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Evolutionary biology and interaction among the anastomosis groups of *Rhizoctonia* spp.

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Abstract

Rhizoctonia solani Kuhn and other *Rhizoctonia* spp. are the plant pathogenic fungi widespread in the world and in both cultivated and noncultivated soils. *Rhizoctonia* spp. are readily isolated from diseased plants and soils, which differ in their pathogenicity, cultural, morphological and physiological characteristics. Identification of species and intraspecific groups (ISGs) is sometimes very difficult, due to the absence of the authentic cultures, which hinders mycological and pathological studies. The genus *Rhizoctonia* can be identified using various techniques such as, sequence analysis of ITS regions, DNA fingerprinting and the rDNA coding sequence. The introduction of the concept of anastomosis groups (AGs) or intraspecific groups has also aided species and subspecies identification. There are 13 different anastomosis groups exists in *Rhizoctonia solani* of which AG 1-4 were strong pathogenic on many plants and AG 6-10 were orchid mycorrhizae. Analysis of restriction fragment length polymorphisms (RFLPs) and the sequences within ribosomal RNA genes (rDNA) among different anastomosis groups of *R. solani* isolates exhibited DNA base sequence homology and diverging evolutionary affinities for hyphal anastomosis. More recently, ribosomal DNA (rDNA) sequences have been used to study the genetic relationships between AG of *R. solani*. The ecology and epidemiology of each ISG of *R. solani* must be investigated in order to gain a better understanding of this important group of fungi.

Keywords: Anastomosis groups, Identification, *Rhizoctonia solani*, *Rhizoctonia* spp.

Introduction

Rhizoctonia solani Kuhn and other *Rhizoctonia* spp. are the plant pathogenic fungi widespread in the world and in both cultivated and noncultivated soils. Many isolates of *Rhizoctonia* spp. are readily isolated from diseased plants and soils, which differ in pathogenicity and morphology, as well as cultural and physiological characteristics. Based on these differences, many species and intraspecific groups (ISGs) have been described; however, identification of species and ISGs is sometimes very difficult, owing to the absence of the authentic cultures, which hinders mycological and pathological studies. Fortunately, this situation has been put in order through the efforts of many researchers through characterization of the genus *Rhizoctonia* using various techniques as sequence analysis of ITS regions, DNA fingerprinting and the rDNA coding sequence. The introduction of the concept of anastomosis groups (AGs) or intraspecific groups has also aided species and subspecies identification.

Rhizoctonia* spp. and *Rhizoctonia solani***Rhizoctonia* spp.**

The genus concept of *Rhizoctonia* spp. was first established by de Candolle (1815) [14] after which, more than one hundred species of it have been described. Based on morphology, dimension of sclerotia and monilioid cells and their pathogenicity these species are distinguished from one another. According to available information, *Rhizoctonia* is considered a genus of basidiomycetous imperfect fungi, characterized as follows (Ogoshi 1975a) [46] branching near the distal septum of cells in young, vegetative hyphae; (b) formation of a septum in the branch near the point of origin; (c) construction of the branch; (d) dolipore septum; (e) no clamp connection; (j) no conidium, except monilioid cells; (g) sclerotium not differentiated into rind and medulla; and (h) no rhizomorph. In terms of these characteristics, only forty-nine of one hundred species of *Rhizoctonia* reported up to now are true *Rhizoctonia* spp., eleven are not, and forty are dubious (Ogoshi 1984 and 1987) [47, 48].

Rhizoctonia isolates are divided into three groups, if the above concept is adopted: One is the multinucleate *Rhizoctonia*, which has three or more nuclei per cell, larger hyphae and teleomorph in the genus *Thanatephorus* Donk. Another is the binucleate *Rhizoctonia*, which has only two nuclei per cell (rarely one or three), smaller hyphae (4-7 µm), and teleomorph in the genus *Ceratobasidium* Rogers.

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The third includes *R. oryzae* and *R. zaeae*, which are multinucleate and have teleomorphs in the genus *Waitea* Warcup and Talbot.

Rhizoctonia solani

R. solani (*Thanatephorus cucumeris*) is the representative of *Thanatephorus* which is multinucleate having three other species, *Thanatephorus sterigmaticus* (Talbot 1965)^[66], *Thanatephorus orchidicola* (Warcup *et al.* 1966)^[69] and *Thanatephorus corchorus* (Tu *et al.* 1977)^[67]. However, these three species are not frequently isolated and are thought to have limited distribution.

In the last two decades some important developments were made in the study of *R. solani*: (a) the concept of *R. solani* as a species became clearer; (b) the concept of intraspecific groups of *R. solani* was introduced and became well established; and (c) studies on the teleomorph of *R. solani* were developed, and the taxonomic classification was determined (Ogoshi 1987)^[48]. Parmeter and Whitney (1970)^[52] gave a detailed description of the characteristics specific to *R. solani*: Teleomorph is *Thanatephorus cucumeris* (Frank) Donk, hyphae are multinucleate, and hyphae and sclerotia have characteristics typical of *Rhizoctonia*.

Intraspecific grouping of *R. solani*

Observations show that *R. solani* is varied in its pathogenicity, sclerotial morphology, cultural appearance on media, physiological characteristics, etc, this fungus has long been thought to have many ISGs, and indeed there have been many attempts to divide *R. solani* into logical groups. These attempts fall basically into two categories: those based on the differences in pathogenicity, cultural appearance, morphology, physiology, or ecology; and those based on hyphal anastomosis on culture media (Ogoshi 1987)^[48].

Morphological and Pathological Grouping was given by Exner (1953)^[17] where she recognized four formae speciales, namely, *solani*, *microsclerotia*, *sasakii*, and *timsii*, in *Pellicularia filamentosa* (*T. cucumeris*). Takahashi & Matsuura (1954)^[65] divided *R. solani* into six groups by morphology (mainly of sclerotia) and pathogenicity, resulting in the addition of formae speciales *betae* and *compacta* to Exner's groups.

Hyphal Anastomosis Grouping are observed when isolates of *R. solani* are paired 2-3 cm apart on a medium (usually 2% water agar) in a petri dish, their mycelia grow and overlap, which can be observed under a light microscope at low magnification. If hyphal fusion occurs, these isolates belong to the same anastomosis group, and often, attraction of hyphae and death of fused cells are observed (McCoy and Kraft 1984)^[38]; Yokoyama and Ogoshi 1984^[47]. If fusion, attraction, and hyphal death do not occur, the isolates belong to different AGs. Accordingly, attraction and hyphal death are reliable clues for detecting hyphal fusion.

Mechanism of Hyphal Fusion

The process of perfect fusion of hyphae of *R. solani* is summarized as follows: hyphal growth, secretion of one or more attracting substances, attraction to the substances, contact of hyphae, cessation of hyphal growth, formation of branchlike projections, dissolution of cell walls, and connection of protoplasts (Yokoyama *et al.* 1983, 1985, 1985a)^[73, 72, 74]. Imperfect fusion differs in that dissolution of cell walls is followed by death of cells (Yokoyama and Ogoshi 1984)^[47]. An isolate of an AG can recognize and fuse only with members of the same AG. At present, four

categories of anastomosis (C3 to C0) defined by Carling *et al.* (1996)^[7] have been accepted by many researchers. These are useful for a better understanding of the genetic diversity of *R. solani* populations, because of the background genetically supported by vegetative or somatic compatibility (VC or SC) of confronted isolates (MacNish *et al.* 1997)^[34]. Each of categories is as follows:

C3: walls fuse; membranes fuse, accompanied with protoplasm connection; anastomosis point frequently is not obvious; diameter of anastomosis point is equal or nearly equal hyphal diameter; anastomosing cells and adjacent cells may die, but generally do not. This category occurs for the same anastomosis group, same vegetative compatibility population (VCP) and the same isolate.

C2: wall connection is obvious, but membrane contact is uncertain; anastomosing and adjacent cells always die. This category occurs in same AG, but not between different VCPs.

C1: wall contact between hyphae is apparent, but both wall penetration and membranemembrane contact do not occur; occasionally one or both anastomosing cells and adjacent cells die. This category occurs between different AGs or in the same AG.

C0: no reaction. This category occurs between different AGs. In general, hyphal fusion occurs at a high frequency (50% \geq) within members of the same AG, with the exception of non-self-anastomosing isolates (Hyakumachi and Ui, 1988)^[24]. On the other hand, hyphal fusion among members of different AGs occurs at either a low frequency (\leq 30%) or no fusion occurs. *Rhizoctonia* isolates giving C3 to C1 reactions in anastomosing test have been taken to be the same AG.

Anastomosis Groups

Martin *et al.* (1983)^[35] found AG1 on tall fescue (*Festuca arundinaceae* Schreb). Martin and Lucas (1984)^[36] found AG1-IA on turfgrass, and AG5 causing brown patch on turfgrass. Hurd and Grisham (1983)^[23] found AG2-IIIB causing brown patch of turfgrass. Oniki *et al.* (1986)^[50] found AG2-2IV causing large patch on turfgrass. Hyakumachi *et al.* (1998)^[1] found *R. solani* AG2-2 IIIB for all their isolates from *Agrostis palustris* Huds. in Japan. Herr and Fulton (1995)^[20] found AG2-2 IIIB from *A. palustris* in Ohio, as well as AG1-IA from tall fescue. Sneh *et al.* (1991) reported AG1 and AG2-2 associated with turfgrasses. Burpee and Martin (1992)^[5] in their review of *Rhizoctonia* species associated with turfgrasses, listed AG1, AG2-2, AG4 and AG5. Zhang and Dernoeden (1995)^[75] cite studies which list six AG on both warm and cool season turfgrasses including: AG1, AG2-2, AG3, AG4, AG5 and AG6. Parmeter *et al.* (1969)^[53] reported that *R. solani* should be divided into AGs 1, 2, 3, and 4, based on hyphal fusion. They also discussed the possibility of the existence of additional anastomosis groups and the possibility of "bridging" isolates, *i.e.* those capable of anastomosis with members of two or more' groups. This speculation has now been verified (Homma *et al.* 1983^[22], Kuninaga *et al.* 1979^[31], Neate and Warcup 1985^[43], Ogoshi 1975^[45], Rovira *et al.* 1986^[58]). Ogoshi (1975)^[45] attempted to divide the Japanese isolates of *R. solani* into groups by hyphal fusion. Tests of hyphal fusions among 255 isolates indicated that 242 could be assigned to one of five AGs (AG-I-AG-5). The remaining 13 isolates were 'not assigned to any AG. AG-2 was further divided into type-1 and type-2 (AG-2-1 and AG-2-2) based on the relative frequency of hyphal fusion, with fusion between two isolates from the same type in AG-2 being frequent, but that of frequency between two isolates from different types in AG-2 being rare (Ogoshi 1975)^[45].

Kuninaga *et al.* (1978) added AG-6 and AG-BI (bridging isolates) to Ogoshi's six groups.

Furthermore, Homma *et al.* (1983) [22] reported an eighth group, AG-7. Recently, Neate & Warcup (1985) [43] reported a ninth group, AG-8, which is thought to be the primary pathogen responsible for "bare patch" of cereals. To date, isolates of *R. solani* have been assigned to 13 anastomosis groups (AG) and some of which include several subgroups and isolates of *R. zae* and *R. oryzae* have been assigned to WAG-Z and WAG-O, respectively (Sneh *et al.* 1991; Carling *et al.* 1999, 2002a [13, 10]). Furthermore, AG-8 is also a "bridging" isolate, as it can fuse with AG-2 and AG-BI, though frequency of fusion depends on isolates and related groups (Rovira *et al.* 1986) [58]. AG-8 and AG-BI differ in their thiamine requirement; the former is thiamine autotrophic and the latter, auxotrophic (discussed in a later section). The behavior of bridging isolates is interesting from the viewpoint of the phylogeny of *R. solani*.

In general, there is no contradiction in the conventional anastomosis grouping system by taking anastomosis frequency into consideration. However, two exceptional cases where anastomosis frequency mismatched with morphological, physiological and pathogenic characteristics have been reported from tobacco (Nicoletti *et al.* 1999) [44] and soybean (Naito and Kanematsu 1994) [41]. These demonstrate the limitations of using hyphal anastomosis as the sole criteria for characterization and identification of closely related fungi. In addition, it is not easy to determine the subgroup of isolates within the same AG because no differences occur in their anastomosis reaction. Thus, in order to determine AGs or subgroups in *R. solani*, genetic analysis using molecular approaches that employ multiple genetic loci is needed.

Isolates of *R. solani* that exhibits DNA base sequence homology and affinities for hyphal anastomosis may represent a diverging evolutionary unit (Kuninaga and Yokosawa 1980) [29]. This hypothesis is supported by analysis of restriction fragment length polymorphisms (RFLPs) and the sequences with in ribosomal RNA genes (rDNA) among different anastomosis groups of *R. solani* (Vilgalys and Gonzalez 1990 [68]; Gonzalez *et al.* 2001 [19]; Carling *et al.* 2002 [12]). More recently, ribosomal DNA (rDNA) sequences have been used to study the genetic relationships between AG of *R. solani*. Boysen *et al.* (1996) [4] studied the relatedness of *R. solani* AG4 isolates based on sequences of the rDNA internal transcribed spacer region (ITS, composed of ITS1, 5.8S, ITS2 regions). Kuninaga *et al.* (1997) sequenced the ITS of 45 Japanese isolates of *R. solani* from different anastomosis groups, and found that isolates of each AG clustered together. Salazar *et al.* (1999 and 2000) [59, 60] sequenced the ITS of *R. solani* AG2 isolates and used these data to examine the relationships between and within AG2 subgroups. These results suggested that sequence analysis of the ITS region could be used to identify AG subgroups.

Characteristics of anastomosis groups and subgroups of *Rhizoctonia solani*

1. AG-1: IA, IB, IC, ID

AG-1 IA (Li and Yan 1990 [32]; Sneh *et al.*, 1991; Fenille *et al.*, 2002 [18]; Naito, 2004 [40]).

Symptoms: sheath blight, foliar blight, leaf blight, web-blight, head rot, bottom rot, and brown patch.

Host: rice, corn, barley, sorghum, potato, barnyard millet, common millet,

soybean, peanut, lima bean, cabbage, leaf lettuce, Stevia, turfgrass, etc.

There is a general tendency to attack aerial parts of the plants by this group of pathogens. Basidiospore infection of rice has been reported, but sclerotia are more important as an infection source. The optimum growth temperature is higher than those of AG-1 IB.

AG-1 IB (Sneh *et al.*, 1991; Naito, 2004 [40]; Yang *et al.*, 2005b [70]).

Symptoms: sheath blight, leaf blight, foliar blight, web-blight, root rot, damping off, head rot, and bottom rot.

Host: corn, sugar beet, common bean, fig, soybean, cabbage, lettuce, apple, pear, marigold.

AG-1 IC (Sneh *et al.*, 1991; Naito, 2004) [40].

Symptoms: damping-off, summer blight, foot rot, crown rot canker, and root rot.

Host: sugar beet, carrot, buckwheat, flax, soybean, bean, cabbage, pineapple and radish.

AG-1 ID (Priyatmojo *et al.*, 2001) [55].

Symptom: leaf spot.

Host: coffee.

This subgroup was recently reported in the Philippines (Priyatmojo *et al.*, 2001) [55]

2. AG-2: 2-1, 2-2 IIIB, 2-2 IV, 2-2 Lp, 2-3, 2-4, 2-BI.

AG-2-1 (Satoh *et al.*, 1997 [61]; Camporota and Perrin, 1998 [6]; Sneh *et al.*, 1991; Rollins *et al.*, 1999 [57]; Khan and Kolte, 2000 [26]; Naito, 2004 [40])

Symptoms: damping-off, leaf rot, leaf blight, root rot, foot rot, bottom rot, and bud rot.

Host: sugar beet, wheat, potato, cowpea, canola, rape, cauliflower, mustard, turnip, pepper, spinach, lettuce, strawberry, tulip, tobacco and clover.

AG-2-2 III B (Sneh *et al.*, 1991; Priyatmojo *et al.*, 2001 [55]; Naito, 2004 [40]).

Symptoms: brown sheath blight, dry root rot, root rot, brown patch, large patch, black scurf, stem rot, stem blight, *Rhizoctonia* rot, damping-off, stem rot, collar rot, and crown brace rot.

Host: rice, soybean, corn, sugar beet, elephant foot yam, saffron, turfgrass, *gladiolus* and ginger.

AG-2-2 IV: (Sneh *et al.*, 1991; Naito, 2004 [40]).

Symptoms: leaf blight, foliage rot, root rot, and stem rot.

Host: sugar beet, carrot, eggplant (*Solanum* Linn), pepper, spinach and turfgrass.

AG-2-2 LP: (Aoyagi *et al.*, 1998) [1].

Symptoms: large patch.

Host: Zoysia grass.

AG 2-3: (Naito and Kanematsu, 1994 [41]; Sumner *et al.*, 2003 [64]).

Symptoms: leaf blight and root rot.

Host: soybean.

AG-2-4: (Sumner, 1985) [63].

Symptoms: crown rot, brace rot, and damping-off.

Host: corn and carrot.

AG-2-BI: (Carling *et al.*, 2002b).

Symptoms: nonpathogenic.

Host: isolates, obtained only from soils and plants in forests.

(Formerly known as AG-BI.)

3. AG 3: PT, TB (Sneh *et al.*, 1991; Kuninaga *et al.*, 2000 [30]).

Symptoms: black scurf, leaf spot, target leaf spot, and damping-off.

Host: potato with black scurf symptoms, tobacco with target leaf spot symptoms.

4. AG-4: HG-I, HG-II, HG-III (Baird, 1996^[3]; Holtz *et al.*, 1996^[21]; Sneh *et al.*, 1991; Fenille *et al.*, 2002^[18]; Ravanlou and Banihashemi, 2002^[56]; Kuramae *et al.*, 2002^[18]; Naito, 2004^[40]).

Symptoms: damping-off, root rot, stem canker, fruit rot, and stem rot.

Host: pea, sugar beet, melon, soybean, common bean, snap bean, lima bean, carrot, spinach, taro, tomato, potato, alfalfa, elephant foot, beans, barley, buckwheat, cabbage, canola, turnip, carnation, cauliflower, Chinese chive, chrysanthemum, corn, cotton, tobacco, turfgrass, wheat and cauliflower.

5. AG-5 (Li *et al.*, 1998^[33]; Demirci, 1998^[15]; Sneh *et al.*, 1991; Ravanlou and Banihashemi, 2002^[56]; Eken and Demirci, 2004^[16]; Naito, 2004^[40]).

Symptoms: root rot, damping-off, black scurf, brown patch, and symbiosis (orchids).

Host: soybean, apple, barley, chickpea, common bean, lima bean, potato, strawberry, sugar beet, tobacco, turfgrass and wheat.

6. AG-6: HG-I, GV (Mazzola, 1997^[37]; Meyer *et al.*, 1998^[39]; Sneh *et al.*, 1991; Carling *et al.*, 1999^[13]; Pope and Carter, 2001^[54]; Naito, 2004^[40]).

Symptom: root rot, crater rot, and symbiosis (orchids).

Host: apple, wheat, carrot, and carnation.

7. AG-7: (Naito *et al.*, 1993^[43]; Baird and Carling, 1995^[2]; Carling, 1997, 2000^[8,9]; Carling *et al.*, 1998)^[11]

Symptoms: damping-off, root rot, and black scurf.

Host: carnation, cotton, soybean, watermelon and potato.

8. AG-8: (Sneh *et al.*, 1991; Naito, 2004^[40]).

Symptoms: bare patch.

Host: barley, potato and wheat.

9. AG-9: (Sneh *et al.*, 1991; Naito, 2004^[40]).

Symptoms: black scurf.

Host: potato, crucifers, wheat and barley.

10. AG-10: (Sneh *et al.*, 1991).

Symptoms: weak pathogenic.

Host: barley and wheat.

11. AG-11: (Kumar *et al.*, 2002).

Symptoms: damping-off and hypocotyls rot.

Host: barley, lupine, soybean, and wheat.

This group is considered as bridging isolates (anastomose with each members of AG-2-1, AG-2 BI, AG-8) (Carling *et al.*, 1996).

12. AG-12: (Kumar *et al.*, 2002)^[28].

Symptoms: symbiosis (orchids).

Host: *Dactylorhiza aristata* (Orchidaceae).

13. AG-13: (Carling *et al.*, 2002a)^[10].

Symptoms: none.

Host: cotton.

Summary

Taxonomic and epidemiological studies of *Rhizoctonia* are important at the level of both species and intraspecific group

in the same way that studies of intraspecific groups (formae speciales) of *Fusarium* have proven vital to our understanding of that important genus of fungi. Taxonomic differences among ISGs of *R. solani* are often closely related to ecological and epidemiological differences. For example, leaf blight of sugar beet in Japan is caused by *R. solani* AG-I IB and AG-2-2 IV, two epidemiologically distinct fungi. The former spreads only by mycelia, and the latter disseminates by both mycelia and basidiospores. Measures to control these two intraspecific groups must be considered accordingly. Life cycles and disease cycles of some ISGs of *R. solani* have been well studied; however, those of most have not.

Rhizoctonia solani includes 13 anastomosis groups, of which AG 1-4 were strong pathogenic on many plants and AG 6-10 were orchid mycorrhizae, new groups are still being identified. Field survival of sclerotia of the sheath-blight fungus of rice (*R. solani* AG-I IA), for example, has been studied for some time, yet the role of basidiospores in the disease cycle was not understood until recently, although spore formation in paddy fields had been frequently observed. A similar situation exists with *R. solani* AG-3 on potatoes, where spore formation on plant stems has been observed, yet their role in the disease cycle is obscure. Interestingly, however, it was reported that spores of AG-3 infected and caused leaf spots on tomato and eggplant (Kodama *et al.* 1982)^[27].

The ecology and epidemiology of each ISG of *R. solani* must be investigated in order to gain a better understanding of this important group of fungi. Descriptions of binucleate *Rhizoctonia* and multinucleate *Rhizoctonia* other than *R. solani* are absent from this report. These fungi are frequently isolated alone or in association with *R. solani*, and many are important plant pathogens. AGs, and possibly ISGs, are contained in other species of *Rhizoctonia* (Ogoshi *et al.* 1979, Oniki *et al.* 1985)^[31, 51], although they are less studied. Further taxonomic and epidemiological examinations of *Rhizoctonia* species are needed, and are anxiously anticipated.

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