vernal grass (*Anthoxanthum odoratum*), yellow oat-grass (*Avena flavescens*), tall oat-grass (*Avena elatior* or, in the botanical section, *Arrhenatherum avenaceum*), crested dog's-tail (*Cynosurus cristatus*), sheep's fescue (*Festuca ovina*), red fescue (*F. rubra*), perennial rye-grass (*Lolium perenne*), Italian rye-grass (*L. italicum*), wood meadow-grass (*Poa nemoralis*), and rough-stalked meadow-grass (*P. trivialis*). All these species are advertised by our seedsmen, but only three, tall oat-grass and the rye-grasses, are used in the United States in more than an incidental way.

The common names are of interest. The species have for the most part retained the English names when grown in this country, but *Agrostis alba*, known in England as bent-grass, is called here redtop; English fine bent-grass (*Agrostis vulgaris*) is called here Rhode Island bent; English cock's-foot is called here orchard grass; English smooth-stalked meadow-grass is called here Kentucky bluegrass or June grass; timothy in England has the alternative name cat's-tail grass. *Cynodon Dactylon*, our familiar southern pasture grass known in the United States as Bermuda grass and in the English West Indies as Bahama grass, is called in England creeping finger-grass. This assumes no agronomic importance there, as the climate is too cool and moist for its best development.

The author is director of the United Kingdom Seed Control Station, a fact reflected in the prominence given to data concerning the seed of grasses. There are two chapters devoted to the subject, one on the valuation and purchase of grass seeds, and one on the specification and compounding of grass seed mixtures. In the botanical section there are cuts illustrating the "seed" (usually the florets) of the commercial species and of the common weed seeds found as impurities in grass seed.

The work is a valuable résumé of British agrostology and should be in the hands of all interested in that subject. However, the problems of grass culture in America are so different from those considered by ARMSTRONG that agrostologists in this country will receive little aid. Our problems have to do with the cultivation of grasses under conditions practically unknown in the British Isles.—A. S. HITCHCOCK.

NOTES FOR STUDENTS

Biology of rusts.—Among recent publications on rusts, GASSNER'S[3] account of his extensive studies in Uruguay gives the first comprehensive picture of the grain rust vegetation of that part of the world. Although the investigations were mostly made in the neighborhood of Montevideo, the observations and

[3] GASSNER, G., Die Getreideroste und ihr Auftreten im subtropischen östlichen Südamerica. Centralb. Bakt. II. 44:305–381. 1915.

———, Untersuchungen über die Abhängigkeit des Auftretens der Getreideroste vom Entwicklungszustand der Nährpflanze und von äuseren Faktoren. *Ibid.* II. 44: 512–617. 1915.

conclusions are applicable not only to Uruguay but also to the adjoining province of Buenos Aires in Argentine, whose climate is similar to that of Uruguay. The geographical and ecological aspects of the subject are presented in two papers. The first deals with the species and biological races of grain rusts in the region under consideration, and with their seasonal distribution. The second treats of the influence of external factors on the occurrence of rusts. Of this long account only the salient features can be noted.

Only 4 species of grain rusts occur in the La Plata region of South America. These are *Puccinia graminis*, *P. triticina*, *P. coronifera*, and *P. Maydis*. *P. graminis* infects strongly wheat, barley, and *Lolium temulentum;* less virulently oats, *Lolium perenne*, *Dactylis glomerata*, and *Alopecurus pratensis;* while rye, European oats, *Lolium multiflorum*, and *Phleum pratense* are rarely infected. On other grasses it is not found. From cultures which seemed to indicate that this rust could be transferred from wheat to barley, and from rye, oats, barley, *Lolium temulentum*, and *Dactylis glomerata* to wheat, the author is inclined to believe that only a single biological race is present, which in its choice of hosts does not coincide fully with any of the established races. Although others have noted variations in the degree of fixity of biological races of rusts in different regions, it may nevertheless be assumed with reasonable certainty that further study will reveal more than one specialized form in the La Plata region, and that forms as distinct in other regions as that on wheat on the one hand, and that on oats and *Dactylis glomerata* on the other, will not be found to be identical in Uruguay. With regard to the occurrence of *Puccinia graminis* on the grain crops, it was found that the fungus was generally absent from both wheat and barley during the winter and spring. Some years wheat is entirely free from this rust, and in general the plants are not attacked until they are nearly mature, so that this rust is of little economic importance in the culture of wheat. It is the only rust that occurs on barley. Rye and oats are rarely attacked, but the native variety of oats suffers more severely than imported European types.

Puccinia triticina occurs only on wheat and rye. It is found on wheat in the fields at all times of the year, and on plants of all ages, except in the earliest stages of growth. Infections on rye are rare and only uredospores are produced. The opportunity to prove by cultures and observations that this rust occurs on rye was unusually favorable, because *P. dispersa*, with which it might be confused, does not occur in the La Plata region.

Puccinia coronifera was found on *Avena sativa*, *A. fatua*, *Lolium perenne*, *L. temulentum*, and rarely on *L. multiflorum*. The biological race on oats is different from that on *Lolium*. A striking difference in susceptibility exists between native oats and European varieties. The native type is only lightly attacked, while the European varieties are entirely destroyed, so that their cultivation in this region is impossible.

Puccinia Maydis occurs in Uruguay only on maize, and not on sorghum. Maize is usually planted from October to January, and the rust begins to appear in December and January. The infection, however, is not sufficiently severe to cause perceptible damage to the crop.

In the second paper, dealing with the influence of external conditions on the occurrence of rust infection, the author points out that in dealing with problems of this kind it is necessary to take into consideration the effect of the state of development of the plant itself. In regard to this question he finds, as others had noted, that, within wide limits, the age of plant organs has little to do with their susceptibility to infection by uredospores and aecidiospores, but that there is, nevertheless, an age limit beyond which infection does not take place. This limit GASSNER finds coincides with that stage of development of an organ at which teleutospore formation begins. Leaves and stems on which the production of teleutospores has begun are no longer capable of infection. This period varies with different rusts. For example, leaves which are producing teleutospores of *Puccinia triticina*, and hence no longer capable of infection by that fungus, can still be infected by *P. graminis*, since teleutospores of *P. graminis* are produced on leaves which have reached a more advanced stage of maturity than those on which teleutospores of *P. triticina* are produced. A peculiar condition of immunity of seedlings of wheat, rye, and oats to the attacks of *P. graminis* was observed. Seedlings of these plants are infected only from January to April. For *P. triticina* and *P. coronifera* and *P. Maydis* no such immunity for the young stages of the host plants was observed. These facts make it imperative that in a study of the influence of seasonal and climatic conditions on the occurrence of rust, only plants of the same state of development should be compared. This condition was met by the author by sowing the various grains at regular intervals throughout the year, so that practically all stages were available for observation at all seasons. The results of this long series of observations can barely be mentioned. It should be stated, however, that the indefiniteness of the results indicates that the problem cannot be settled by observation alone, and that an experimental analysis with control of all the factors involved is necessary before the effect of the individual constituents of the environment can be determined. In general GASSNER believes that the environment acts not directly on the fungus itself, but indirectly through the effect on the host. He finds that the yearly seasonal changes do not affect the occurrence of these 4 grain rusts alike. *P. graminis* is found from the beginning of summer to the beginning of winter; *P. triticina* and *P. coronifera* are to be found producing new infections at all seasons; while *P. Maydis* occurs from midsummer until autumn. A favorable effect of high relative humidity for rust development could not be observed, for the period of highest relative humidity, the winter, was also the period of least rust development. It is, of course, a question to what extent the effect of humidity was obscured by other factors, especially low temperature. In general, high temperatures appear to influence the host plant in such a way as to favor rust development, but isothermal periods in spring and in autumn are not characterized by equal intensity of rust development. It may be a matter of considerable significance to agriculture that the addition of fertilizers does not increase the susceptibility of the grains to rust infection. High moisture content of the soil was favorable for rust development. Slope and drainage consequently had an influence only in so far as the soil moisture content was affected thereby.

A more direct attack upon the problem of the influence of environmental factors on the development of rusts was undertaken by MAINS.[4] In his work the effect on *Puccinia coronata* and *P. Sorghi* of a number of factors, partly external and partly internal to the host, was studied under controlled conditions. It was found that low temperatures (13–15°) retard the development of these rusts, and that there is also an upper limit in the neighborhood of 30° beyond which growth of the parasite does not take place. Both wet soil and a saturated atmosphere favor the development of rusts, to the highest degree when both factors are present simultaneously. Absence of any of the mineral elements necessary for plant growth does not prevent infection, but decreases the number of pustules produced. The light relations are of special interest as giving an indication of the mode of nutrition of rusts. Light as such is not necessary for the development of the parasite; if, however, the host has been depleted of carbohydrates by being kept in the dark, no rust development takes place. Light, therefore, acts indirectly in so far as it is necessary for the production of carbohydrates for the nourishment of the fungus. For the same reason, rust does not develop in the absence of carbon dioxide on plants which have been deprived of carbohydrates. *Puccinia Sorghi* develops in the dark on sterile seedlings of *Zea Mays* and upon pieces of leaves supplied with solutions of starch, cane sugar, dextrose, maltose, and dextrin, but is not able to grow upon these substances directly. From these interesting experiments the author concludes that rusts are dependent for their nourishment upon some of the intermediate products of carbohydrate metabolism in leaves.

In continuation of his observations on the wintering of rust fungi, TREBOUX[5] reports a number of cases in the vicinity of Riga of the hibernation of rusts by means of a persistent mycelium. The observations were made in February, March, and April, when the melting snow had uncovered the host plants, and before infection from external sources had been possible. When the host plants were brought into a warm room further development of unopened sori was observed in *Puccinia dispersa* on *Secale cereale* and *S. montanum; P. obscura* on *Luzula pilosa* and *L. campestris; P. arenariae* on *Moehringia trinervia; P. Poarum* on *Poa pratensis* and *P. annua; P. agropyrina* on *Agropyrum repens; Uredo Airae* on *Aira caespitosa;* and *Thecopsora Pirolae* on *Pirola rotundifolia*. In addition to these, field observation showed the

[4] MAINS, F. B., The relation of some rusts to the physiology of their hosts. Amer. Jour. Bot. 4:179–220. *pls. 2.* 1917.

[5] TREBOUX, O., Überwintering vermittels Mycels bei einigen parasitischen Pilzen. Mycel. Centralb. 5:120–126. 1914.

development of uredinia in early spring from persistent mycelia of *Puccinia glumarum* on *Secale cereale; P. coronata* on *Agrostis vulgaris* and *Agropyrum repens; P. Carduorum* on *Carduus crispus; Uredo Festucae* on *Festuca ovina;* and probably also of *Melampsora Lini* on *Linum catharticum*, and *P. bromina* on *Bromus mollis.*

In the neighborhood of Vienna, HECKE[6] finds that, as ERIKSSON and HENNING have occasionally observed in Sweden, *Puccinia glumarum* sometimes persists through the winter by means of hibernating mycelium in the leaves of wheat. In 1914, rust pustules were observed in abundance on the old leaves in March, and from that time the rust was present continuously. No such interruption of continuity between the spring outbreak and the summer outbreak as was reported by ERIKSSON was observed. An abundance of wintering mycelium the author regards as one of the conditions determining the occurrence of rust epidemics or "rust years."

Brief notes on the wintering of the timothy rust, *Puccinia Phleipratensis*, have been published by MERCER[7] and by HUNGERFORD.[8] MERCER states that in North Dakota it is difficult to find uredospores of this rust after the first hard frost, and that the fungus is not active until late July. The new pustules are on new growths in all cases, and therefore do not arise from hibernating mycelia, by means of which ERIKSSON and HENNING believe this rust lives through the winter in Sweden. Uredospores from rusted timothy straw exposed to the weather, but kept from moisture by means of open tin cylinders, did not germinate at any time from October to March.

In Wisconsin, HUNGERFORD finds that this rust behaves quite differently. Here uredospores capable of germinating were collected in the field in the months of October, November, December, January, and March. On plants that were taken up in March, sori developed on the new growth and also on flecked places on the old leaves. The latter undoubtedly arose from a hibernating mycelium.

MAINS[9] reports the wintering of *Coleosporium* (in Michigan?) by means of hibernating mycelia. Uredospores capable of germination were collected in February and May. On plants brought in during January, new pustules developed on the old rosette leaves.

The fact that the position of spore pustules of rusts, whether on the upper or the lower surface of infected leaves, is usually included in the diagnosis of

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[6] HECKE, L., Zur Frage der Überwinterung des Gelbrostes und das Zustandekommen von Rostjahren. Naturw. Zeitschr. Forst.- u. Landwirtsch. 13:213–220. 1915.

[7] MERCER, W. H., Investigations of timothy rust in North Dakota during 1913. Phytopath. 4:20–22. 1914.

[8] HUNGERFORD, C. W., Wintering of timothy rust in Wisconsin. Phytopath. 4:337–338. 1914.

[9] MAINS, F. B., The wintering of *Coleosporium Solidaginis*. Phytopath. 6:371–372. 1916.

species has led GREBELSKY[10] to undertake a study of this characteristic, in order to determine its constancy for given species and to discover the factors influencing the distribution of the sori. A statistical study of 42 species of rusts gave evidence that with few exceptions the uredinia are formed on the stomate-bearing side of the leaf. Especially striking illustrations are found in such forms as *Melampsora Larici-retusae*, which infects two species of willows, *Salix reticulata* with stomata only on the lower surfaces of the leaves, and *S. retusa* with amphigenous stomata. Here the distribution of the uredinia corresponds to that of the stomata, exceptions occurring only in leaves on which the infection is unusually severe. Some cases are noted, among them *Puccinia glumarum*, in which the sori do not occur on both sides of the leaves, although the stomata are amphigenous.

In a number of plants examined histologically it was found that the young sori always originate beneath the stomata; coating parts of the stomatal surfaces with wax led to the suppression of sori. By turning leaves with amphigenous stomata, but on which sori were normally produced on one side only, the author was able to shift the position of the sori to the other side of the leaves. Mere cultivation in the greenhouse induced sori normally present on one side of a leaf to become amphigenous. This result is attributed to the absence, on plants grown in the greenhouse, of wax coating by which the author believes the formation of sori is normally suppressed on the most heavily coated side of the leaf.

Some time ago, MORGENTHALER[11] showed that the production of teleutospores by rusts was determined by conditions internal to the host rather than by external factors. Further evidence of this relation has been brought out by GASSNER[12] in his studies of the South American grain rusts. The observations on *Puccinia triticina*, *P. coronifera*, *P. graminis*, and *P. Maydis* all indicate that teleutospore formation is associated with a definite state of maturity of the infected organ. Particularly clear and striking evidence that seasonal changes have little influence was obtained in the case of *P. triticina* and *P. coronifera*. On plants sown at intervals throughout the year, these rusts regularly produce uredospores followed by teleutospores. In *P. triticina* on wheat, production of teleutospores begins shortly before the appearance of the ear. This fact is particularly noticeable in varieties requiring different lengths of time for development. Seasonal influence is evident only in so far as it affects the development of the host. The teleutospores of *P. coronifera* on oats are also formed at the time of the appearance of the head, but with *P. graminis* on wheat, barley, and oats teleutospore formation does not begin

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[10] GREBELSKY, F., Die Stellung der Sporenlager der Uredineen und deren Wert als systematisches Merkmal. Centralb. Bakt. II. 43:645–662. *figs. 12*. 1915.

[11] Rev. BOT. GAZ. 56:162. 1913.

[12] GASSNER, G., Die Teleutosporenbildung der Getreiderostpilze und ihre Bedingungen. Zeitschr. Bot. 7:65–120. 1915.

until the plants have reached a more advanced state of development. In general, the production of teleutospores appears to be associated with the depletion of the carbohydrates of the leaves. A direct influence of climatic or seasonal factors does not appear to exist.

DIETEL,[13] in the third instalment of his studies on the conditions affecting the germination of teleutospores, reports that the teleutospores of *Puccinia Malvacearum* germinate and form sporidia only in a saturated atmosphere. If the degree of saturation is only slightly below 100 per cent, normal germination does not take place. Furthermore, germination takes place only when water is abundantly supplied through the pedicels. When leaves of *Althea rosea* bearing rust sori were suspended in a saturated atmosphere in a bottle, but with the stems projecting into the air through the cork, no germination took place, although the leaves remained turgid. When the petioles were immersed in water, germination of the teleutospores in the sori began immediately. The author's interpretation of these observations is that the water necessary for germination is supplied to the teleutospores through the pedicels, but that an adequate supply is possible only under conditions of complete turgor of the host, and in a saturated atmosphere. The sporidia of *Puccinia Malvacearum*, it was noted, lose their vitality in one hour in an atmosphere of 90 per cent saturation, and in 10–16 hours even in a saturated atmosphere.

An unusual case of mycelial distribution is reported by FISCHER[14] for *Puccinia Dubyi*. The mycelium of micropuccinias is usually strictly localized, but in *P. Dubyi* FISCHER finds that the mycelium extends from the older infected leaves of the host (*Androsace*) through the stems to the newly formed whorls where new sori are produced. Instead of one crop of teleutospores usual in micropuccinias, this form produces a succession of sori through the season.

FROMME[15] reports that the germ tubes of the uredospores of *Puccinia Rhamni* are negatively geotropic, and that as a rule the germ tubes grow out from the pores on the non-illuminated side of the spore. Of 200 germ tubes issuing from spores illuminated on one side, 86 per cent had grown away from the light. The germ tubes of spores in darkness grew equally well in all directions. This property of the germ tubes undoubtedly is of significance in the process of infection.

Remarkable morphological changes in *Puccinia Ellisiana* and *P. Andropogonis* due to the influence of the host have been reported by LONG.[16] Both of

[13] DIETEL, P., Versuche über die Keimungsbedingungen der Teleutosporen einiger Uredineen III. Centralb. Bakt. II. **42**:698–705. 1915.

[14] FISCHER, E., Beitrage zur Biologie der Uredineen. 6. Mycol. Centralb. **5**:113–119. 1914.

[15] FROMME, F. D., Negative heliotropism of urediniospore germ tubes. Amer. Jour. Bot. **2**:82–85. *figs. 2.* 1915.

[16] LONG, W. H., Influence of the host on the morphological characters of *Puccinia Ellisiana* and *P. Andropogonis*. Jour. Agric. Research **2**:303–319. 1914.

these rusts have their telial generations on species of *Andropogon*, and are distinguishable by evident morphological differences in their uredospores. *P. Ellisiana* has its aecidial generation on species of *Viola*, while the aecidial generation of *P. Andropogonis* occurs on species of *Pentstemon*. LONG now finds that *P. Ellisiana* will readily produce aecidia on *Pentstemon* also, but these aecidia resemble those of *P. Andropogonis*. More remarkable still is the fact that when plants of *Andropogon* are reinfected with aecidiospores of *P. Ellisiana* from *Pentstemon*, the resulting uredospores have all the characteristics of uredospores of *P. Andropogonis*. This rust can then not again be readily transferred to its original aecidial host, the violet. Conversely, *P. Andropogonis* can be made to infect species of *Viola*, but with great difficulty. If the aecidiospores thus obtained are sown on *Andropogon*, the resulting uredospores have all the characteristics of *P. Ellisiana*. In each case the morphological characteristics of the telial generation are determined by the aecidial host. From these facts the author concludes that *P. Ellisiana* and *P. Andropogonis* are but forms of one species. Since the transfer of *P. Ellisiana* to *Pentstemon* takes place readily, while the transfer of *P. Andropogonis* to *Viola* is accomplished with difficulty, he believes that in nature the transformation of *P. Ellisiana* to *P. Andropogonis* through the aecidial host, *Pentstemon*, is continually going on. The possible bearing of this discovery on the unexplained phenomena in the life histories of many rusts, and its consequent economic importance, are at once apparent.

Rust sori produced entirely within the tissue of the host do not seem to be of uncommon occurrence. To the number of known cases ADAMS[17] adds one of the occurrence of internal uredinia of *Uromyces Caryophyllinus* in the leaves of carnations, and COLLEY reports the finding of internal telia of *Cronartium ribicola* in the petioles of infected currant leaves. To COLLEY'S list of investigators who have reported internal sori of rusts should be added the names of BEAUVERIE,[18] who described internal sori in the seeds of grains and other grasses, and of REYNOLDS,[19] who mentions internal telia of *Puccinia Xanthii* in the leaves of *Xanthium canadense*.

In view of ARTHUR'S[20] recent revision of the rusts of the type of the orange rust on the blackberry in the United States, KUNKEL'S[21] paper, in which he clears up the anomalous situation created by his discovery[22] that the most

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[17] ADAMS, J. F., Internal uredinia. Mycologia **8**:181–182. *pl. 1.* 1916.

[18] BEAUVERIE, J., Les germes de Rouilles dans l'intérieur des semencis de gramineés. Rev. Gen. Bot. **25**:11–27. *figs. 10.* 1914.

[19] REYNOLDS, E. S., Relations of parasitic fungi to their host plants. BOT. GAZ. **53**:365–395. 1912 (p. 381).

[20] ARTHUR, J. C., Orange rusts of *Rubus*. BOT. GAZ. **68**:501–515. *fig. 1.* 1917.

[21] KUNKEL, L. O., Further studies of the orange rusts of *Rubus* in the United States. Bull. Torr. Bot. Club **43**:559–569. *fig. 1.* 1916.

[22] Rev. BOT. GAZ. **60**:80–81. 1915.

common orange rust of the blackberry is a short cycle form of the type of *Endophyllum*, needs merely to be mentioned here. The discovery of this rust, now known as *Kunkelia nitens* (Schwein.) Arthur, is a striking illustration of the proposition of TRANZSCHEL and of FISCHER, which may be generalized in the statement that the aecidial hosts of long cycle rusts often bear short cycle rusts whose teleutospores resemble one of the spore forms of the long cycle rust.

BARTHOLOMEW[23] finds that the mycelium producing the thin-walled spores which occur together or separately in the uredinia of the fern rust *Hyalopsora Polypodii* is binucleate throughout, and that there is therefore no reason for regarding the two spore forms as other than uredospores.

A very extensive investigation of the biological forms of *Puccinia graminis* in the area extending from the upper Mississippi valley through the northern great plains to the intermountain area of Washington and Idaho has been made by STAKMAN and PIEMEISEL.[24] Uredospores of *P. graminis* from about 30 species of grasses in this region were systematically sown on the common cereals and a number of other grasses, and in like manner uredospores from the cereals were sown on a large number of other grasses. The results of the many hundreds of cultures are tabulated in a readily comprehensible form. Six biological forms were isolated; of these, one, *P. graminis Tritici compacti*, is new. The others are the forms formerly distinguished, namely, *P. graminis Tritici*, *P. graminis Secalis*, *P. graminis Avenae*, *P. graminis Agrostis*. The extent of this work and the thoroughness with which it was carried out place the problem of the differentiation of biological races of *Puccinia graminis* in a much clearer light than has heretofore been accomplished. It is found that each biological form attacks a group of grasses not necessarily related. Within each group all degrees of susceptibility exist; the range from complete susceptibility to complete immunity is therefore gradual. The groups susceptible to the various biological races overlap considerably, so that the same grass may be host to a number of biological races of rust. Thus barley, rye, and *Bromus tectorum* have been infected by all of the 6 races of *P. graminis;* while oats has been infected by all except *P. graminis Tritici compacti*. The forms can nevertheless be differentiated by means of other grasses which are distinctly susceptible to some and immune to others of the biological races. These facts will probably explain the apparently different degrees of specialization of the forms of *P. graminis* by observers in different geographical regions. Within the region studied by the authors, no geographical specialization was observed. —H. HASSELBRING.

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[23] BARTHOLOMEW, E. T., Observations on the fern rust *Hyalopsora Polypodii*. Bull. Torr. Bot. Club **43**:195–199. *figs. 3.* 1913.

[24] STAKMAN, E. C., and PIEMEISEL, F. J., Biologic forms of *Puccinia graminis* on cereals and grasses. Jour. Agric. Research **10**:429–495. *pls. 7.* 1917.