

VARIATION OF NITROGEN AND CARBOHYDRATE CONSTITUENTS DURING THE DEVELOPMENT OF HIMANTHALIA ELONGATA (L.) S. F. GRAY

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Seasonal variations in the chemical composition of brown algae have been studied by various workers (Lapicque, 1919; Lunde, 1940; Black, 1948a, 1948b, 1949, 1950a, 1950b, 1954a, 1954b; Channing and Young, 1952, 1953; Øy, 1951; Smith and Gordon Young, 1953; Wort, 1955). Black and Dewar (1949) correlated the physical and chemical properties of the sea water with the chemical constitution of algae. In all these investigations, however, no indication of the age, stage of development or sex of the plants is given.

Moss (1950) found that marked changes in the chemical composition of *Fucus vesiculosus* were associated with the development of the reproductive structures. In later work Moss (1952) noted that during the Spring a variation in chemical constituents occurred in several developmental stages of *Himantalia elongata* collected at the same time from the same habitat.

Black (1954a) has shown that at certain times of the year gradients of carbohydrates, proteins and mineral matter occurred along the frond of *Laminaria saccharina*. Studying the variation of nitrogen in *F. vesiculosus* and *L. saccharina*, Jacobi (1954) observed horizontal and vertical gradients of nitrogen, water content and fresh weight. During the time of sporulation the frond of *L. saccharina* showed a higher percentage of soluble nitrogen than during the time of vegetative growth. Jacobi suggested that ontogenetic factors were more decisive in bringing about variations in chemical composition of brown algae than the availability of nutrients in the sea water as postulated by Black and Dewar (1949). For *Himantalia elongata* similar variations in chemical constituents occur along the length of the plant (Jones, 1956). The same author noted that the mature vegetative tissues of the plant were lower in nitrogen content than the actively growing reproductive tissues, and that the male receptacles were higher in nitrogen content than the female receptacles.

No work appears to have been carried out to determine the variation of chemical constituents during the growth and development of brown algae from germination to maturity and senescence. For such a study, therefore, the brown alga *Himantalia elongata* has been selected, for it enables an independent study to be made of the variation in chemical composition of both vegetative and reproductive tissues during the growth and development of the plant.

MATERIALS AND METHODS

*Collection of material*

Samples of *Himantalia elongata* were collected from St. Mary's Island, Northumberland, at low water as the tide receded. All samples were returned to the

laboratory in large glass vessels, thus ensuring that the plants, prior to analysis, were fully turgid. During 1954, the following major stages of growth and development of the plant were investigated:

1) The development of the young vegetative buttons until they produced receptacles at the end of the year. At St. Mary's Island, the young receptacles made their appearance during September to October.

2) The maturation of the plants in their second year of growth. During this period the receptacles grow rapidly in the summer months and develop receptacles containing the gametes.

For analysis, samples were sorted into their respective stages of development. Each sample contained at least 100 individuals. Wherever possible the vegetative buttons were separated from the receptacles and analyzed separately so that variations in chemical composition throughout the development of both vegetative and reproductive tissues could be studied. Because of the difference in nitrogen content of male and female receptacles of *Himanthalia* (Jones, 1956), for the mature plants only female ones were used.

#### *Analytical procedure*

Methods of analysis were those described previously (Jones, 1956). Fucoidin as combined L-fucose, however, was estimated by the improved method of Black, Cornhill, Dewar, Percival and Ross (1950).

#### *Expression of experimental results*

For the purpose of this study it was considered that the results would lend themselves best for interpretation if they were expressed on a unit plant basis.

## RESULTS

### 1. *Young developing plants*

During the development of the young vegetative button there is a gradual increase in fresh and dry weight until the young receptacles make their appearance in October (Table I). Thereafter the weight of the button remains comparatively steady. The receptacles, however, increase in both fresh and dry weight after their initial appearance.

The total nitrogen of the young plants gradually increases throughout the year. In the button the protein content steadily increases, while the non-protein nitrogen increases with the growth of the button until October, when, at the time of receptacle initiation, it falls appreciably (Fig. 1). The relationship between the protein and non-protein is illustrated in Figure 2. During the period January to August the ratio rapidly decreases, suggesting a building-up of non-protein constituents. From August to the end of the year, the ratio increases indicating a synthesis of protein. This synthesis precedes the development of the young receptacles, which are themselves rich in protein and non-protein nitrogen. The build-up of a soluble non-protein reserve, of which peptide nitrogen is the chief constituent, is therefore clearly indicated during the early stages of the development of the button.

TABLE I

Variation of constituents during the development of young plants, 1954

Month		Weight of plants gm./unit plant		Nitrogenous constituents mg./unit plant						Carbohydrate constituents mg./unit plant				Total ash mg./unit plant
		Fresh	Dry	Total N	Protein N	Non-protein N	Volatile base N	Free amino N	Peptide N	Alginic acid	Mannitol	Laminarin	Fucoidin	
January	B	0.54	0.07	1.02	0.87	0.15	0.04	0.04	0.07	13.9	3.9	1.4	5.1	28.0
February	B	0.72	0.11	1.48	1.25	0.23	0.06	0.06	0.10	—	12.1	—	—	—
March	B	—	—	—	—	—	—	—	—	—	—	—	—	—
April	B	0.78	0.14	2.02	1.68	0.34	0.08	0.09	0.15	26.1	13.6	2.7	10.0	56.0
May	B	—	—	—	—	—	—	—	—	—	—	—	—	—
June	B	1.69	0.24	3.71	2.79	0.92	0.31	0.15	0.35	43.8	32.4	5.1	18.6	91.0
July	B	2.00	0.32	4.62	3.58	1.04	0.45	0.24	0.61	56.0	41.5	7.0	20.5	112.0
August	B	1.80	0.31	4.31	3.06	1.25	0.38	0.15	0.50	58.3	43.1	12.3	28.0	108.0
September	B	1.96	0.38	4.67	3.67	1.00	0.36	0.19	0.50	64.8	47.8	34.5	31.4	110.0
October	B	1.62	0.33	4.44	3.69	0.75	0.21	0.25	0.31	71.5	36.6	27.0	20.7	97.0
November	B	1.76	0.36	5.16	4.24	0.92	0.17	0.14	0.33	82.0	25.1	21.5	22.5	120.0
November	R	0.15	0.03	0.56	0.33	0.23	0.02	0.02	0.03	4.0	2.0	—	1.7	8.0
December	B	2.00	0.36	5.32	4.58	0.74	—	—	—	83.0	24.4	11.1	26.0	127.0
December	R	0.32	0.04	0.91	0.53	0.28	—	—	—	6.6	2.4	0.5	2.6	13.0

B = Button.  
R = Receptacles.

Throughout the growth of the young plant the alginic acid content increases even after the production of the receptacles. The other carbohydrate substances, namely mannitol, laminarin and fucoidin gradually increase during the early months of the year, then become more concentrated during the summer months, no doubt the result of active photosynthesis. Between August and October the vegetative but-

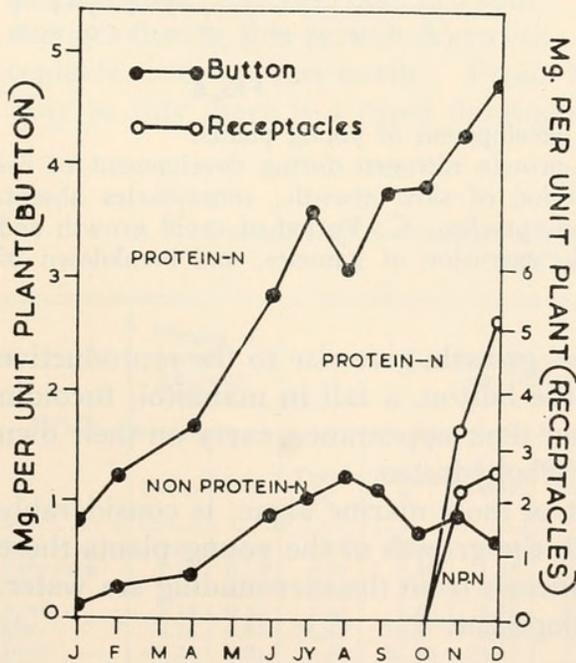


FIG. 1

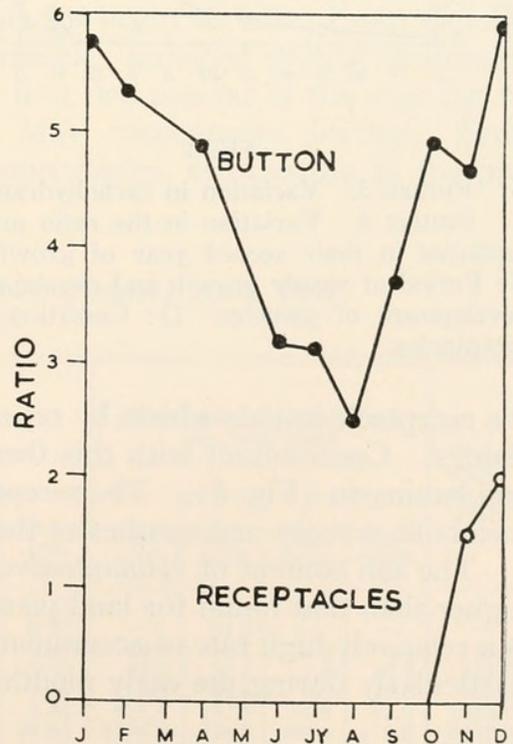


FIG. 2

FIGURE 1. Variation in nitrogen during development of young plants.

FIGURE 2. Ratio protein:non-protein nitrogen during development of young plants.

tions exhibit a fluctuation in carbohydrates associated with the production of the receptacles. It is seen that the laminarin falls to a much lower level after receptacle formation in October. A similar fall in mannitol and fucoidin also occurs at this time. In the young receptacles the mannitol and fucoidin increase during the last two months of the year.

These latter results indicate the building-up of a reserve of carbohydrates throughout the early months of the year, which, with the increased photosynthesis during the summer, reaches a high concentration in the button. However, with the advance of the winter months this reserve is utilized for the rapid development of

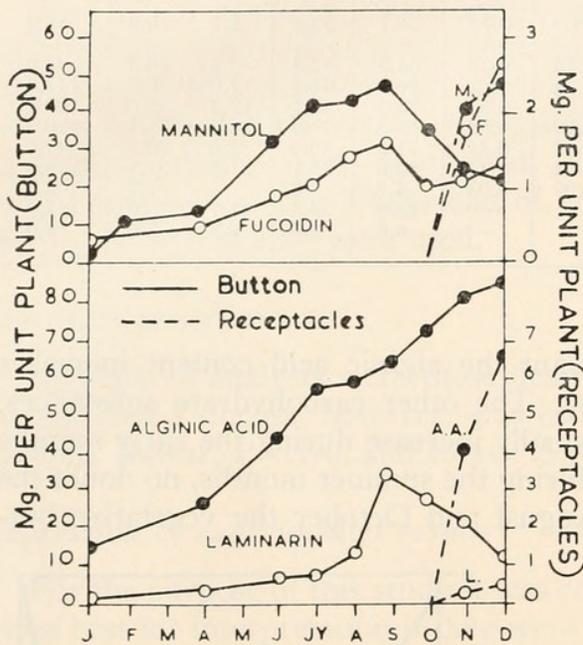


FIG. 3.

FIGURE 3. Variation in carbohydrates during development of young plants.

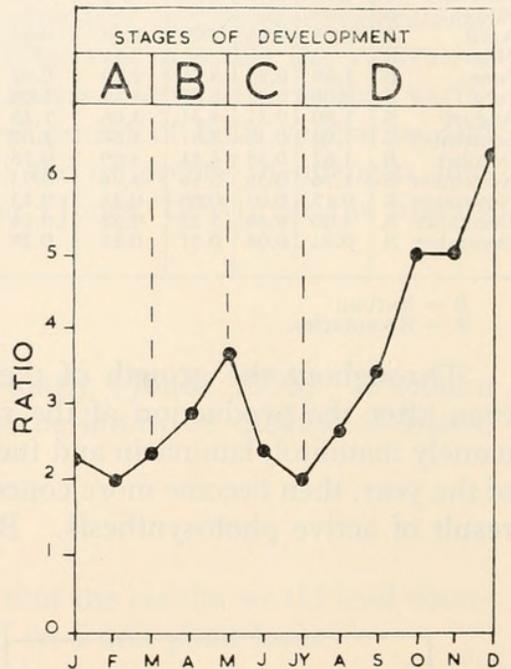


FIG. 4.

FIGURE 4. Variation in the ratio protein:non-protein nitrogen during development of receptacles in their second year of growth. A: Period of slow growth; conceptacles absent. B: Period of steady growth and development of conceptacles. C: Period of rapid growth and development of gametes. D: Cessation of growth, extrusion of gametes, and breakdown of receptacles.

the receptacle initials which, by repeated apical growth, give rise to the reproductive thongs. Concomitant with this there is, in the button, a fall in mannitol, fucoidin and laminarin (Fig. 3). The receptacles, after their appearance, carry on their own metabolic activity and synthesize their own carbohydrates.

The ash content of *Himanthalia*, like that of most marine algae, is considerably higher than that found for land plants. With the growth of the young plants there is a relatively high rate of accumulation of minerals from the surrounding sea water, particularly during the early months of development.

### 2. The mature plants

In the mature plants, during the second year of growth, the button remains relatively constant in fresh and dry weight (Table II). The receptacles, however, ex-

TABLE II  
Variation of constituents during development of mature plants, 1954  
(The vegetative button)

Month	Weight of plants gm./unit plant		Nitrogenous constituents mg./unit plant						Carbohydrate constituents mg./unit plant				Total ash mg./unit plant
	Fresh	Dry	Total N	Protein N	Non- protein N	Volatile base N	Free amino N	Pep- tide N	Alginic acid	Man- nitol	Lami- narin	Fu- coidin	
January	2.19	0.39	4.95	4.07	0.88	0.21	0.21	0.53	83.3	39.0	18.0	42.4	125.0
February	2.51	0.45	5.68	4.77	0.71	0.15	0.17	0.42	—	37.8	—	42.6	162.0
March	2.17	0.40	5.40	4.47	0.83	0.16	0.16	0.38	88.4	22.1	—	23.5	147.0
April	1.88	0.38	4.58	4.00	0.58	0.12	0.12	0.33	88.7	25.6	8.1	—	136.0
May	2.17	0.40	5.02	4.29	0.73	0.13	0.22	0.40	88.7	28.5	—	23.3	144.0
June	1.97	0.37	4.92	4.29	0.63	0.13	0.20	0.31	83.4	32.8	—	27.9	138.0
July	1.95	0.40	5.60	5.06	0.54	0.12	0.21	0.32	88.0	30.6	—	—	116.0
August	1.95	0.38	5.41	4.85	0.56	0.10	0.19	0.25	84.0	29.1	9.5	33.9	105.0
September	—	—	—	—	—	—	—	—	—	—	—	—	—
October	1.81	0.35	4.74	4.23	0.51	0.11	0.26	0.20	77.5	21.5	—	—	100.0
November	1.62	0.33	4.81	4.37	0.44	0.13	0.18	0.18	75.2	20.9	7.3	30.5	95.0
December	1.64	0.33	4.77	4.32	0.45	—	—	—	—	—	—	—	—

hibit marked changes. During the early months of the year, growth of the receptacles, as determined by the fresh and dry weights, is slow, but steady. In the spring and early summer there is an increase in both fresh and dry weights, reaching a climax during the month of July, when the fresh weight of the receptacles has increased some five-fold. This increase is not due to water uptake and turgor extension of the cells alone because a similar five-fold increase in the dry weight also occurs (Table III). After the month of July, with the approach of the winter months, the fresh and dry weights of the receptacles begin to fall. From October to December this decrease is rapid. The receptacles undergo several anatomical changes during this period of growth. For the first two months of the year the receptacle tissue is non-fertile. From March to May, conceptacles develop. From May to July there is a rapid development of conceptacles, terminating in the pro-

TABLE III  
Variation of constituents during development of mature plants, 1954  
(The receptacles).

Month	Weight of plants gm./unit plant		Nitrogenous constituents mg./unit plant						Carbohydrate constituents mg./unit plant				Total ash mg./unit plant
	Fresh	Dry	Total N	Protein N	Non- protein N	Volatile base N	Free amino N	Pep- tide N	Alginic acid	Man- nitol	Lami- narin	Fu- coidin	
January	0.67	0.08	2.24	1.56	0.68	0.07	0.08	0.23	—	—	—	—	—
February	1.19	0.14	3.85	2.50	1.35	0.10	0.15	0.42	—	11.2	—	—	—
March	1.58	0.19	5.32	3.73	1.59	0.14	0.22	0.60	30.6	18.7	2.2	6.3	81.0
April	2.14	0.27	7.63	5.65	1.98	0.17	0.32	0.60	34.6	23.2	2.6	10.8	134.0
May	9.76	0.87	24.57	19.11	5.46	1.04	1.16	1.91	143.9	59.4	6.9	28.5	446.0
June	26.24	2.81	78.51	55.38	23.13	7.64	3.85	8.46	477.4	152.5	31.8	82.9	1324.0
July	112.80	14.97	347.00	231.14	115.86	40.00	21.26	41.62	2776.5	938.5	308.4	473.0	6719.0
August	101.50	13.37	251.49	182.50	68.99	14.97	11.17	23.40	2535.0	1458.8	266.0	764.8	6000.0
September	95.80	13.89	243.91	189.46	54.45	12.83	10.69	21.81	2868.3	830.1	314.3	923.5	6376.0
October	89.50	12.28	203.47	169.21	34.26	7.00	9.70	11.79	2773.5	746.6	391.7	—	5511.0
November	58.62	7.60	126.38	105.81	21.20	3.57	3.80	8.44	2009.4	266.0	195.3	—	3405.0
December	16.00	2.05	34.60	29.86	4.74	—	—	—	540.8	51.3	43.3	—	906.0

duction of antheridia and oogonia. By August the receptacles are "ripe" throughout their entire length, except for some 5 to 6 cm. above the button which remains sterile. Growth ceases and there is a gradual extrusion of the gametes in a basipetal sequence. Disintegration from the tips of the receptacles then follows. This occurs comparatively slowly over the months of August to October, but thereafter very quickly, so that by January of the next year only a few plants remain, the majority having completely disintegrated.

Very little change, if any, occurs in the nitrogenous constituents of the button in the second season after it has reached maturity. Most of the nitrogen in the button is in the form of protein; very little non-protein nitrogen is present. The receptacles show great fluctuations in their nitrogen content (Table III). The protein and non-protein nitrogen increases steadily during the early months of the year, but from March to July there is a rapid increase, particularly in protein. From August to the end of the year the nitrogen content decreases. The ratio protein:non-protein nitrogen (Fig. 4) shows a correlation between the ratio and the stage of development reached by the receptacles. During the early months of the year when growth of the receptacles is slow but steady, the ratio gradually rises in favor of protein synthesis within the receptacles. Between May and July the ratio falls sharply and this is coincident with the period of rapid growth and development of gametes within the receptacles. This suggests that the early synthesis of protein is associated with extra receptacle tissue, and that, at a later date, this protein is broken down to soluble constituents and transported to the receptacles where re-synthesis takes place in the production of the gametes, resulting in the increase in the ratio from August to the end of the year. From October onwards the gradual extrusion of the gametes and the wearing away of receptacle tissue keep pace with one another and the ratio continues to rise. It is seen that the peptide nitrogen exceeds the free  $\alpha$ -amino nitrogen in the soluble non-protein constituents of the mature receptacles.

During the production of the receptacles there was a proportion of the soluble non-protein nitrogen which could not be accounted for. Nitrate nitrogen could not be detected in the plants at any stage of development. It was therefore considered to be some nitrogenous substance associated with reproduction such as nucleic acid.

In the button the carbohydrates remain relatively constant throughout the year. Like the young vegetative button the "old" tissue remains high in alginic acid content. The mannitol is low, similarly laminarin and fucoidin, the latter being higher than the laminarin and similar in magnitude to the mannitol. Throughout their growth the receptacles are particularly low in fucoidin and laminarin. Alginic acid is the major constituent of the receptacle tissue, mannitol being slightly lower. During the early months of the year there is little change in the content of alginic acid and mannitol. However, with increased photosynthesis in the spring and summer months both these constituents increase rapidly. After the extrusion of the gametes the alginic acid and mannitol are considerably reduced.

With the increased growth the accumulation of inorganic ions by the developing receptacles occurs during the months of January to July and thereafter falls following the disintegration of the tissue. The mature button remains comparatively uniform in mineral ash content throughout the year, although there is a tendency toward a falling-off during the latter part of the plant's existence.

## GENERAL DISCUSSION

During the present investigation, variations in chemical constituents have been followed throughout the development of *H. elongata*. Other workers have generally selected their plants at certain times of the year, or have used well established and fully developed plants for their investigations, failing to include the young stages. This is particularly the case where the grapnel has been used for collection, for this method selects only the larger algae. The number of individuals analyzed from one habitat is also of great importance. The results obtained by Black (1949, 1950b) for the Laminariaceae were based on results of the chemical analysis of two plants per month. Baardseth and Haug (1952) have since shown that certain constituents of marine algae vary considerably from one plant to another in a uniform

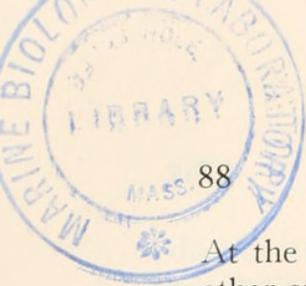
TABLE IV

*Expression of results obtained for the receptacles of mature plants during the months of April and August 1954*

Month	Protein N	Ash	Alginic acid	Mannitol	Laminarin	Fucoidin
a. Results expressed as mg. per gm. dry weight						
April	21.04	500.0	128.0	86.6	13.4	39.9
August	13.65	445.7	189.6	109.6	19.9	32.2
Month	Protein N	Ash	Alginic acid	Mannitol	Laminarin	Fucoidin
b. Results expressed as mg. per unit plant						
April	5.63	134.0	34.6	23.2	2.6	10.8
August	182.50	5959.0	2535.0	1458.8	266.0	430.5

population, even when collected from the same habitat. The ash and alginic acid contents of 55 *L. digitata* plants which they collected at one time showed variations as great as those obtained by Black throughout the whole year.

The majority of studies concerning the chemical composition of marine algae have been carried out by chemists concerned with the possible utilization of algae for industrial purposes. These studies, based on the variation of chemical constituents expressed as a percentage of the dry weight, have led to considerable misconceptions of the physiological problems of growth and development in marine algae. For example, Black (1948a, 1948b, 1949, 1950b) found that the Laminariales and the Fucales exhibit a decrease in "crude protein" content expressed as a percentage of the dry weight, during the period of rapid growth. He attributed this decrease of protein to the lack of nitrate in the sea water at that time of the year. One can hardly accept the statement made by Black (1950b, p. 52) that "rapid growth of the plant results in a decrease in the crude protein content." Where an increase in growth occurs, increase in protoplasm must be the determining factor. An increase in protoplasm with a decrease in protein is difficult to imagine, particularly as protein is one of the major components of protoplasm.



At the time of maximum growth in *Laminaria* and *Fucus* the carbohydrates and other substances, particularly ash, are high. An increase in these other substances will result in an *apparent* decrease in the protein content expressed on a dry weight basis. Had Black expressed his results on a unit plant basis a truer picture of growth and the variations accompanying growth and development would have been made, as the examples for the receptacles of *Himanthalia* illustrate (Table IV). A decrease in protein, ash and fucoidin content between April and August occurs when the results are expressed on a dry weight basis. In the actual plant, however, these constituents have greatly increased over this period (Table IVb). As a result of such an increased synthesis of metabolic products the plant has increased in size, form and reproductive development.

Parke (1948), in her studies on the growth of *L. saccharina*, found that the plant reached its maximum weight during June to July after the period of rapid growth. Plants were found reproducing at all months of the year, but the greatest number were found during October and March. Black (1948b, 1949) found that for the fucoids the maximum dry weight of the plants occurred during the period May to June. For *Himanthalia*, the present author recorded maximum fresh and dry weight values during the months July and August. At all these times of maximum weight the plants commence their reproductive phase, producing either spores or gametes. The development of the reproductive tissues will therefore exert a considerable influence upon the chemical composition of the plants.

Moss (1950, 1952) showed that for *F. vesiculosus*, and later for *Himanthalia elongata*, reproduction definitely influenced the chemical composition of the plants. Jacobi (1954) found that when *F. vesiculosus* and *L. saccharina* were grown under favorable conditions, seasonal variations in nitrogen similar to those published by Black occurred, and that prior to reproduction a mobilization of protein was evident. In *L. saccharina* a higher percentage of soluble nitrogen was recorded for the reproductive tissue than the adjacent vegetative tissue. This led Jacobi to conclude that the increase in nitrogen content of the plant was most probably due to the development of the reproductive tissues which are higher in nitrogen during spore production or gamete formation.

The present work on the change in chemical composition during the growth and development of *Himanthalia* substantiates the findings of Moss (1952) and Jacobi (1954). During the first year of growth the young vegetative plants gradually build up a reserve of nitrogen and carbohydrate constituents which are utilized for receptacle production. The young receptacles, after their initiation in October, continued to grow steadily until the following year, when, during the months of April to July, they grew very rapidly and reached maturity. The fucoidin, mannitol and laminarin, accumulated during the summer months in the young vegetative buttons, on the appearance of the young receptacles, were greatly depreciated, suggesting they were utilized in the production of reproductive tissues. Associated with the receptacle formation there was a rapid synthesis of protein from the non-protein constituents. In the button and also in the developing receptacles the alginic acid content continued to increase. After the establishment of the receptacles the composition of the vegetative button throughout the second year of growth remained relatively constant.

With the increase in the sea temperature and the increased photosynthesis

during the early summer months active metabolism resulted in the extensive growth of the receptacles. The two polysaccharides, fucoidin and laminarin, were very low during this period. Alginic acid, mannitol and mineral ash, however, continued to increase. Utilizing the inorganic nitrogen sources of the surrounding sea water, the receptacles synthesized amino acids and peptides which were later utilized in protein synthesis during the formation of the gametes in the conceptacles. The plant by August reached maturity and the gametes were extruded in a basipetal sequence. This process was accompanied with one of disintegration of receptacle tissue, resulting in a reduction in the chemical composition of the receptacle, until, by December, little remained other than the sterile bases attached to the senescent button. The whole plant then quickly decomposed.

The high ash content of the tissues, particularly of the receptacles, is of interest for the ash content of land plants is usually only represented by about 5 per cent of the dry matter of the plant (Thomas, 1949). Unlike land plants, marine algae are immersed in their nutritive medium, the sea water. In many cases seaweeds concentrate elements several thousand times the concentration found in the surrounding sea water (Black and Mitchell, 1952). The mineral ash consists of inorganic salts, presumably in solution in the cell sap, and cations in combination with such organic substances as alginic acid and fucoidin. Again the reproductive tissues exhibit differences from the vegetative tissues of the plant, insofar as they were found to be considerably higher in ash content. The receptacles contained as much as 50 per cent of their dry weight in mineral ash. Similar high results were found for the receptacles of *F. vesiculosus* (Moss, 1950), particularly when the receptacles were ripe.

The effect of the onset of reproduction upon the chemical composition of plants is not only to be found in marine algae. Variations in nitrogen with development of reproductive tissue have been found to occur in land plants. McCalla (1933), growing wheat in water cultures, found a decrease in nitrogen in the vegetative parts of the plant after the ears had emerged. These findings were later confirmed by Miller (1939) who showed that from the end of May onwards the inflorescences of winter wheat were the only aerial parts of the plants to gain in nitrogen, whereas the stems and leaves lost their nitrogen progressively. Blanck, Giesecke and Heukeshoven (1933) and Blanck and Giesecke (1934) found that maturation of the oat plant was accompanied by a redistribution of nitrogen, which first decreased in the roots and later in the stems and leaves while, on the other hand, it accumulated in the inflorescences. In the barley plant Richards and Templeman (1936) also indicated a pronounced movement of nitrogen from the vegetative parts to the developing grain.

It appears, therefore, that in the life history of *Himantalia elongata* from germination to maturity and senescence separate parts of the plant undergo their own ontogenetic changes which greatly affect the chemical composition of the plant.

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## SUMMARY

1. Monthly variations in chemical constituents have been followed throughout the development of *Himanthalia elongata*.

2. Nitrogen, laminarin, mannitol, alginic acid and fucoidin increase during the first year's growth of the vegetative button.

3. Associated with receptacle initiation, the carbohydrate and nitrogen reserve of the button is utilized and there is a synthesis of protein from the non-protein constituents.

4. The young receptacles build up a reserve of non-protein materials which are later utilized in protein synthesis during the formation of the gametes.

5. It was concluded that during the life history of *Himanthalia elongata* from germination to maturity and senescence, separate parts of the plant undergo their own ontogenetic changes which are correlated with changes in the chemical composition.

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