1976)
CE-QUAL-R1	X	X	X	X	X		X		X			X		WES (EWQOS) (1982)
CLEAN	X	X	X	X	X		X		X				X	Bloomfield et al. (1973)
CLEANER	X	X	X	X	X		X		X				X	Scavia & Park (1976)
MS.CLEANER	X	X	X	X	X	X	C & Si	N & P	X*	6-51*		X		Park et al. (1980)
DEM	X	X	X				X		X		X			Feigner & Harris (1970)
DOSAG3	X	X	X				X		X		X			Duke & Masch (1973)
EAM	X	X	X	X	X	X	X		X			X		Tetra Tech (1979, 1980)
ESTECO	X	X	X	X	X		X		X		X			Brandes & Masch (1977)
EXPLORE-1	X	X	X	X			X		X		X			Baca et al. (1973)
HSPF	X	X	X	X	X		X		X			X		Johanson et al. (1980)
LAKECO	X	X	X	X	X		X		X		X			Chen & Orlob (1975)
MIT Network	X		X	X			X		X		light			Harleman et al. (1977)
QUAL-II	X	X	X				X		X		X			Roesner et al. (1981)
RECEIV-II	X	X	X	X			X		X		light	nutrients		Raytheon (1974)
SSAM IV		X	X	X			X		X			X		Grenney & Kraszewski (1981)
WASP	X	X	X	X		X	X		X		X			Di Toro et al. (1981)
WQRRS	X	X	X	X	X		X		X			X		Smith (1978)
Bierman	X	X	X	X		X	Si	N & P	X**	6-52**	light	nutrients		Bierman et al. (1980)
Canale	X	X	X	X		X	X		X		X			Canale et al. (1975, 1976)
Jorgensen	X	X	X	X	X			X		6-53	X			Jorgensen (1976)
Lehman	X	X	X	X	X	X		X		6-53	X			Lehman et al. (1975)
Nyholm	X	X	X	X				X		6-54, 55	light		nutrients	Nyholm (1978)
Scavia	X	X	X	X		X	X		X			X		Scavia et al. (1976)

*Fixed stoichiometry Michaelis-Menten formulation used for carbon and silicon, with variable stoichiometry formulations for nitrogen and phosphorus.
**Fixed stoichiometry Michaelis-Menten formulation used for silicon, with variable stoichiometry formulations for nitrogen and phosphorus.

Several different formulations have been used to compute nutrient limitation factors in variable stoichiometry models. As with fixed stoichiometry models, the limitation factors may range from 0 to 1. Most models assume a minimum internal stoichiometric nutrient requirement at which growth is zero. This minimum level is often called the minimum cell quota or subsistence quota. Algal growth (and the nutrient limitation factors) are assumed to increase with increasing internal nutrient levels above the minimum cell quota until the maximum growth rate is attained. Some type of hyperbolic function is typically used to express this saturation type relationship.

The following expressions have been used to determine growth limitation factors in variable stoichiometry models:

$$f(q) = \frac{q}{K_1 + q} \tag{6-56}$$

$$f(q) = \frac{(q - q_{min})}{K_2 + (q - q_{min})} \tag{6-57}$$

$$f(q) = \left(1 - \frac{q_{min}}{q}\right) = \left(\frac{q - q_{min}}{q}\right) \tag{6-58}$$

$$f(q) = \frac{q - q_{min}}{q_{max} - q_{min}} \tag{6-59}$$

$$f(q) = \left[\frac{(q - q_{min})}{K_3 + (q - q_{min})}\right]\left[\frac{K_3 + (q_{max} - q_{min})}{(q_{max} - q_{min})}\right] \tag{6-60}$$

where $f(q)$ = nutrient limitation factor

q = internal nutrient concentration, mass nutrient/biomass algae

q_{min} = minimum internal stoichiometric requirement (cell quota), mass nutrient/biomass algae

q_{max} = maximum internal nutrient concentration, mass nutrient/biomass algae

K_1, K_2, K_3 = half-saturation constants for growth limitation

Equation (6-56) is equivalent in form to the Michaelis-Menten relationship except that the internal rather than the external nutrient concentration is the independent variable. This equation is used in MS.CLEANER for both nitrogen and phosphorus limitation (Park et al., 1980). Equation (6-57) also has the same form as the Michaelis-Menten relationship, but the independent variable is the internal nutrient concentration in excess of the minimum cell quota. This equation is used by Bierman (1976) and Bierman et al. (1973, 1980) for nitrogen and phosphorus. Equation (6-58) was originally developed by Droop (1968), and it is used in several models including Lehman et al. (1975), Jorgensen (1976), Jorgensen et al. (1978, 1981), and Canale and Auer (1982) for all nutrients simulated in these models. Equation (6-58) can be derived from Equation (6-57) by assuming $K_2 = q_{min}$, as was demonstrated by Rhee (1973, 1978) for phosphorus and nitrogen (Bierman, 1981). Equations (6-59) and (6-60) are used by Nyholm (1978) for nitrogen and phosphorus, respectively. Note that Equation (6-59) is a linear rather than hyperbolic relationship. Also, Equation (6-60) is similar to Equation (6-57) since the second factor in Equation (6-60) is a constant once q_{min}, q_{max}, and K_3 are defined.

Since variable stoichiometry formulations have not been widely used, data for the model parameters are limited. Values for the various half-saturation constants are presented in Table 6-12. Note that the half-saturation constants (K_1, K_2, and K_3) have different values since the corresponding equations are different. Minimum cell quotas and maximum internal nutrient concentrations are tabulated in Tables 6-13 and 6-14.

The ways in which variable stoichiometry formulations are used varies between different models. Some models use variable stoichiometry formulations only for phosphorus and nitrogen, combining them with conventional Michaelis-Menten kinetics for carbon and silica (Park et al., 1980; Bierman et al., 1980), while other models use variable stoichiometry formulations for all nutrients modeled (Lehman et al., 1975; Jorgensen, 1976). In a few cases, different internal nutrient formulations are used for different nutrients in the same model (Nyholm, 1978). In some models,

TABLE 6-12. HALF-SATURATION CONSTANTS FOR VARIABLE STOICHIOMETRY FORMULATIONS

Nutrient	Half-Saturation Constant Type	Value	Algal Type	Reference
Phosphorus	K_1	0.005 g/m^3	Total Phytoplankton	Desormeau (1978)
	K_2	0.724×10^{-7} μmole/cell 0.0005 mg/mg (D.W.)	Diatoms	Bierman et al. (1980)
		0.312×10^{-8} μmole/cell 0.0005 mg/mg (D.W.)	Green Algae	
		0.148×10^{-7} μmole/cell 0.0005 mg/mg (D.W.)	Flagellates	
		0.488×10^{-8} μmole/cell 0.0007 mg/mg (D.W.)	Blue-greens (N-fixing)	
		0.566×10^{-8} μmole/cell 0.0007 mg/mg (D.W.)	Blue-greens (non N-fixing)	
	K_3	0.003 mg/mg (D.W.)	Total Phytoplankton	Nyholm (1978)
Nitrogen	K_1	0.05 g/m^3	Total Phytoplankton	Desormeau (1978)
	K_2	0.801×10^{-5} μmole/cell 0.025 mg/mg (D.W.)	Diatoms	Bierman et al. (1980)
		0.345×10^{-6} μmole/cell 0.025 mg/mg (D.W.)	Green Algae	
		0.163×10^{-5} μmole/cell 0.025 mg/mg (D.W.)	Flagellates	
		0.377×10^{-6} μmole/cell 0.025 mg/mg (D.W.)	Blue-greens (N-fixing)	
		0.438×10^{-6} μmole/cell 0.025 mg/mg (D.W.)	Blue-greens (non N-fixing)	
	K_2	0.14×10^{-7} μmole/cell	Diatoms	Bierman (1976)
		0.14×10^{-7} μmole/cell	Green Algae	
		0.23×10^{-7} μmole/cell	Blue-greens (N-fixing)	
		0.14×10^{-7} μmole/cell	Blue-greens (non N-fixing)	

carbon and silica are not included as potentially limiting nutrients (Nyholm, 1978).

The combined effects of multiple limiting nutrients in variable stoichiometry models are dealt with in the same basic ways as in fixed stoichiometry models (i.e., multiplicative formulation (Equation (6-26)), minimum formulation (Equation (6-27)), or harmonic mean formulation (Equation (6-28)). However, when a minimum (or threshold) formulation is used, the limiting nutrient is often determined by comparing the internal

TABLE 6-13. MINIMUM CELL QUOTAS

Algal Type	Minimum Cell Concentration				Units	References
	Nitrogen	Phosphorus	Carbon	Silicon		
Total Phytoplankton	0.015-0.02	0.001-0.003	0.15-0.18		mg/mg (D.W.)	Jorgensen (1976, 1983)
	0.015	0.001	0.15-0.4		mg/mg (D.W.)	Jorgensen et al. (1978, 1981)
	0.04	0.00146			mg/mg (D.W.)	Nyholm (1978)
			0.3-0.7**		mg/mg (D.W.)	Jorgensen (1981)
Diatoms	0.520×10^{-7}	0.20×10^{-8}			µmoles/cell	Bierman (1976)
	0.801×10^{-5} 0.025	0.724×10^{-7} 0.0005			µmoles/cell mg/mg (D.W.)	Bierman et al. (1980)
	$6. \times 10^{-7}$**	$0.9\text{-}30. \times 10^{-9}$**		$0.2\text{-}40. \times 10^{-7}$**	µmoles/cell	Lehman et al. (1975)
		0.45-0.6**			$\mu g/mm^3$ cell volume	Jorgensen (1979)
Green Algae	0.520×10^{-7}	0.20×10^{-8}			µmoles/cell	Bierman (1976)
	0.345×10^{-6} 0.025	0.312×10^{-8} 0.0005			µmoles/cell mg/mg (D.W.)	Bierman et al. (1980)
		$1.7\text{-}4.5 \times 10^{-9}$**			µmoles/cell	Lehman et al. (1975)
		>0.5**			$\mu g/mm^3$ cell volume	Jorgensen (1979)
Blue-green Algae	$0.520\text{-}0.853 \times 10^{-7}$	$0.583\text{-}1.34 \times 10^{-9}$			µmoles/cell	Bierman (1976)
	$0.377\text{-}0.438 \times 10^{-6}$ 0.025	$0.488\text{-}0.566 \times 10^{-8}$ 0.0007			µmoles/cell mg/mg (D.W.)	Bierman et al. (1980)
	1.1×10^{-7}**	2.5×10^{-9}**			µmoles/cell	Lehman et al. (1975)
		>0.5**			$\mu g/mm^3$ cell volume	Jorgensen (1979)
Dinoflagellates	3.9×10^{-7}** *	$11. \times 10^{-9}$**			µmoles/cell	Lehman et al. (1975)
Flagellates	0.163×10^{-5} 0.025	0.148×10^{-7} 0.0005			µmoles/cell mg/mg (D.W.)	Bierman et al. (1980)
Chrysophytes	$0.18\text{-}0.3 \times 10^{-7}$**	0.5×10^{-9}**			µmoles/cell	Lehman et al. (1975)
Benthic Algae		0.0005			mg/mg (D.W.)	Auer and Canale (1982)

**Literature values.

TABLE 6-14. MAXIMUM INTERNAL NUTRIENT CONCENTRATIONS

Algal Type	Maximum Cell Concentration				Units	References
	Nitrogen	Phosphorus	Carbon	Silicon		
Total Phytoplankton	0.08-0.12	0.013-0.03	0.6		mg/mg (D.W.)	Jorgensen (1976, 1983) Jorgensen et al. (1978, 1981)
	0.1	0.02			mg/mg (D.W.)	Nyholm (1978)
	0.08-0.12**	0.013-0.035**			mg/mg (D.W.)	Jorgensen et al. (1981)

**Literature values.

phosphorus to internal nitrogen ratio with a threshold ratio, rather than computing the growth limitation factor for each nutrient and using the smallest value.

Table 6-11 compares the growth formulations used in several variable stoichiometry and fixed stoichiometry models. The comparisons show which limiting factors are included, which formulations are used to compute nutrient limitation, and how multiple limiting factors are combined.

6.4.4.3 Nutrient Uptake In Variable Stoichiometry Models

In fixed stoichiometry models, the nutrient composition of the algal cells is assumed to remain constant, so nutrient uptake is directly related to the algal growth rate by the stoichiometric ratio of nutrient mass to cell biomass. The nutrient uptake rate can then be expressed as:

$$v = \mu\, q_c \tag{6-61}$$

where v = nutrient uptake rate, mass nutrient/mass algae-time
μ = algal growth rate, 1/time
q_c = constant internal nutrient concentration, mass nutrient/biomass algae

The growth rates are assumed to be functions of the external nutrient supplies (plus temperature and light) as computed by Michaelis-Menten type relationships (Equation (6-50)).

In contrast, nutrient uptake rates in variable stoichiometry models are functions of both internal nutrient levels in the cells and external nutrient concentrations in the water. The general relationship is typically of the form:

$$v = v_{max}(T_{ref})\ f(T)\ f(q,s)\ f(L) \tag{6-62}$$

where $v_{max}(T_{ref})$ = maximum nutrient uptake rate at reference

temperature T_{ref}, mass nutrient/mass algae-time

f(T) = temperature function for uptake

f(q,s) = nutrient uptake limitation function

q = internal nutrient concentration, nutrient mass/cell biomass

s = external nutrient concentration, mass/water volume

f(L) = light limitation function for uptake

The temperature and light functions for uptake are essentially the same as those used for algal growth.

Variable stoichiometry models are distinguished primarily by the specific formulations used for the uptake limitation function f(q,s). These functions define the feedback between uptake rates and both internal and external nutrient levels. Some formulations attempt a more mechanistic approach, while others tend to be empirically based. In general, the uptake rates increase with the external nutrient supplies but at the same time decrease as the internal nutrient levels approach their saturation values. Uptake rates approach zero when either external nutrients are depleted or when internal nutrients reach their maximum saturated levels. However, neither of these conditions can persist since nutrients are continually recycled and since phytoplankton growth increases the algal biomass relative to the internal nutrient mass which in effect reduces the internal nutrient concentrations under conditions of restricted uptake.

The following formulations have been used to express internal and external nutrient effects on uptake rates in variable stoichiometry models:

$$f(q,s) = (q_{max} - q)\left(\frac{s}{K_{u1} + s}\right) \tag{6-63}$$

$$f(q,s) = \left(\frac{q_{max} - q}{q_{max} - q_{min}}\right)\left(\frac{s}{K_{u2} + s}\right) \tag{6-64}$$

$$f(q,s) = \frac{1}{\left(1 + \frac{K_{u3}}{s}\right)\left(1 + \frac{C_i}{K_i}\right)}$$

$$= \left(\frac{K_i}{K_i + C_i}\right)\left(\frac{s}{K_{u3} + s}\right)$$

$$= \left(\frac{K_i}{K_i + q\ f_i}\right)\left(\frac{s}{K_{u3} + s}\right) \qquad (6\text{-}65)$$

$$f(q,s) = \left(\frac{K_i}{K_i + (q - q_{min})}\right)\left(\frac{s}{K_{u3} + s}\right) \qquad (6\text{-}66)$$

$$f(q,s) = \left(\frac{1}{1 + K_a\ q_d}\right) - \left(\frac{1}{1 + K_a\ s}\right) \qquad (6\text{-}67a)$$

with

$$q_d = q_{dmin}\ e^{\left(\frac{q}{q_{min}} - 1\right)} \qquad (6\text{-}67b)$$

where q_{max} = maximum internal nutrient concentration, mass nutrient/biomass algae

q_{min} = minimum internal stoichiometric requirement (cell quota), mass nutrient/biomass algae

q_d = internal available nutrient concentration, mass nutrient/volume

q_{dmin} = minimum internal available nutrient concentration, mass nutrient/volume

C_i = internal concentration of uptake inhibitor, mass nutrient/biomass algae

f_i = fraction of total internal nutrient concentration which acts as an inhibitor to nutrient uptake (this corresponds to the acid-soluble polyphosphate fraction of total internal phosphorus, or the cellular free amino acid fraction of total internal nitrogen)

K_{u1}, K_{u2}, K_{u3} = half-saturation constants for nutrient uptake, mass nutrient/volume water

K_i = half-saturation constant for inhibition of nutrient uptake, mass nutrient/biomass algae

K_a = affinity coefficient, volume/mass nutrient

Equation (6-63) is used by Koonce and Hasler (1972), Equation (6-64) by Lehman et al. (1975) and Jorgensen (1976), Equation (6-65) by Rhee (1973) and Park et al. (1980), Equation (6-66) by Di Toro (1980), Auer and Canale (1982), and Canale and Auer (1982), and Equations (6-67a) and (6-67b) by Bierman et al. (1973, 1980).

Maximum nutrient uptake rates and half-saturation constants for uptake are presented in Tables 6-15 and 6-16. Minimum cell quotas and maximum internal nutrient concentrations were presented previously in Tables 6-13 and 6-14. Some of the more model specific parameters are presented in Table 6-17.

Although variable stoichiometry models more realistically represent nutrient uptake and cell growth than fixed stoichiometry models, they do it at the expense of additional model complexity and computational costs. Algal growth computations in variable stoichiometry models require shorter time steps since the time scale for nutrient uptake is on the order of hours while the time scale for algal growth is on the order of days. Also, spatial variability in external and internal nutrient concentrations complicates transport since algae with different internal stoichiometries will be transported into the same model segment, requiring some type of averaging procedure at each time step.

Another criticism of variable stoichiometry models is that more model coefficients are required than in fixed stoichiometry models. Several coefficients are required for both the uptake and growth formulations. Since these coefficients must describe the response of species assemblages rather than the single species evaluated in laboratory experiments, they must be determined largely by model calibration. This introduces additional uncertainty in the model results. Also, the data base for variable stoichiometry coefficients is much smaller than for conventional Michaelis-Menten parameters.

TABLE 6-15. MAXIMUM NUTRIENT UPTAKE RATES

Algal Type	Maximum Uptake Rate				Units	References
	Nitrogen	Phosphorus	Carbon	Silicon		
Total Phytoplankton	0.15	0.0014	0.55		1/day	Jorgensen (1983)
	0.012-0.03	0.0014-0.008	0.40-1.21		1/day	Jorgensen et al. (1978, 1981)
	0.14	0.1			1/day	Desormeau (1978)
	0.01-0.035**	0.003-0.01**	0.2-0.7**		1/day	Jorgensen et al. (1978)
	0.01-0.035**	0.003-0.01**	0.2-1.4**		1/day	Jorgensen (1981)
	0.0024**	0.02-2.95**			µmoles/hr	Jorgensen (1979)
Diatoms	0.015	0.024			1/day	Bierman (1976)
	0.125	0.500			1/day	Bierman et al. (1980)
	0.72-4.32**				1/day	Jorgensen (1979)
	$0.3\text{-}120.\times10^{-8}$**	$0.7\text{-}8.\times10^{-9}$**		$2.6\text{-}950.\times10^{-9}$**	µmoles/cell-hr	Lehman et al. (1975)
	$1.52\text{-}8.33\times10^{-6}$**			$0.073\text{-}26.6\times10^{-6}$**	µmoles/cell-hr	Jorgensen (1979)
Green Algae	0.060	0.133			1/day	Bierman (1976)
	0.125	0.500			1/day	Bierman et al. (1980)
	$2.2\text{-}10.6\times10^{-8}$**	$1.2\text{-}4.\times10^{-8}$**			µmoles/cell-hr	Lehman et al. (1975)
	$2.14\text{-}5.56\times10^{-6}$**				µmoles/cell-hr	Jorgensen (1979)
Blue-green Algae	0.040	0.042-0.059			1/day	Bierman (1976)
	0.125	0.500			1/day	Bierman et al. (1980)
	0.042×10^{-6}**				µmoles/cell-hr	Jorgensen (1979)
Flagellates	0.125	0.500			1/day	Bierman et al. (1980)
Chrysophytes	$1.4\text{-}3.8\times10^{-8}$**	2.4×10^{-7}**			µmoles/cell-hr	Lehman et al. (1975)
		$2.01\text{-}13.9\times10^{-9}$**			µmoles/cell-hr	Jorgensen (1979)
Coccolithophores	$4.\text{-}9.\times10^{-10}$**				µmoles/cell-hr	Lehman et al. (1975)
Benthic Algae		0.045			1/day	Auer and Canale (1982)

**Literature values.

TABLE 6-16. HALF-SATURATION CONSTANTS FOR NUTRIENT UPTAKE

Phytoplankton Group	Half-Saturation Constant				References
	Nitrogen (mg/l)	Phosphorus (mg/l)	Carbon (mg/l)	Silicon (mg/l)	
Total Phytoplankton	0.2	0.02-0.03	0.5		Jorgensen (1976, 1983)
	0.2	0.02	0.5-0.6		Jorgensen et al. (1978)
	0.05	0.07			Desormeau (1978)
	0.0014-0.007**	0.0028-0.053**			Jorgensen (1979)
Diatoms	0.030*	0.060*			Bierman et al. (1980)
	0.0028-0.105**	0.18-0.053		0.022-0.098**	Lehman et al. (1975)
	0.0014-0.130**				Eppley et al. (1969)
	0.0042-0.105**	0.0002-0.053**		0.0053-0.098**	Jorgensen (1979)
Green Algae	0.030*	0.020*			Bierman et al. (1980)
	0.0024-0.02**	0.019-0.155**			Lehman et al. (1975)
	0.0014-0.02**				Eppley et al. (1969)
	0.0024-0.02**	0.0009-1.500**			Jorgensen (1979)
Blue-green Algae	0.030*	0.015-0.060*			Bierman et al. (1980)
	0.980**				Lehman et al. (1975)
	0.0067-0.980**				Jorgensen (1979)
Dinoflagellates	0.0015-0.133**				Lehman et al. (1975)
	0.0015-0.144**				Eppley et al. (1969)
	0.0014-0.133*				Jorgensen (1979)
Flagellates	0.030*	0.060*			Bierman et al. (1980)
	0.007-0.077**				Jorgensen (1979)
Chrysophytes	0.0014-0.0084**	0.016-0.496**			Lehman et al. (1975)
	0.0014-0.0084**				Eppley et al. (1969)
	0.0014-0.0084**	0.009-0.496**			Jorgensen (1979)
Coccolithophores	0.0014**				Lehman et al. (1975)
	0.0014-0.0028**				Eppley et al. (1969)
	0.0014-0.0043**				Jorgensen (1979)
Bacillariophyceae	0.0063-0.120**				Jorgensen (1979)
Benthic Algae		0.125			Auer and Canale (1982)

*Apparent half-saturation values under nutrient-starved conditions.
**Literature values.

TABLE 6-17. MODEL-SPECIFIC NUTRIENT UPTAKE PARAMETERS

Nutrient	Model Parameter Type	Model Parameter Value	Algal Type	Reference
Phosphorus	K_i	0.0001 g/m^3	Total Phytoplankton	Desormeau (1978)
	K_i	0.0007 mg/mg (D.W.)	Benthic Algae	Auer and Canale (1982)
	f_i	0.01%	Total Phytoplankton	Desormeau (1978)
	K_a	0.518×10^6 l/mol 0.167×10^7 l/mol $0.518\text{-}2.0 \times 10^6$ l/mol 0.518×10^6 l/mol	Diatoms Green Algae Blue-green Algae Flagellates	Bierman et al. (1980)
	K_a	0.50×10^6 l/mol 0.50×10^6 l/mol $0.90\text{-}1.0 \times 10^6$ l/mol	Diatoms Green Algae Blue-green Algae	Bierman (1976)
	q_{dmin}	0.5 µg/l 0.5 µg/l 0.5 µg/l 0.5 µg/l	Diatoms Green Algae Blue-green Algae Flagellates	Bierman et al. (1980)
	q_{dmin}	0.215×10^{-7} mol/l cell vol. 0.215×10^{-7} mol/l cell vol. 0.107×10^{-7} mol/l cell vol.	Diatoms Green Algae Blue-green Algae	Bierman (1976)
Nitrogen	K_i	0.0005 g/m^3	Total Phytoplankton	Desormeau (1978)
	f_i	0.05%	Total Phytoplankton	Desormeau (1978)
	K_a	0.100×10^7 l/mol 0.100×10^7 l/mol 0.100×10^7 l/mol 0.100×10^7 l/mol	Diatoms Green Algae Blue-green Algae Flagellates	Bierman et al. (1980)
	K_a	0.10×10^7 l/mol 0.10×10^7 l/mol 0.10×10^7 l/mol	Diatoms Green Algae Blue-green Algae	Bierman (1976)
	q_{dmin}	3. µg/l 3. µg/l 3. µg/l 3. µg/l	Diatoms Green Algae Blue-green Algae Flagellates	Bierman et al. (1980)
	q_{dmin}	0.267×10^{-6} mol/l cell vol. 0.267×10^{-6} mol/l cell vol. 0.267×10^{-6} mol/l cell vol.	Diatoms Green Algal Blue-green Algae	Bierman (1976)

Di Toro (1980) and Di Toro and Connolly (1980) have shown that since the time scale for nutrient uptake is a fraction of the time scale for algal growth and is usually much smaller than the time scale for changes in external nutrient concentrations, many of the complexities of variable stoichiometry models can be avoided by assuming cellular equilibrium with