The Origin of 'Golden' Oak.

BY

HELEN STUART WILLIAMSON.

(Imperial College of Science and Technology.)

With Plate X and four Figures in the Text.

THE specimen of oak which was the origin of this investigation was sent to the Timber Department of the Imperial College by Dr. Butler. The wood showed yellow coloration externally and extending internally for two or three millimetres. The specimen was seasoned heartwood of *Quercus robur*. Externally there appeared to be rather fluffy mycelium, some black sporangia, and small round yellow bodies.

METHODS OF ISOLATION OF THE FUNGUS.

Three fungi were isolated from the surface of the wood, viz. a species of *Aspergillus*, *Penicillium luteum* forming yellow ascocarps, and a new fungus, with yellow conidia in long chains, which has been named *Eidamia catenulata* (4). Dilution plates of potato extract agar, inoculated from a needle drawn across the surface, gave a species of *Aspergillus*, one colony of *Penicillium luteum*, and *Eidamia catenulata* in the first dilution, with only the last-named fungus in the second and third dilution plates. This fungus is characterized by its very long chains of yellow conidia. The conidia are oval and measure 3.5 to 5μ by 2.5 to 3.5μ , whereas those of *Penicillium luteum* (7, 7A) are rounder and measure 2.4 to 2.8μ by 1.6 to 2.4μ .

In all the cultures of *Eidamia catenulata* obtained in this way, hyphae bearing hyaline spores also occurred, so single spore cultures were obtained both from the conidia and from the hyaline spores. In each case both types of spores were produced on the resulting growth, and later examination revealed the same hypha bearing both conidiophores and single hyaline spores on branches. In this way it was proved that *Eidamia catenulata* possesses two types of spores.

In order to isolate from inside the wood the fungus causing the yellow coloration, a piece three inches in length was sawn from the original board

and soaked in running water for six hours. It was then placed for a minute in alcoholic mercuric chloride, to kill any external spores, washed in sterilized water, and placed on a glass ring in a potato dish. All the glass used had been previously treated with mercuric chloride. A little sterile water was left in the bottom of the dish to keep the air sufficiently moist. In a week to ten days a mycelium could be seen emerging from the cut surface of the wood. This was a growth from inside the wood and proved on microscopic and cultural examination to be identical with the fungus, *Eidamia catenulata*, isolated from the wood externally. The wood was left for several months in these moist conditions and the yellow colour spread throughout. No other fungus was found arising from the wood. Single spore cultures were obtained from the conidia produced on this mycelium, and subcultures of these were used in all subsequent experiments.

ARTIFICIAL PRODUCTION OF THE GOLDEN COLOUR IN WOOD.

In order to test the effect of *Eidamia catenulata* on the heartwood of normal oak, small pieces of *Quercus robur* (about one cubic inch) were placed one above the other in wide test-tubes. These were sterilized by dry heat at 180° C. Sterile water was then poured in and the wood left to soak for some hours, after which all but 10 c.c. of the water was poured off. This left enough water at the bottom of each tube to supply a sufficiently moist atmosphere for the fungus. The degree of moisture would vary in the different blocks of wood according to the position in the tube, the moisture decreasing from the lowest block upwards. The blocks were then inoculated with spores of *E. catenulata* and left at laboratory temperature. In a week the fungus was growing well, and the oak soon had the yellow colour externally, owing to the production of many chains of yellow conidia. In four months the wood was definitely yellow, and cubes split after six months showed exactly the same golden colour seen in some of the original 'golden' oak which had been left in damp air. In these experiments a control tube of oak which had been treated in exactly the same way as the other tubes, apart from inoculation, was kept for comparison. This wood showed no change in colour or alteration in contents as far as could be seen macroscopically and microscopically.

The difference of moisture in the different blocks was not sufficient to make marked changes in the growth of the fungus and consequent colour of the wood. In this the effect of *E. catenulata* on oak is not comparable to that of the unknown fungus causing 'brown' oak. In the latter Professor Groom (2) found that the brown colour was assumed only when the heartwood contained moisture exceeding a certain minimum and falling short of a certain maximum. The blocks in the middle of each column in the tubes inoculated with the unknown fungus changed to the brown colour, and not those at the base or top of the tubes.

From the fact that *E. catenulata* is the fungus produced from the original specimen of golden oak after careful external sterilization, and that oak inoculated with this fungus becomes the same golden colour as the original specimen, it can be concluded that the golden colour in oak is caused by *Eidamia catenulata*. The other fungi found on the original specimen are growing externally only. This conclusion is confirmed by an examination of sections of the original oak and artificially infected oak.

A few other woods, such as chestnut, beech, were inoculated in the same way with this fungus. The effect on beech is to darken somewhat the colour of the wood, whereas the chestnut becomes a marked golden colour.

MORPHOLOGY OF *EIDAMIA CATENULATA*.

The morphology of this fungus is fully described in the paper dealing with the genus *Eidamia* (4). It may be summarized here as follows:

(1) The mycelium is composed of septate branched hyphae, varying in size from $3\ \mu$ to $10\ \mu$ in width, and having thin or thick walls according to the medium supplied. (2) Two types of spores occur, conidia which are yellow in colour and hyaline spores. (3) The conidia are narrow to broadly elliptical, pointed at both ends, and vary in size from 4 by $2\ \mu$ to 7 by $3.5\ \mu$. There may be as many as 100 in one chain, and balling of the spores may occur. (4) The conidia are borne on sterigmata which are slender, slightly swollen at the base, and vary in size from 8 – $16\ \mu$ in length and 1 – $2.5\ \mu$ in width at the base. (5) The sterigmata may be borne singly on a hypha or on a short branch or a number at the head of a slightly swollen branch, or a *Penicillium* type of conidiophore may occur. (6) The hyaline spores are borne directly on the hypha or at the end of a branch or may be intercalary. They are round or slightly pear-shaped, with fairly thick walls, and vary in size from 7.5 by $8.5\ \mu$ to 14 by $10\ \mu$ or $18\ \mu$ diameter. (7) The colour of the culture varies from pale cream, old gold, to cinnamon brown, according to the medium used, the age of growth, and the temperature of incubation.

PHYSIOLOGICAL CHARACTERISTICS OF *EIDAMIA CATENULATA*.

Details of the experiments on the physiology of this fungus are given in the paper dealing with the genus *Eidamia*, and may be briefly summarized here. (1) *E. catenulata* is capable of hydrolysing starch, and grows on soluble pectin. (2) This fungus can grow on various sugars such as glucose, lactose, maltose, galactose, fructose, mannose, and sucrose, and it causes an appreciable inversion of cane sugar. (3) A moderate growth is obtained on peptone, which becomes considerable when glucose is added to the peptone. (4) Asparagin can be used by the fungus as a source of nitrogen only in the presence of mineral salts, and ammonia is liberated. (5) *E. catenulata* is highly tolerant of acids, being able to grow at a hydrogen-ion concentration

of 1.16. Its optimum pH value is between 2 and 3, and its minimum is 8.2. (6) There is evidence that the fungus is capable of utilizing certain acids, such as malic, tartaric, citric, and gallic. Its growth on tannic acid is practically the same as on the control nutrient medium, showing tolerance of the acid but giving no evidence of utilization. (7) The yellow colour of the conidia is insoluble in ether, chloroform, alcohol, and water. These physiological characteristics are important in the consideration of the fungus in relation to the oak.

E. CATENULATA IN THE WOOD.

The cellulose acetate method (8) was the one usually employed in order to soften the oak and obtain sections with the fungus uninjured. Small cubes of the infected oak, at different stages after inoculation, or of the original specimen after soaking, were de-aerated under water. They were left in pure acetone for two hours, and then placed in a solution of cellulose acetate in acetone. After six to ten days these could be cut on the Jung sliding microtome. This time could be about halved if the tubes containing

TEXT-FIG. 1. Longitudinal section of wood-vessel showing hyphae with globules of secretion and chains of conidia. $\times 290$.

the blocks in the cellulose acetate were placed in an incubator at 40°C . Sections were cut about 10μ thick and placed in acetone to dissolve out the cellulose acetate, followed by alcohol to replace the acetone. After this they were stained, usually with a saturated aqueous solution of safranin followed by light green in clove oil. The fungal hyphae took up the light green very well. Another stain which proved useful was a slight variation on that recorded by E. E. Hubert (5) for staining fungi in wood. The sections were placed in Bismarck brown (2 per cent. in 70 per cent. alcohol) for about two minutes, washed with distilled water, dehydrated, and then left in a solu-

tion of methyl violet in clove oil for three minutes. The violet stain was differentiated in clove oil followed by cedar oil and Canada balsam.

It was found possible, after the use of cellulose acetate to soften the wood, to embed in paraffin, and cut with a Cambridge rocking microtome. The small blocks were transferred from cellulose acetate to acetone for a few hours, and then placed in 95 per cent. butyl alcohol as given by Mlle Larbaud (6), after which the blocks were passed through two baths of pure butyl alcohol, to the second of which paraffin was added. Embedding followed the usual process, and sections were mounted and stained in the usual way.

Hand sections were also made from the wood before it was subjected to any softening process. These were examined in air to obtain fungal hyphae and spores in position in the large vessels. Text-fig. 1 gives an illustration of the results obtained by such sections. The wall of the vessel is lined with a mass of hyphae from which hyphae, bearing sterigmata and conidia, protrude into the lumen. This section was taken from some of the original 'golden' oak which had been soaked and left in damp air for eight months. The conidia are the shape, size, and colour of those of *Eidamia catenulata*. On the hyphae occurred glistening yellow globules of a substance exuded, in all probability, owing to the activity of the fungus, since the wood cells are dead. A substance similar in appearance also occurs in oak inoculated with spores of *E. catenulata*.

Normal heartwood of *Quercus robur* shows large vessels in the spring wood and smaller vessels in the autumn wood, with fibres, wood parenchyma, and medullary rays of the two types, multiseriate and uniseriate. Tannin is present in cells of the medullary rays and in some of the wood parenchyma. A little starch is scattered sporadically in medullary ray cells or in wood parenchyma.

GROWTH OF THE FUNGUS IN THE WOOD.

By examining sections from oak at different intervals of time after inoculation with *E. catenulata* it was possible to trace its course through the

TEXT-FIG. 2. Radial section of wood showing hyphae passing through pits in the walls of the tracheides. $\times 290$.

wood. The hyphae advance along the medullary rays, and they may be found in ray cells when they are absent from all neighbouring cells. They run in a transversely radial direction, always passing through the pits in the

end cell-walls, with occasional branches passing to the wood parenchyma in the vicinity. The passage through the pits in radial section is illustrated in Text-fig. 2. Finally the tracheides, wood-vessels, and fibres are entered, and here the hyphae appear to travel longitudinally, in the main, though fairly numerous lateral branches into surrounding cells do occur (Pl. X, Fig. 2).

The hyphae, as a rule, are septate and branched, with occasionally a swollen irregular appearance with frequent septation, such as was found

TEXT-FIG. 3. Tangential section showing hyphae and hyaline spores. $\times 290$.

when the fungus was growing on synthetic agar at 25°C . The frequent presence of hyaline spores of all sizes was noted in the medullary ray cells and in the wood parenchyma and vessels, both in the older infections and in the original 'golden' oak. Comparisons of the dimensions of these hyaline spores and those of *E. catenulata* showed the same range of variation, though the smaller sizes were perhaps more abundant in the wood than in cultures. Text-fig. 3 shows hyaline spores in medullary ray cells and wood parenchyma in tangential sections of oak.

Conidia also occur frequently in infected oak. Text-fig. 4 shows the lumen of a vessel of the original 'golden' oak with conidia scattered and in

chains. These were measured and found to be $3-4\ \mu$ by $2-3\ \mu$, whilst those on hyphae growing out of the wood were $3.5-5\ \mu$ by $2.5-3.5\ \mu$. The slight difference in size may be due to the fixing and softening process the wood underwent prior to sectioning.

TEXT-FIG. 4. Lumen of wood-vessel showing pits, hyphae, and chains of conidia. $\times 500$.

PRODUCTION OF YELLOW SUBSTANCE.

(a) *In the Wood.*

Reference has already been made to the glistening yellow globules seen on hyphae in vessels of the wood. The same phenomenon occurs in fibres, vessels, and wood parenchyma seen in microtome sections. The hyphae in a cell may be studded with roundish small masses of a substance which may retain a yellow colour or may be stained red or yellow-red with safranin. Sometimes only one hypha in a cell will have this appearance. In other stages the substances will take the form of an irregular mass completely covering a portion of the hypha. Where this substance is present in quantity the hyphae are often somewhat disorganized, and refuse to take up the light green stain taken by normal living hyphae. Instead they are often stained dark red by safranin. In one cell may be found hyphae staining light green, some disorganizing hyphae staining red, and irregular masses of a somewhat refractive substance which may or may not stain red with safranin. Finally cells are found which are completely filled with a yellow or red yellow substance in which it is sometimes possible to see broken mycelium (Pl. X, Fig. 3).

In transverse section infected oak shows refractive contents in the medullary rays, wood parenchyma, fibres, and even lining the vessels (Pl. X, Fig. 1). These refractive bodies sometimes have a crystalline appearance, in other cells they are more granular in structure, and again it may not be possible to make out any definite structure at all. They vary in colour, being yellow generally, tangerine, or red-brown to brown occasionally. In transverse section these substances appear to occur in islands of cells surrounded by areas of comparatively empty cells, and this corresponds with

the fact that the course of the hyphae is generally vertical in the wood, so that islands of vessels and tissue containing hyphae would occur.

Tests for tannin show that many of these cells contain some 'tannin body' as well as the refractive substance, often masking the yellow colour. It is possible to dissolve out the tannin and obtain cells still showing yellow or tangerine-coloured contents.

These bodies agree, in certain reactions, with the behaviour of the material known as 'wood-gum'. They are insoluble in water, alcohol, ammonia, chloroform, acetic acid, concentrated nitric, hydrochloric, and sulphuric acids. In most of these cases tannin is dissolved out and the refractive substance, yellow, light orange, or red-brown, remains. Strong potash dissolves some of the cell contents, leaving pale yellow or tangerine-coloured substances in the medullary rays and some patches of cells. Whether this 'tannin', so often present along with the yellow substances, is the same as the 'tannin' in uninfected oak it is impossible to say with the micro-chemical tests available.

The yellow colour of the wood may be due to two factors, the yellow substance exuded by the fungus and the yellow colour of the conidia. Colour may be produced in wood by fungi due to the colour of the mycelium, such as certain species of *Graphium* may produce on oak, pine, &c. Other cases have been recorded in which the fungus exudes a soluble pigment which, according to Hedgecock (3), is absorbed by the lignified cell-walls so that the wood is actually stained. Hedgecock describes *Penicillium aureum* which may produce a yellow colour in oak. This fungus exudes a soluble pigment in the form of granules and also possesses a mycelium, which may have swollen cells and bear conidiophores, consisting of a whorl of branch hyphae bearing sterigmata and long chains of oval conidia. The points of difference between this fungus and *Eidamia catenulata* are as follows :

(1) *P. aureum* is dimorphous, having a mycelium with grey-green coloured fruiting clusters and also a sterile mycelium which can be lemon-colour or orange-red according to the acidity or alkalinity of the medium. *E. catenulata* has a colourless mycelium and its fruiting clusters are yellow. (2) The swollen cells in the mycelium of *P. aureum* have no thick walls and do not separate from the hyphae, so cannot be compared with the hyaline spores of *E. catenulata*. (3) The conidia in *P. aureum* are $3-4\ \mu$ by $1.5-2\ \mu$ and contain a blue-green pigment which is soluble in hot alcohol, whereas those of *E. catenulata* measure $4-7\ \mu$ by $2-3.5\ \mu$, and possess a yellow colour insoluble in alcohol, &c. (4) The yellow pigment exuded by the hyphae of *P. aureum* is soluble in slightly acid or alkaline water, hot alcohol, &c., and is absorbed by the lignified cell-walls. In *E. catenulata* the hyphae exude a yellow substance which is insoluble in acid or alkali; and is stored in the cell cavities as a refractive yellow or orange 'gum', and there is no staining of the cell-walls.

Beside the yellow substance in the infected oak there occurred in certain cells, generally in small groups, dark granular masses. These were found in normal heartwood as well as in infected wood, and their distribution did not appear to be related to the hyphae at all. These patches appear to be slightly more numerous in the infected wood, but apparently their occurrence was not sufficiently great to cause any darkening in the colour of the wood. The dark substance was insoluble in hydrochloric, nitric, and acetic acids, but soluble in strong potash. Its nature was not discovered. This substance was noted in 'brown' oak by Professor Groom.

(b) *In Culture Media.*

It has been found that, when grown on prune agar, malt agar, potato glucose agar, and synthetic starch agar, the fungus produces roundish refractive yellow or brown bodies. These bodies are very noticeable among the aerial hyphae. They are larger than the hyaline spores as a rule and do not dissolve in alcohol, water, or chloroform, and do not stain with iodine, Sudan III, Scharlach red, or alkannin. In fact they behave in the same way as the yellow substance produced in wood. Cultures on potato mush agar and on a synthetic sugar medium produce globules of yellow viscid substance of somewhat the same nature.

The yellow colour does not extend to the medium in any of these cases. The only exception to this is oak-sawdust agar (4 per cent. or 10 per cent. sawdust) infected with *E. catenulata*, where yellow coloration of the medium begins to show after three to four weeks' growth. It may be that this is the only medium possessing the requisite properties that result in the production of the yellow colour in the wood.

THE ACTION OF THE FUNGUS ON THE CELL-WALL.

A certain amount of splitting of the middle lamella is visible in sections of infected wood, but it has not been possible to prove this to be due to fungal action. One case was noted in which a hypha was growing along such a split between two cells, but it is doubtful whether this was more than accidental. The splitting in sections may be due to some slight weakening of the tissue by the fungus, or by the process of softening, making it more susceptible to the action of the knife.

The fungus passes from cell to cell through the pits, and no case of any other method of passage was found. There is no evidence to show whether the hypha pierces the middle lamella of the pit or excretes an enzyme to dissolve it. The fungus is capable of growing on and using up soluble pectin, and may possibly have some action on the middle lamella.

Many tests were made to see if any delignification of the cell-wall by the fungus occurred, but none was observed. The wall region just round

the pits was particularly scrutinized and no cellulose reaction due to the fungus could be found. It was noted that, with the iodine-sulphuric acid test, the reaction for cellulose occurred wherever a wall had been broken or distorted or strained by the action of the knife or the pressure of the microtome holder. This made the test difficult to interpret, and great care had to be taken in observing the path of the hyphae and the walls in contact with them. The conclusion that the fungus has no power of delignification was reached.

SOURCE OF FOOD IN THE WOOD.

The fungus is growing in seasoned heartwood of oak. The food available is the pectic substance of the middle lamella; the pectic bodies, glucosides, tannins, cellulose, and lignin in the walls; the tannin bodies in the medullary rays and wood parenchyma cells; any starch or waste products which may have been contained in the cells and dried in the process of seasoning. The amount of food material is necessarily small, and the chief bulk would be comprised by the lignified walls and the tannin with glucosides and other impurities in the cells. The small quantity of the food is not a deterrent to the growth of *E. catenulata*, as the fungus can grow on media with minute quantities of salts only, on starvation media suggested by Coon (1), and even on dilute hydrochloric acid in distilled water.

There is no evidence that the fungus is capable of delignifying the cell-walls, and it shows no appreciable growth on cellulose, so the lignin and cellulose are probably not utilized. Certain deductions as to its method of nutrition in the wood may be made from the study of its behaviour in various nutrient constituents, an aspect which has already been dealt with in considerable detail elsewhere.

The fungus has been shown to be capable of growth in almost pure soluble pectin derived from apples. Hence it is not improbable that the pectic bodies in the walls of the wood may supply a certain amount of nourishment. The middle lamella is not disorganized by the fungus, which seems to attack it only at the pits and that action may be physical, therefore that lamella cannot be regarded as a source of food.

Any sugar or glucoside would be readily used, as it has been demonstrated that *E. catenulata* grows freely on glucose and can invert cane sugar.

This fungus can hydrolyse starch, but the quantity available is extremely minute, being scattered sporadically in ray cells and wood parenchyma. It is able to grow to a certain extent in an acid medium containing no other source of nutriment. It is highly tolerant of certain acids (limits being pH 1.16 to pH 8.2) and is probably able to utilize malic, citric, tartaric, and gallic acids. Any trace of gallic acid in the oak can be utilized. Growth also occurs in a solution containing from 0.1 to 2 per cent.

tannic acid. A consideration of these facts makes its growth on oak more accountable, since the tannic acid present in the wood is no deterrent to its activity—though it may be the factor that inhibits the growth of *E. viridescens* on oak, since with that fungus appreciable growth was not obtained in tannic acid at higher percentages than 0.1.

The 'tannin' bodies probably contain glucosides and other impurities which act as food for the fungus. These bodies themselves do not appear to decrease, and in fact, from micro-chemical tests, would appear to be more prevalent in the infected wood. It may be that the clearing away of the impurities in the 'tannin' bodies by the fungus leaves the tannin itself more free to take up the ferric chloride, so producing the apparent increase in tannin. Without chemical analyses of the normal and infected oak it is not possible to be definite on this point.

The physiological evidence points to the source of food in the wood being any soluble pectic bodies, glucosides, starch, proteid, and any organic salts that may be present.

SUMMARY.

Eidamia catenulata has been isolated from the specimen of 'golden' oak, both externally and internally. Since this fungus is the only one growing from inside the oak when external sterilization has been applied, and it also produces the golden colour when grown on normal oak, the conclusion has been reached that the golden colour in the specimen of oak investigated is due to the activity of *E. catenulata*.

This fungus in the infected tissue gives rise to a yellow substance as globules exuded along the hyphae. This accumulates in the cells and may finally fill them completely, with accompanying disorganization of the hyphae. This yellow substance somewhat resembles in its reactions the material termed 'wood-gum'.

The hyphae advance in the heartwood along the medullary rays in a transversely radial direction and in the wood parenchyma, fibres, and vessels longitudinally in the main. Passage from cell to cell takes place only through pits in the walls, and there appears to be no delignification or attack on the walls themselves.

The source of food for the fungus in the heartwood of oak is probably soluble pectic bodies, glucosides, any gallic acid, starch, proteids, or organic salts that may occur.

E. catenulata produces conidiophores with oval yellow conidia in long chains and also hyaline spores borne singly or in pairs, generally terminally, on lateral branches of the mycelium.

In conclusion I desire to thank Professor Groom for passing on to me the original specimen of 'golden' oak on which this investigation has been based.

LIST OF REFERENCES.

1. COONS, G. H.: Factors involved in Growth and Pycnidium Formation. Journ. Agric. Research, v. 713, 1916.
2. GROOM, P.: 'Brown' Oak and its Origin. Annals of Botany, xxix. 393, 1915.
3. HEDGECOCK, G. G.: Studies upon some Chromogenic Fungi which discolour Wood. Missouri Bot. Gard. Report, xvii. 59, 1906.
4. HORNE, A. S., and WILLIAMSON, H. S.: The Morphology and Physiology of the Genus *Eidamia*. Annals of Botany, xxxvii. 393, 1923.
5. HUBERT, E. E.: A Staining Method of Hyphae of Wood-inhabiting Fungi. Phytopathology, xii. 440, 1922.
6. LARBAUD, Mlle: Nouvelle technique pour les inclusions et les préparations microscopiques des tissus végétaux et animaux. Comptes Rendus, xxi. 1317, 1921.
7. WEHMER, C.: (1) Zur Morphologie und Entwicklungsgeschichte des *Penicillium luteum* Zuk., eines überaus häufigen grünen Schimmelpilzes. Ber. d. deut. Bot. Ges., xi, 499, 1893.
- 7 A. ———: (2) Die Arten der Gattung *Penicillium*. Lafar's Handbuch der Techn. Mykol., iv. 227, 1907.
8. WILLIAMSON, H. S.: A New Method of Preparing Sections of Hard Vegetable Structures. Annals of Botany, xxxv. 139, 1921.

EXPLANATION OF FIGURES IN PLATE X.

Illustrating Mrs. Williamson's paper on the Origin of 'Golden' Oak.

Fig. 1. Transverse section of *Quercus robur* infected with *Eidamia catenulata*, showing islands of cells filled with a yellow or tangerine coloured, somewhat refractive substance. The large vessel also shows some of the same substance lining the wall.

Fig. 2. Tangential section of *Quercus robur* showing hyphae of *E. catenulata* running longitudinally and passing through pits in the cell-walls.

Fig. 3. Tangential section of *Quercus robur* showing excreted globules on the hyphae of the fungus. One wood parenchyma cell is full of this substance and shows remains of disorganizing hyphae.

1.

2.

3.

Huth lith et imp.

WILLIAMSON-GOLDEN OAK.

Williamson, Helen Stuart. 1923. "The origin of 'golden' oak." *Annals of botany* 37, 433–444. <https://doi.org/10.1093/oxfordjournals.aob.a089857>.

View This Item Online: <https://www.biodiversitylibrary.org/item/270686>

DOI: <https://doi.org/10.1093/oxfordjournals.aob.a089857>

Permalink: <https://www.biodiversitylibrary.org/partpdf/319094>

Holding Institution

New York Botanical Garden, LuEsther T. Mertz Library

Sponsored by

BHL-SIL-FEDLINK

Copyright & Reuse

Copyright Status: Public domain. The BHL considers that this work is no longer under copyright protection.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.