

The pros and cons of monoculture fungus farming, in *Termitomyces*

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Abstract

Many organisms work together with organisms of other species, to be able to compete better for resources. Such a cooperation is called obligatory mutualism if both partners depend on each other for survival. An amazing form of mutualism is observed between *Termitomyces* and termites who cultivate these fungi. The termites cultivate the fungi on combs, which are constructed from plant material in chambers. The termites consume persistent plant material and put their faeces on the rims of these combs. The fungi are grown in monocultures on these combs where they extract the nutrients. Afterwards, the termites eat the fungi and the degraded plant material, thereby utilising the extracted nutrients. In other fungi than *Termitomyces*, research has shown that long-term cultivation in monocultures can lead to lower fungal growth and spore formation. This may indicate possibilities of increasing or maintaining production of the fungus when grown in a mixed culture. To select for plant components on which a mixed culture could be maintained, the degradation possibilities needed to be found. Therefore different *Termitomyces* strains were tested on 35 diverse substrates. To show the long term effect of cultivation in monocultures an evolution experiment on *Termitomyces* was performed. The fungi were examined during many generations and no obvious negative effect of long-term monoculture cultivation was shown. Next to that, the cultures were tested on rich and poor media to distinguish between different ways of selection. No clear difference in productivity in monocultures because of the influence of substrate degradation by the fungus was observed.

Key words: *Termitomyces*, termites, symbiosis, mutualism, substrate degradation, monoculture, *Microtermes*, *Macrotermes*, *Odontotermes*.

General Introduction

Organisms are in competition for resources to survive. Many organisms work together with other organisms, to compete better. Cooperation between individuals from different species is called mutualism [1]. This mutualism can be obligatory, if it is necessary to survive for both involved organisms [2]. Symbioses are close beneficial relationships between organisms, which can grow up to highly integrated and coevolved relationships between two species [1]. Symbiosis often implicate exchanging goods and services between both partners and most likely result into the gain of new abilities by at least one of the involved organisms [2].

An amazing form of symbiosis is observed in agriculture: growing and maintaining organisms of other species to feed upon appears only a few times in the animal kingdom [3]. Three insect orders independently evolved around 50-million years ago the ability to cultivate fungi. These insect orders are ants, ambrosia beetles and termites. Next to insects, also *Littoraria irrorata*, a marine snail from the North America's Atlantic Ocean, has fungal growing behaviour [4]. More recently, around 10,000 years ago, also humans started farming, which can be improved by learning from other agricultural systems [3]. Growing mushrooms on a larger scale can help solving food shortages on a global scale, mostly because they are high in proteins and essential minerals, but low in calories [5]. A nice example of agriculture that can be explored by humans more is between *Termitomyces* and the *Macrotermitinae* the subfamily of termites that cultivate these fungi. *Termitomyces* species have a high nutritional value compared to other mushrooms, and can therefore have a high nutritional importance. For example the protein content of *Termitomyces letestui* is 3.9g per 100g, compared to other edible fungi: 3.0g, 1.9g and 2.3g per 100g in *Agaricus bisporus*, *Cantharellus cibarius* and *Pleurotus florida* respectively [5].

The termites cultivate the *Termitomyces* in well-protected gardens in their nests [6] (Shown in Figure 1). The fungi grow on combs, which are constructed from plant material in chambers. The termites have division of labour between old and young workers [7]. The old workers take hard to decompose plant material from outside the nest. This plant material is consumed by the young workers who put their faeces on the rims of the comb. On the comb, consisting of materials the termites themselves could not decompose, the fungi are grown [8]. The young workers eat the fruiting bodies, called nodules, produced by the fungus. The fungus is restricted in reproducing sexually because the nodules cannot grow out and are eaten before they reach maturity [9]. These nodules contain vegetative spores that can survive the termites' digestion tract and are dispersed on the substrate in the faeces of the termites. Because of this way of inoculating the fungus it will face repeating and very strong bottlenecks and is expected to stay in monoculture [9]. The fungus will be selected by the termites to produce more nodules, because this leads to more food and more inoculation material [9]. At a later stage, the old workers also eat the old comb with the degraded plant material and the fungal mycelium it contains [8]. A main part of the decomposition and mineral cycling in Old World tropical areas is due to the termite-fungus mutualism and this relationship is therefore of major ecological importance [8].

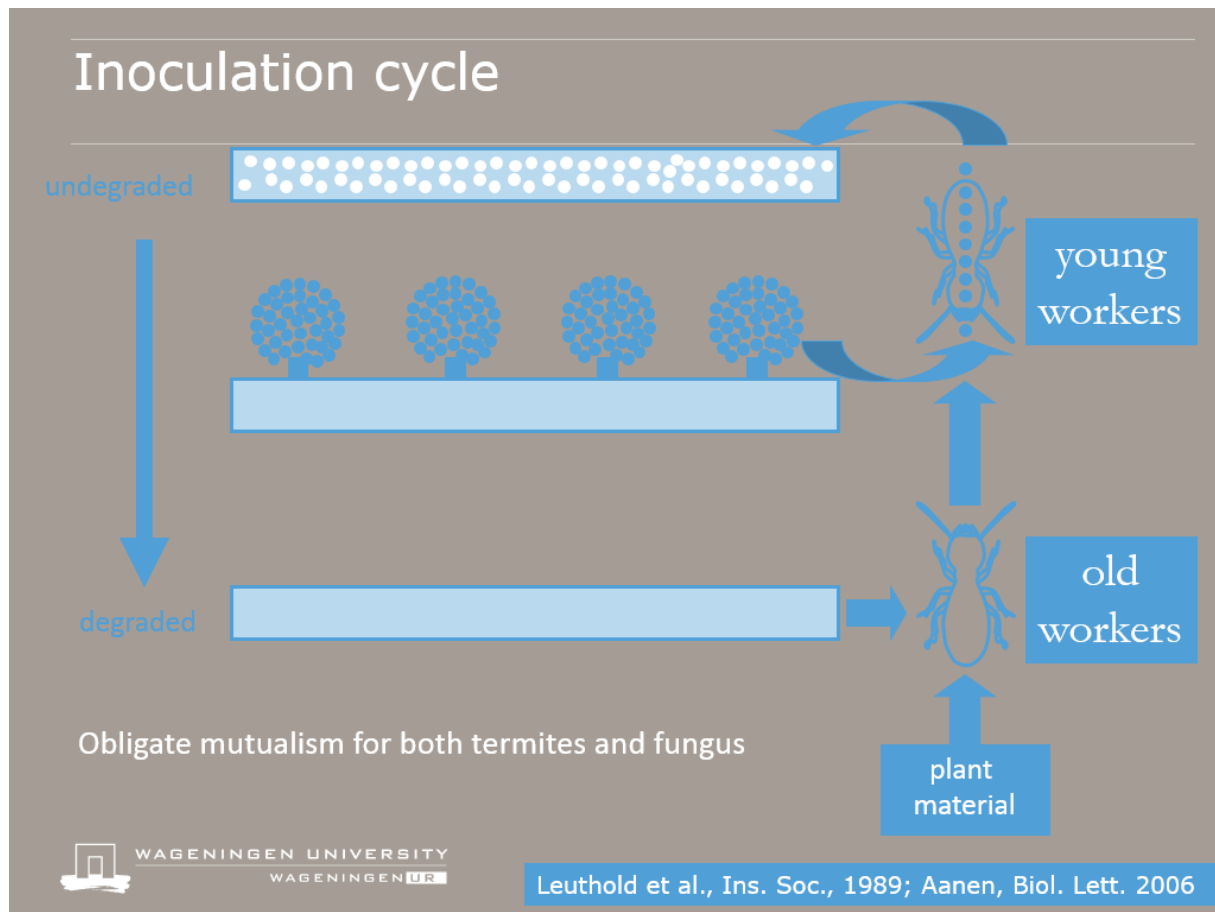


Figure 1 - Inoculation cycle. Shown is the plant material that brought into the nest by old workers on the lower right. Young workers consume the plant material, which is mixed with the fungus in their guts. They their faeces on the combs, where the fungus grows. Nodules are formed and again consumed by young workers. Old combs are eaten by old workers. Picture by Duur Aanen.

Termitomyces has been found to be cultivated by the termites in monocultures [9]. A monoculture excludes the need for competition with other strains. Because separate mycelia are from the same fungus there is synergism when fusing. Fungi in monoculture have enhanced efficiency of spore production. The short-term fitness interests of fungi and termites are maximised [6]. On the other hand, monoculture farming can have negative sides. A negative aspect of a monoculture is the small spectrum of substrate degradation possible. Furthermore, a mixed culture could have the advantage of having a larger spectrum of the substrates that can be degraded. Next to that a monoculture is more susceptible for diseases than a mixed culture. This monoculture breeding gives space for cheating. Because the surrounding colonies are genotypic identical, cheaters can fuse with other mycelia to enhance the efficiency of producing spores, at the cost of mycelial growth. In *Neurospora*, it has been shown that long-term cultivation in monocultures leads to lower fungal growth and spore formation (Bastiaans et al., in prep.).

To look more into the possible advantages and disadvantages of monoculture fungus farming two main questions were examined.

- Is there an advantage for a mixed culture compared to a monoculture?
 - Which substrates can be degraded by the fungus?
 - Is there variation among strains in which substrates they can handle?

- Which substrates are suitable for a mixed culture?
- What are the effects on fungal growth and spore formation of long-term cultivation of *termitomyces* in a monoculture?
 - Which substrate is suitable for a long-term evolution experiment?
 - Which effect does density have on fungal growth and spore formation?

To answer these questions three experiments were performed. First, to find suitable substrates to test the mixed cultures on, a substrate experiment was performed, in which different *termitomyces* strains were grown on 35 different substrates. The expectation was to find two fungi, one fungus that grows well on one substrate and less on another, and a second fungus that grows well on the substrate that the first fungus grows less on and vice versa. Second, a mixed substrate experiment was performed, in which two suitable substrates were mixed and a mixed culture was tested for growth on this mixed substrate. Expected was that it might be able for both fungi to live together, both using the substrate in the mix that suits them best. Third, an evolution experiment was performed, in which weekly propagation of 10 evolution lines were performed to see the long term effects on growth and spore formation. Two scenarios were suggested, it could be like in *Neurospora* where it has been shown that long-term cultivation in monocultures leads to lower fungal growth and spore formation. But it could also be that because of the differences in cellular structure.

Substrate experiment

Termites nor their gut microbes are able to degrade lignin [10]. The gut microbes of the termites are however able to degrade the products released by the depolymerisation of lignin, which can be done externally, prior to ingestion, by the fungus [11]. The ruminant hypothesis states that when young workers eat the nodules the fungal enzymes and spores in these nodules are mixed with the foraged plant material and enzymes of termite and bacterial origin. This way of mixing works as an external rumen for the termites. It benefits both the fungus and the termites, because the degradation of the plant material can be very efficient in this way and so a good food source is prepared. The enzymes produced by the fungus are concentrated in the nodules, and since these are consumed by the termites the asexual spores from the nodules are used to inoculate the fresh combs. The old combs are consumed by old workers, which provides them with fungal biomass and nitrogen-enriched plant material. The exact role of the termite gut bacteria remains to be studied in more detail [12]. To see which nutrients different *Termitomyces* strains can degrade they were tested in this study on 35 different substrates. An overview was made between the substrate degradation done by diverse *Termitomyces* strains.

Materials and methods

The fungal strains that were used have been collected during several field trips in South Africa, and are in storage at -80°C in tubes with pepton-glycerol. The fungal strains were taken out of the tubes with sterilised tweezers and placed on MYA plates. These were incubated at 25°C for ten days, until they grown sufficiently to harvest.

A selection was made on growth speed, to be sure that no very poorly growing fungal strains were used. The ITS region of these strains has been sequenced in previous studies. The sequences described before [13] have been compared, to make a proper selection of a broad spectrum of fungi to be studied. The selected strains were put on new MYA plates, two replicates were made, so enough material was produced. A drop of 50µl of fungal suspension was transferred onto the plate with the substrate, to test for the degradation ability. For the 35 different substrates two replicates were made. Photos were taken from the end result to compare the different substrates and the different strains.

Media

- MYA (Malt Yeast extract Agar). The composition of this medium is: 20g malt extract, 2g yeast extract and 15g agar per litre demineralised water.
- 36 substrates were tested for fungal growth in the substrate degradation experiment. These substrates were formed by the addition of 35 different carbon sources, and no carbon source to a minimal medium. A complete list of these carbon sources is attached in the appendix. The composition of the minimal medium is: 6g NaNO₃, 1.5g KH₂PO₄, 0.5g MgSO₄·7H₂O, 0.5g KCl, 1mg FeSO₄, 1mg ZnSO₄, 1mg CuSO₄, 1mg MnCl₂ and 15g agar per litre demineralised water. This minimal medium was autoclaved at 110°C for 15 minutes. The 35 different carbon sources were sterilized separately from the minimal medium in an autoclave at 110°C for 15 minutes. This was sterilized separately to make sure no reaction between the carbon sources and the ingredients of the minimal medium, especially the agar, occurred. Also 2 ml vitamin solution and 1ml trace elements were added to one litre media.

Strains

- The *Microtermes*-symbionts T40b, T41a, T42e, T43e, T46b, T47a, T48a, T49c, T50a, T51g, T52a, T53b, T54a and T55c were sequenced before [13], T56b were sequenced.
- The *Macrotermes*-symbionts T58, T63 and T64 were sequenced.
- The *Odontotermes*-symbionts T67a, T68a, T70a, T71a, T72a, T73b and T75 were sequenced.

A broad spectrum of the sequenced fungi was studied in this experiment. Two replicates were made of every strain-substrate combination.

Results

The experiment was severely infected due to problems in the lab, so that no results were obtained for some strains, and in some cases not for all substrates for a strain. In the end of this experiment the growth of the various *Termitomyces* strains was determined in a semi-quantitative way by making photographs (Appendix), to get an overview of the substrates they can degrade.

Discussion

Per strain it is very clear that some of the substrates are easy to degrade, and others cannot be used by the fungus to grow. Generally, the more complex substrates are a good source for the fungi, the most simple sugars are good for growing for some of the strains, while growth is reduced on the more complex sugars. Comparing the strains, no clear differences are visible. Also between the symbionts of different genera (*Microtermes*, *Macrotermes* and *Odontotermes*) no clear differences are visible. This indicates that the fungi are not really species specific considering the differences in degradation abilities of the termite and their gut microbes. This might be caused by the last common ancestor of the genus *Microtermes* being relatively recent. Next to that, the fungal symbionts of species of fungus-growing termites are not monophyletic despite the vertical transmission mode which should lead to a high degree of host specificity. Besides the vertical transmission also horizontal transmission has occurred, leading to one of the symbionts associated with *Microtermes* being spread through several different genera [12]. Not only *Microtermes* but also *Macrotermes* has a strain that is spread and associated with at least four not monophyletic termite lineages. *Macrotermes bellicosus* is not only clonally propagated, but it also has occasional recombination with other *Macrotermes* strains [12]. Not only vertical transmission is found, an example is the termite *Macrotermes natalensis* which is highly specific and has a single, sexually reproducing *Termitomyces* strain. The transmission mode and the specificity correlated with it should be further studied as should the influence of these on the interactions between the termite and the fungus.

Evolution experiment

In other fungi than *Termitomyces*, for example *Neurospora* research has shown that long-term cultivation in monocultures leads to lower fungal growth and spore formation (Bastiaans et al., in prep.). To see whether this is also the case in *Termitomyces* an evolution experiment was performed. The fungus was examined to determine the possible negative effect of long-term monoculture cultivation. This was done in two different ways to distinguish between continuous growth and repeating inoculation of newly formed spores as the termites do. When there is a negative effect of this monoculture system it may indicate that the termites are essential to prevent this negative effect in nature. The objective of this section was therefore to find whether *Termitomyces* productivity changes when cultivated for a long time in a monoculture.

Materials and methods

When the fungus has grown sufficiently, it starts forming spores. To start with a culture originating from a single spore a series of dilutions (1x, 5x, 25x, 125x, 625x, 3125x) was made and one single spore was selected to be used as a starting point for all the evolution lines.

The evolution lines were grown in two different ways, both with five lines. The first growing way is on race tubes. These are plastic tubes with medium on which the fungi were inoculated on one side. The fungus can then continuously grow in a linear way. The second growing method is on plates. Every week the fungus was inoculated via asexual spores on the plate and spread evenly. When the spores were formed after one week they were harvested with a blade and suspended in 500 microliter saline, and in 600 microliter pepton-glycerol stored in the freezer at -80°C. 50 microliter of the suspension was then applied on a new plate. The plates were incubated for one week at 25°C. These lines were prepared in two different densities. With a lower density the hyphae of different spores a lower chance to connect, which will reduce the opportunity for cheating.

The ten eppendorf-tubes stored in the -80°C freezer from the last generation of all 10 lines and one eppendorf-tube containing the starting line were taken out of the freezer and spread on MYA plates, three plates per tube were prepared. After two weeks the plates contained enough material and were harvested.

The quantity of the material used was standardised. A dilution series was made (1x, 5x, 25x, 125x, 625x, 3125x) to create single spore cultures which can be examined for variations. In these dilution series the effect of density on the different lines (which were grown in both high and low density) was made visible. The least diluted plates in this dilution series were compared for the size and number of nodules with the program ImageJ.

5 µl of the non-diluted solution was inoculated in the middle of a MYA plate, 3 replicas per strain. The radial growth was measured so the growth speed can be determined. This was also performed with a single spore culture from the dilution series. Also some substrates from the substrate test were tested. These were simple sugars on which the fungus was able to grow before the evolution experiment. These were glucose, galactose, mannose, and cellobiose. On the more complex substrates the fungus should be able to find something that can be degraded so it has no use to test these.

Media

The fungus were tested on a rich and a poor medium.

- The rich medium that was used is MYA (Malt Yeast extract Agar). The composition of this medium is: 20g malt extract, 2g yeast extract and 15g agar per L demineralised water.
- The poor medium that was used is cellulose. This medium has 1% cellulose in the minimal medium used for the substrate degradation experiment.
- Glucose, Galactose, Mannose and Cellobiose as used in the substrate degradation experiment.

Strains

The *Macrotermes*-symbiont T63 was used for this experiment. From the initial strain, five lines were made with two replicates to start the evolution experiment.

Results

On the poor medium the growth was not sufficient, so no results were obtained from there.

In the end of this experiment the growth and spore production was measured to see whether the *Termitomyces* productivity changes when cultivated for a long time in a monoculture. A comparison was made between the productivity for the different strains, seen in figure 2. Comparing the strains shows that the radial growth of most of the strains is like the ancestral strain. Strain D and J showed no growth after the full period of the experiment, A and E have a significantly lower radial growth than the ancestral strain.

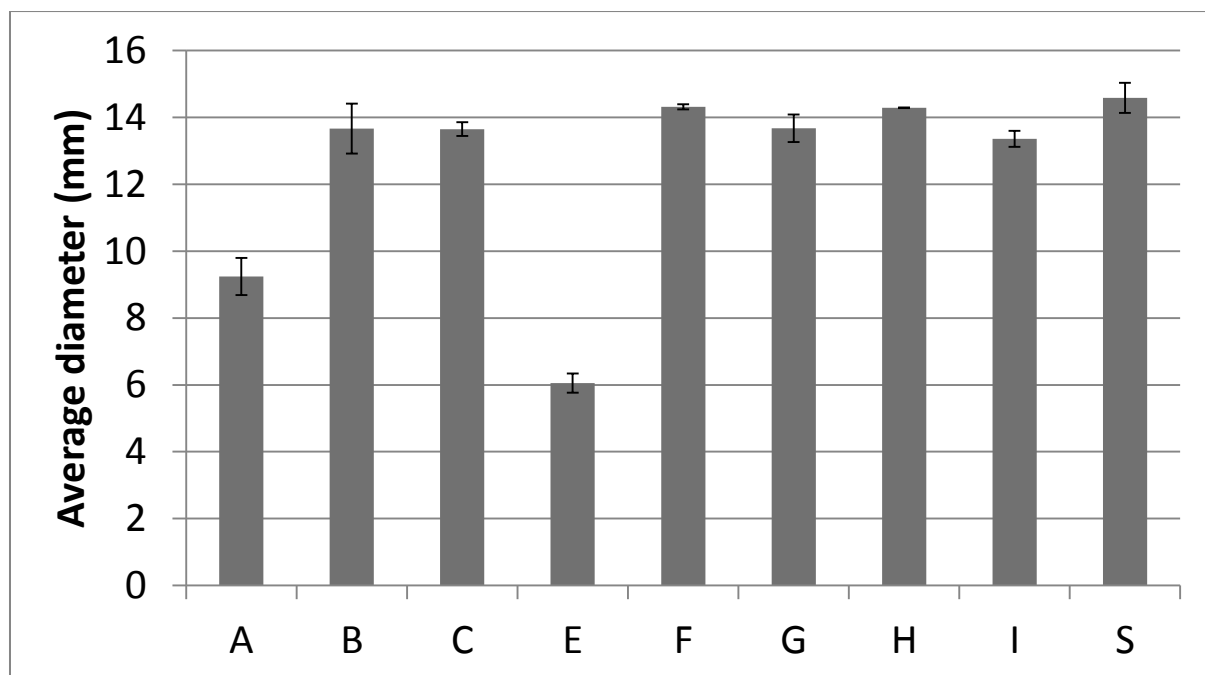


Figure 2 – Radial growth. The error bars represent the standard error obtained from three replicates. The letters on the x-axis is the name of the line represented, A to I respectively, S is the ancestral strain. The y-axis represents the average diameter in mm.

The yield was measured using the program ImageJ. This takes into account the number of nodules as well as their size. A representation of the results are shown in figure 3. Comparing the strains shows

that the yield of the strains A, E and G is like the ancestral strain. Strain B has a significantly lower yield and C, F, H and I have a significantly higher yield.

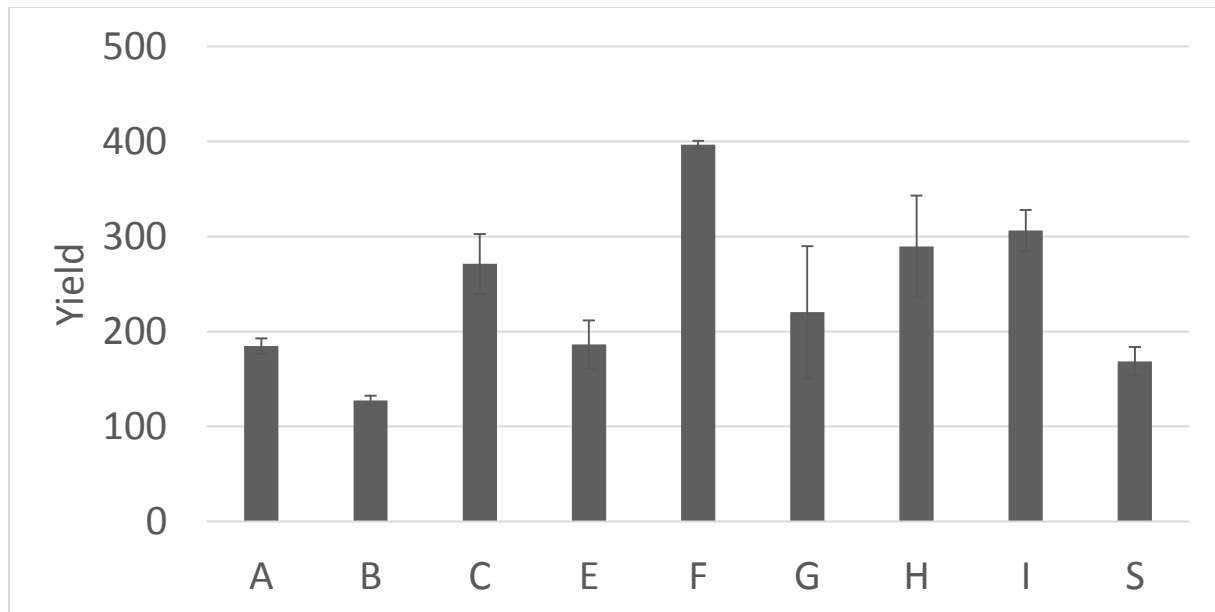


Figure 3 – Yield. The error bars represent the standard error obtained from three replicates. The letters on the x axis is the name of the line represented, A to I respectively, S is the ancestral strain.

We observed that large and small colonies appeared in all evolution lines. To see if this difference in size was stable, colonies were transferred to new plates. Two large and two small colonies were selected per strain. Of these colonies, three pieces of 1 mm were taken and put on a new plate. The diameter was measured of the newly formed colonies, and displayed in figure 4. It is shown that for the different strains the large colonies are after transferring larger than the small colonies after transferring. There are big differences between the sizes of the colonies and there is also variance between the size of the large and the small colonies from one strain.

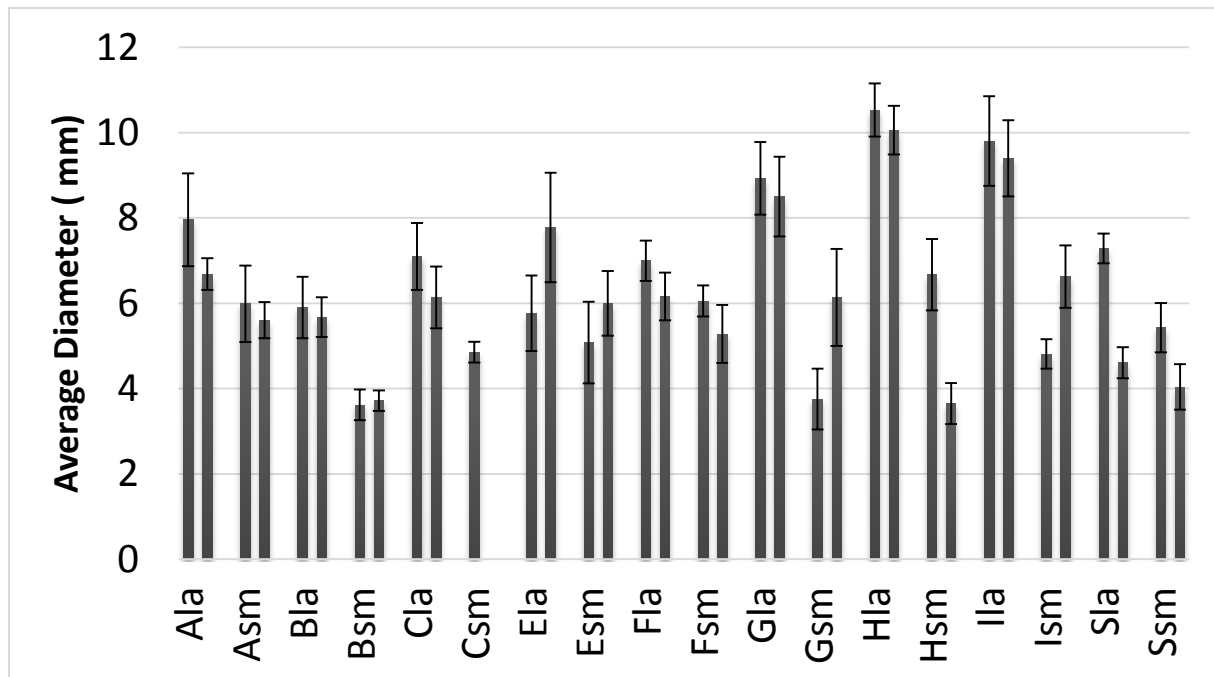


Figure 4 - Colony size. The first letter of the name on the x axis is the name of the strain represented, A to I respectively, S is the ancestral strain. The addition 'la' indicates a large colony transferred, 'sm' indicates a small colony. Two bars are per name on the x-axis, while two colonies were taken to test. The error bars represent the standard error obtained from the three replicates.

Discussion

The evolution lines differ from each other in radial growth. The lines A, D, E and J are evidently smaller compared to ancestral line, so it seems that the fungal growth was lowered as was expected following the observations in *Neurospora*. Why evolution lines D and J went totally down should be studied to observe the collapse of these colonies. It can be argued that this might be because of cheaters, if cheaters take over the colony and not enough enzymes are produced to degrade the substrate, the colony might collapse. The other lines on the other hand show similar growing properties as the ancestral line, no negative effects are visible. The results concerning the yield are also not unambiguous. Some evolution lines differ evidently from ancestral line, others show similar properties. Both increased and decreased yield is observed in the evolution lines. Therefore it cannot be confirmed that the long-term cultivation in monocultures leads to lower fungal growth and yield in *Termitomyces*. The changed properties in some strains may indicate that the termites have a crucial role in the growth of the colony. The role of the termites might also explain the observations that the fungus grown in low density does not show less possibility for cheating. A possible role the termite can play is the choice for nodules to harvest. A nodule probably starts from just a few cells. When a cheating cell is in this nodule the nodule will have less enzymes because the cheater does not produce the enzyme, but only spores to multiply itself [12]. The differences with the observations in *Neurospora* may also be caused because of the differences in cellular structure. *Neurospora* does not produce separated cells when growing, the cells are connected with septa. This makes it easy for organelles and nuclei to disperse in the colony, this does not happen in *Termitomyces*.

The colony size seems repeatable with this first pilot study. In one strain it shows that the transferred pieces from the large colonies grow bigger than the transferred pieces from the small colonies. Between strains the differences are in the same direction, although not in the same amplitudes. It needs to be noticed that the large and small colonies are not only observed in the evolution lines, but

also in the ancestral line. The cause of the different colony sizes is unknown as is the influence on the density on cheating. More research on this topic will be needed, and performed by Luuk Croijmans in his Bachelor thesis.

Mixed substrate experiment

Because *Termitomyces* is cultivated in monocultures they have quite a limited spectrum of substrate degradation possible within one nest. When two different *Termitomyces* strains with different substrate degradation capabilities are put in a mixed culture, this spectrum could be broadened. To see whether it is possible for two different strains to complement each other, mixed cultures were grown together on a mixed medium with the two substrates the fungi found to degrade best in the substrate degradation experiment. The objective of this section was therefore to see whether a broader spectrum of substrate degradation was created by mixing complementing *Termitomyces* strains on a mixed substrate.

Materials and methods

Two *Termitomyces* strains that show different degradation capabilities were put together on a plate with a mixed medium, containing both the substrates that are degraded well by one fungus and badly by the other. The strains selected are T64 and T71. In the substrate experiment it was shown that T64 grows well on Arabinogalactan and not on Starch. T71 on the other hand grows well on Starch and not on Arabinogalactan. The fungi were applied in 5 different proportions, to both the substrates as well as to a mix of both the substrates. The possibility of two different strains to complement each other was examined to see whether a broader spectrum of substrate degradation was created.

Results

The combination of both fungal strains show higher number of colonies than when applied to the substrate as a monoculture (figure 5). The spore germination on Starch is clearly lower than on Arabinogalactan and the mixed substrate.

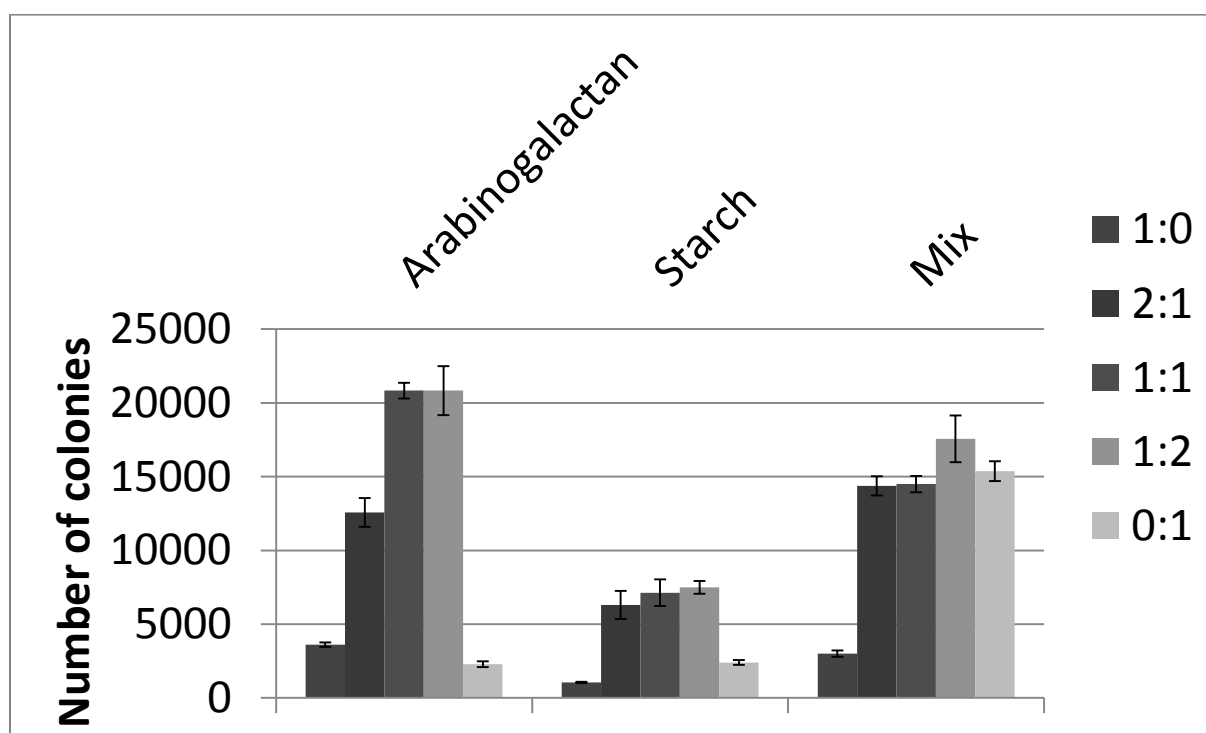


Figure 5 - Number of colonies in substrate experiment. The error bars represent standard error obtained from 3 replicates. The different coloured bars represent the 5 proportions, 1:0 is 1X strain T64: 0X strain T71, 2:1 is 2X strain T64: 1X strain T71, 1:1 is 1X strain T64: 1X strain T71, 1:2 is 1X strain T64: 2X strain T71, 0:1 is 0X strain T64: 1X strain T71.

strain T71. They are all applied in the same concentration. The substrate on which the fungi are grown is displayed on top.

Next to spore germination, the nodule production on these substrates was observed and shown in the following photographs. In figure 6 the photographs are shown of the fungi in three different proportions on the mixed substrate and of the 1:1 proportion on the three different substrates. The combination of both fungal strains on the mixed substrate does show enhanced nodule formation compared to the monoculture of T61, but not compared to the monoculture of T74. The nodule formation of the 1:1 proportion on the mixed substrate is not different from the nodule formation on Arabinogalactan, on Starch the nodules do appear to be a bit smaller.

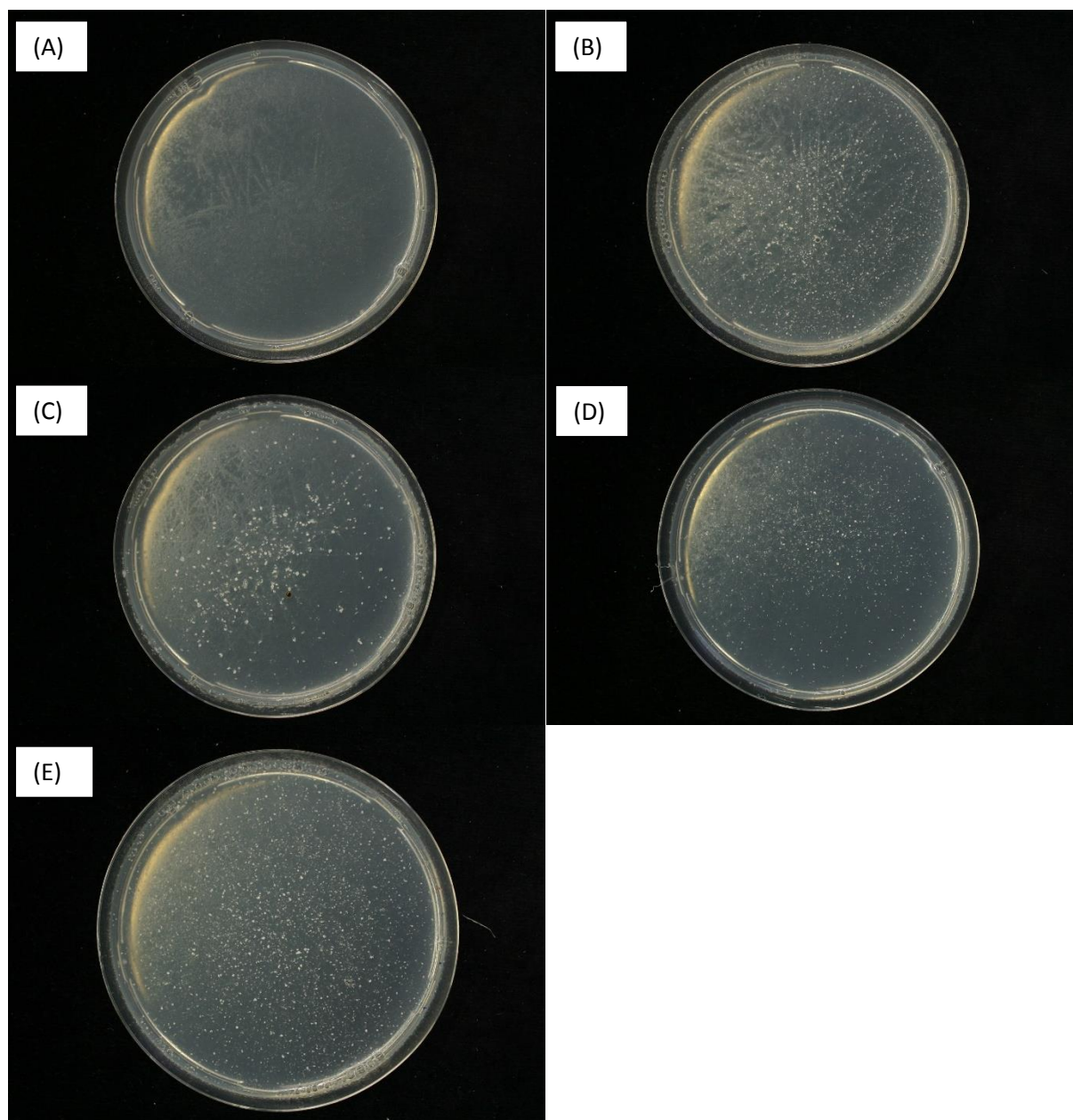


Figure 6 – Nodule formation on mixed substrate. (A) Proportion of 0:1 on mixed substrate. (B) Proportion of 1:1 on mixed substrate. (C) Proportion of 1:0 on mixed substrate. (D) Proportion of 1:1 on Starch. (E) Proportion of 1:1 on Arabinogalactan.

Discussion

The two fungal strains complement each other to germinate better than one does on the same substrate without the other fungus. The nodule formation on the other hand does not show the same trend as the number of colonies. The nodule formation seems to be similar to the lower yield observed in mixed cultures relative to monocultures by Aanen et al (2009) [6]. A possible explanation is that the strains were selected for growth on the substrate, not nodule formation. This may cause cells that germinate and grow faster have a higher advantage than the cells that have a higher yield. Based on the higher numbers on the mixed substrate than on starch, it may be possible to define a substrate on which both of the fungal strains can grow when mixed together, but on which they cannot grow by themselves. The experiment should be repeated with more strains and other substrates, to get more insight in the degradation of the substrates. It will also be very interesting to test, next to the different proportions, more dilutions to test different patch sizes. The density of the fungus may lead to differences in ability to cooperate or use enzymes produced by another, which may lead to changes in the substrate usage. It is needed to not only select the fungal strains on growth but also on nodule formation on the different substrates.

Final conclusion

To examine the pros and cons of monoculture fungus farming in *Termitomyces* three experiments were performed.

A substrate experiment was performed to find the degradation possibilities of the fungi. In an experiment, different *termitomyces* strains were grown on 35 different substrates. An overview with pictures showing the fungal growth was made. Some strains can use the simple sugars well for growing, while others seem to use them not as well. Overall, most strains are able to grow well on the more complex substrates, these substrates contain several components which the fungi are able to degrade. The complex sugars are not suitable for most strains to grow on. Between the different symbionts (*Microtermes*, *Macrotermes* and *Odontotermes*) no clear differences are visible. This indicates that the fungi are not really species specific considering the differences in degradation abilities of the termite and their gut microbes.

A mixed substrate experiment was performed, in which two substrates were mixed and a mixed culture was tested for growth on this mixed substrate. Arabinogalactan and starch were found to have complementary growth by the *termitomyces* strains T64 and T71. The two fungal strains complement each other to germinate better on the mixed substrate than they do on the same substrate without the other fungus. The nodule formation on the other hand does not show the same trend as the number of colonies.

An evolution experiment was performed, in which weekly propagation of 10 evolution lines were performed to see the long term effects on growth and spore formation. The fungi were examined during many generations and no obvious negative effect of long-term monoculture cultivation was shown. Next to that, the cultures were tested on rich and poor media to distinguish between different ways of selection. No clear difference in productivity in monocultures because of the influence of substrate degradation by the fungus was observed.

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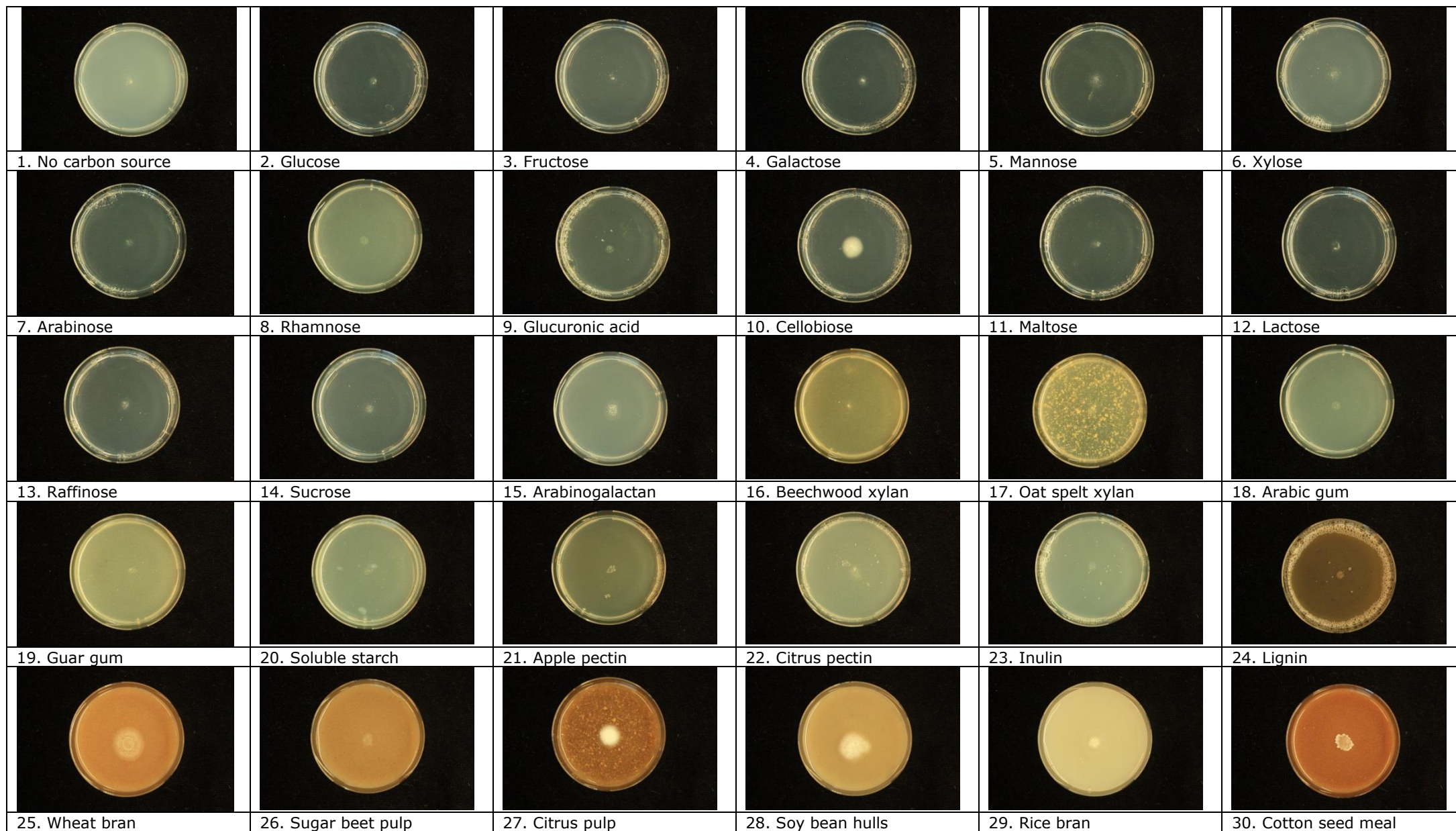
Appendix

List of substrates:







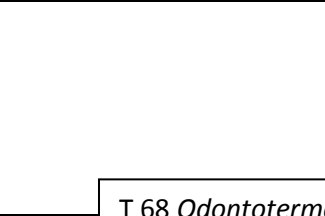
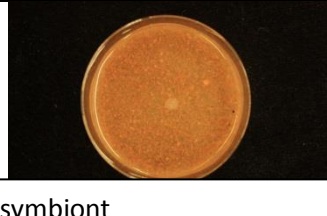

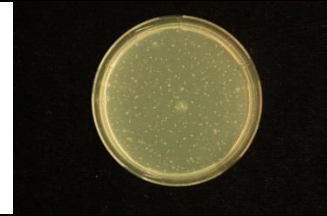
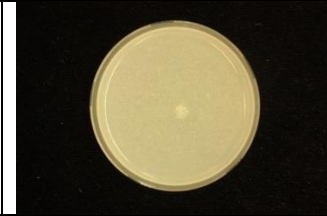
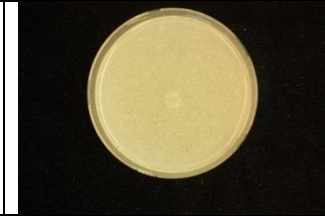
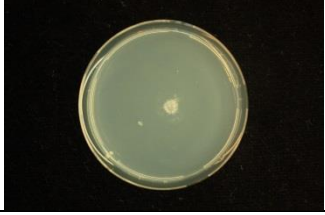
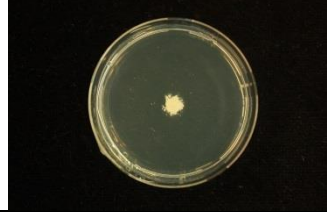
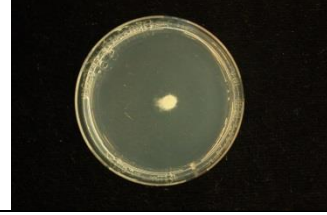
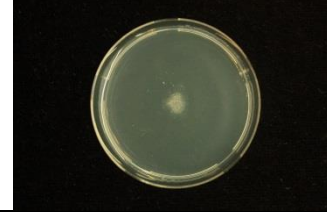
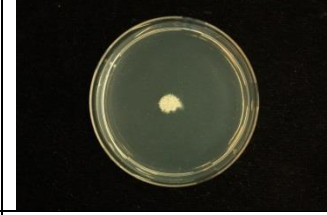
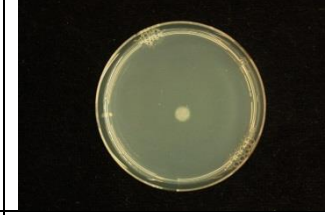
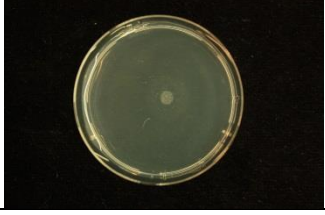
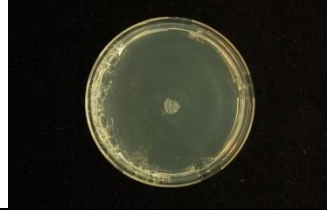


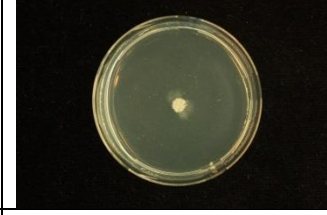
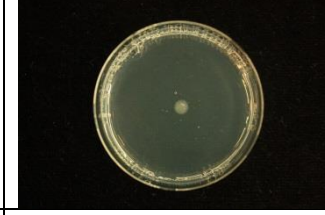

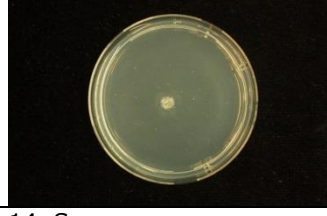
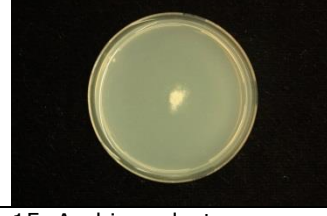
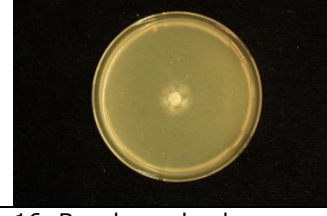
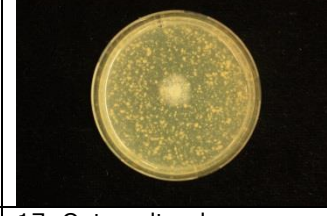
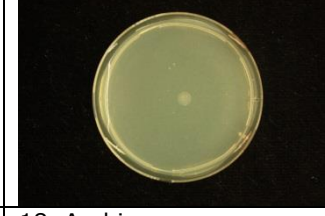
1. No carbon source
2. Glucose (25mM)
3. Fructose (25mM)
4. Galactose (25mM)
5. Mannose (25mM)
6. Xylose (25mM)
7. Arabinose (25mM)
8. Rhamnose (25mM)
9. Glucuronic acid (25mM)
10. Cellobiose (25mM)
11. Maltose (25mM)
12. Lactose (25mM)
13. Raffinose (25mM)
14. Sucrose (25mM)
15. Arabinogalactan (1%)
16. Beech wood xylan (1%)
17. Oat spelt xylan (1%)
18. Arabic gum (1%)
19. Guar gum (1%)
20. Soluble starch (1%)
21. Apple pectin (1%)
22. Citrus pectin (1%)
23. Inulin (1%)
24. Lignin (1%)
25. Wheat bran (3%)
26. Sugar beet pulp (3%)
27. Citrus pulp (3%)
28. Soy bean hulls (3%)
29. Rice bran (3%)
30. Cotton seeds meal (3%)
31. Alfalfameel (3%)
32. Corn gluten (3%)
33. Oat hulls (3%)
34. Casein (1%)
35. Cellulose (1%)
36. Chitin (1%)

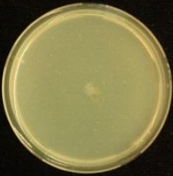

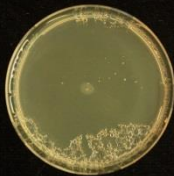

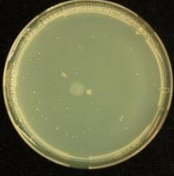
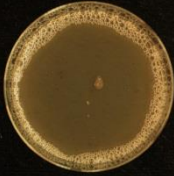


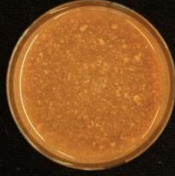



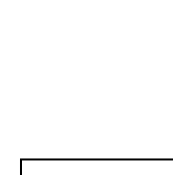
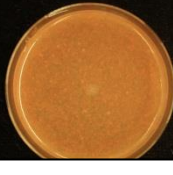
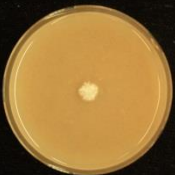
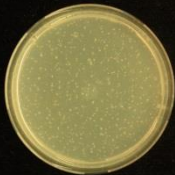
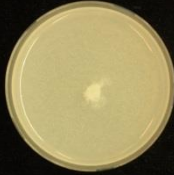
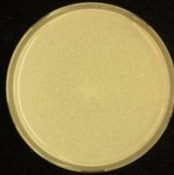
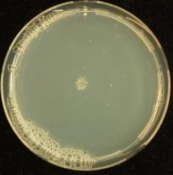
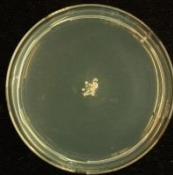
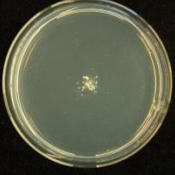
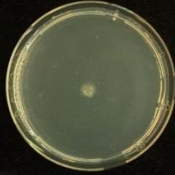
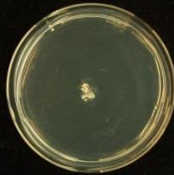
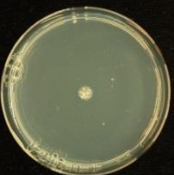
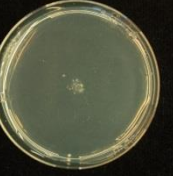
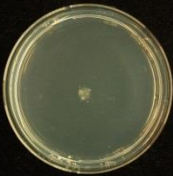
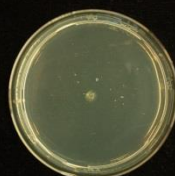
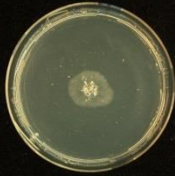
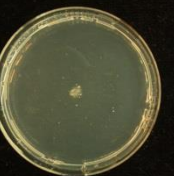
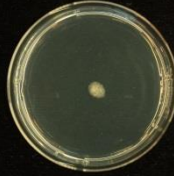
Overview substrate experiment

Per strain an overview of the 36 substrates is made.

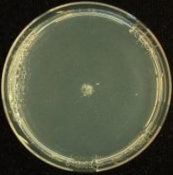
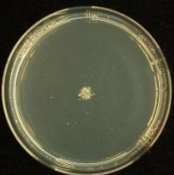
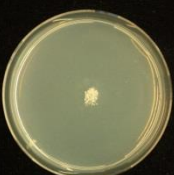
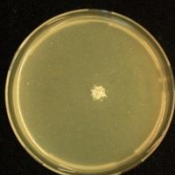
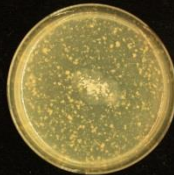
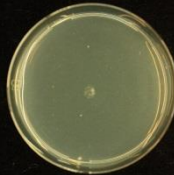
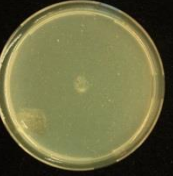
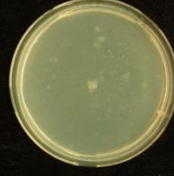
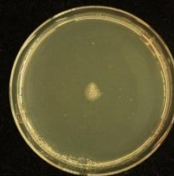
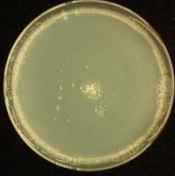
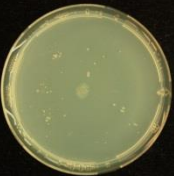
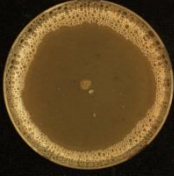


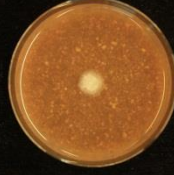



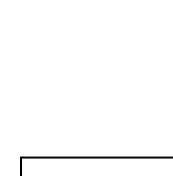
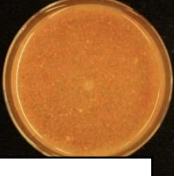




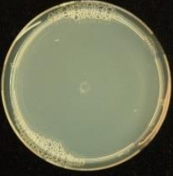
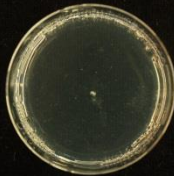
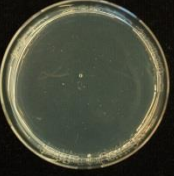
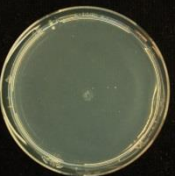
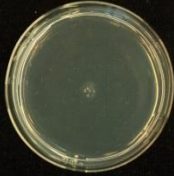
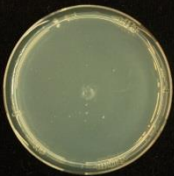


<div>T 67 <i>Odontotermes-symbiont</i></div>					
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin

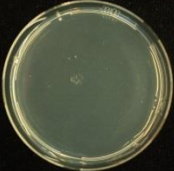
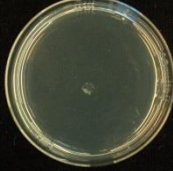



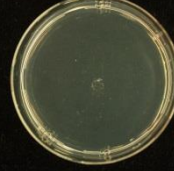
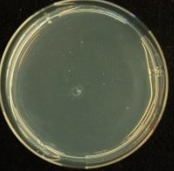
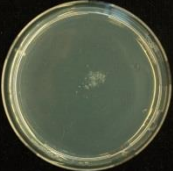
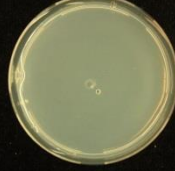
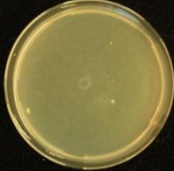
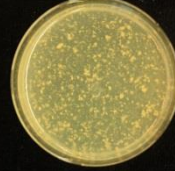
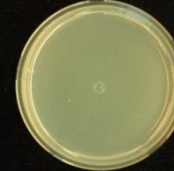
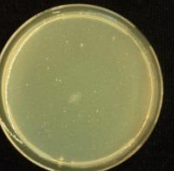
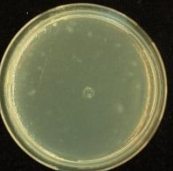
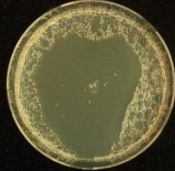
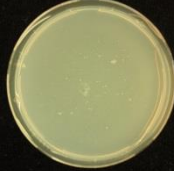
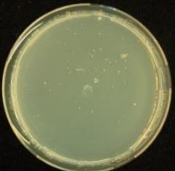
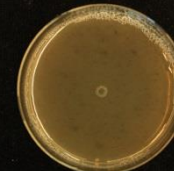


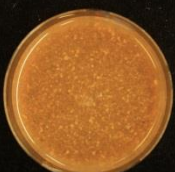









					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
	T 68 <i>Odontotermes</i> -symbiont				
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose
					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose
					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum

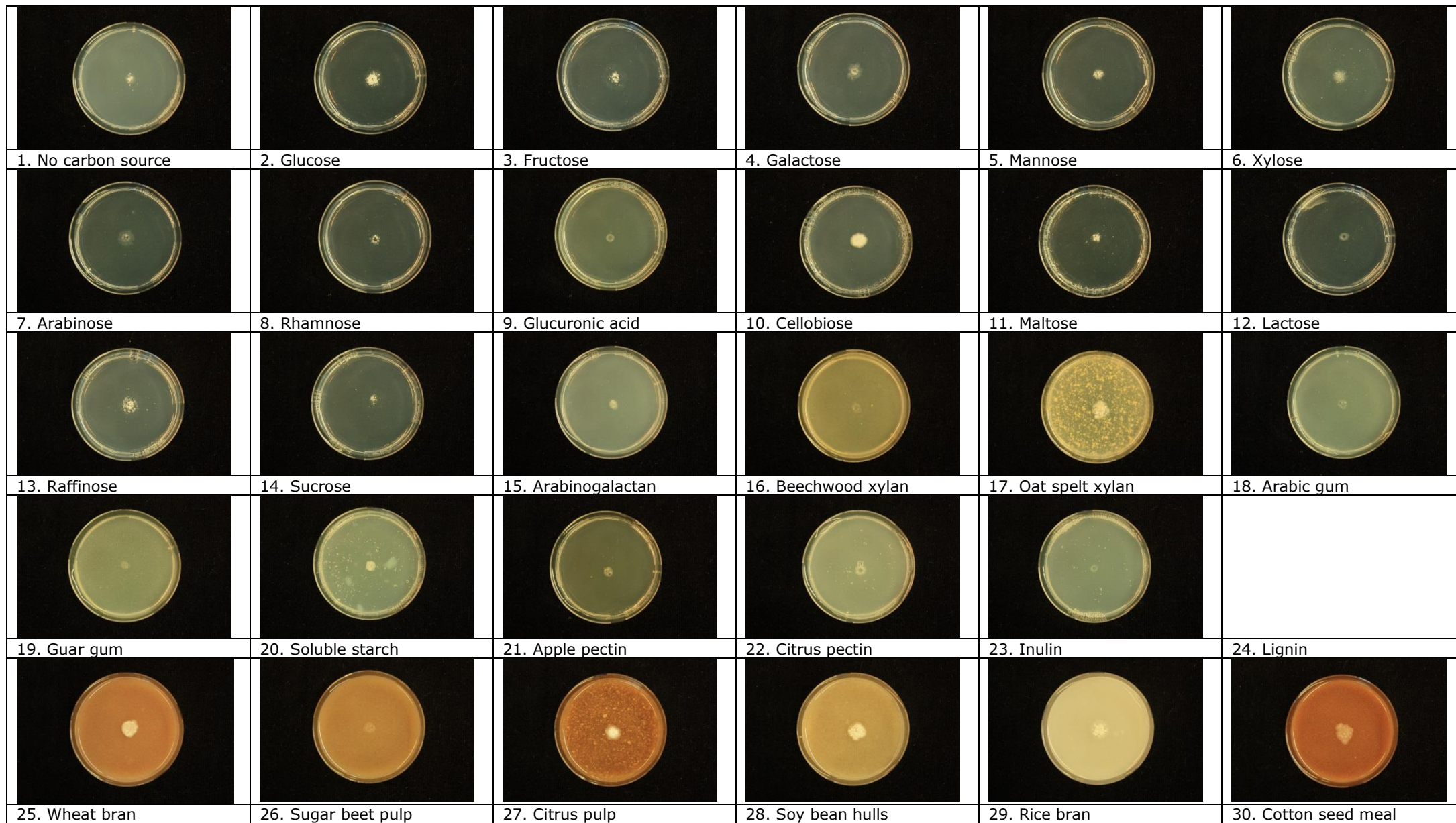
					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin
					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose
					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose



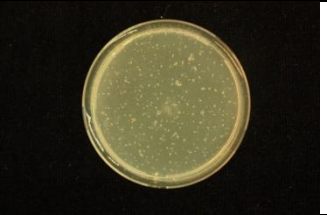


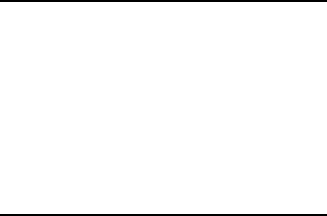
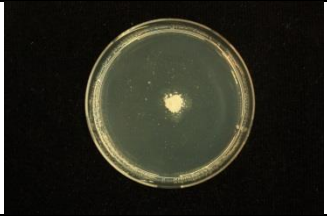

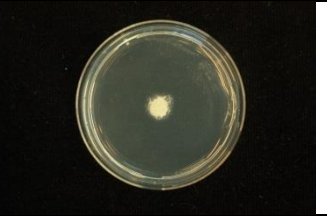


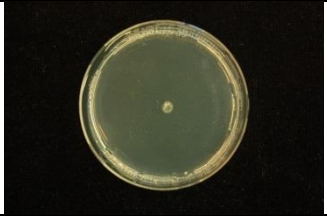

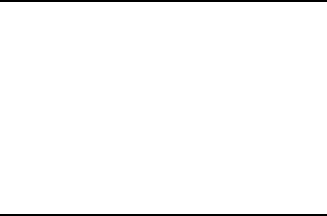
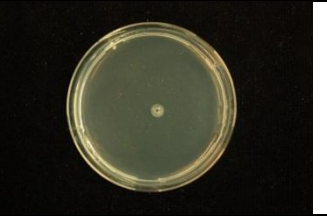
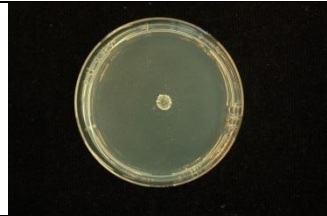
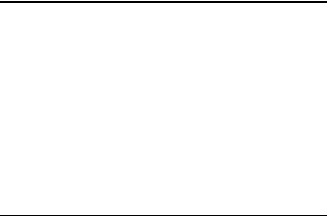
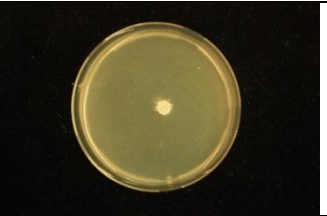
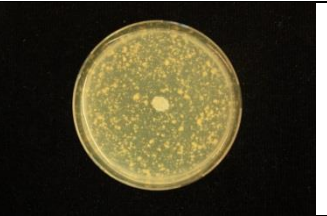
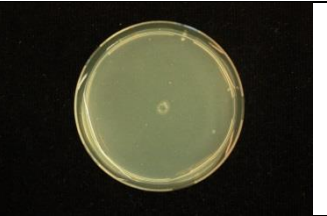

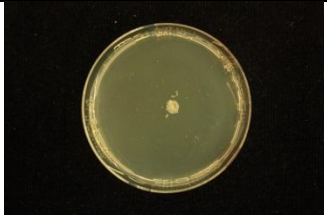


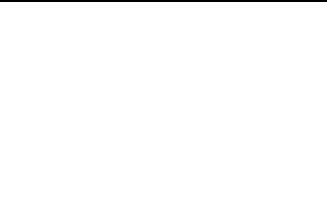
T 58 *Macrotermes-symbiont*





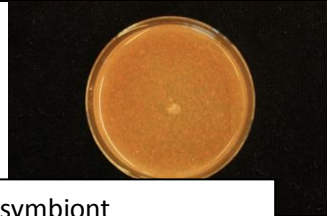



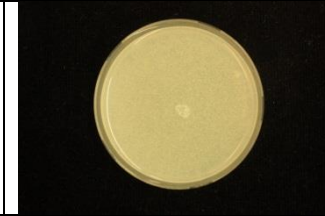

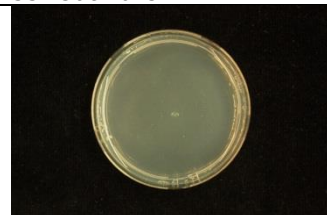

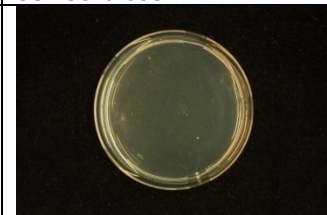
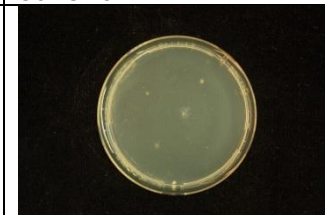
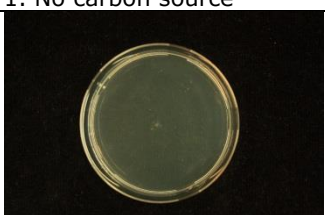


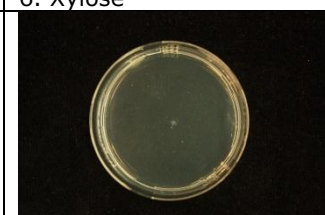


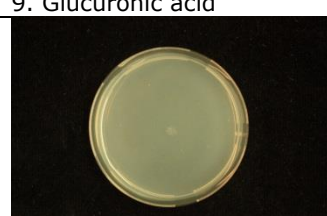



					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum
					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin
					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose

T 41 *Microtermes*-symbiont


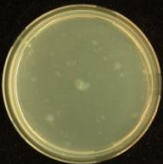










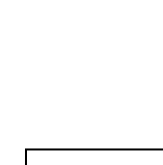





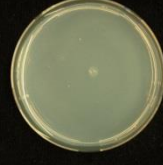
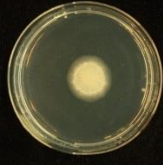
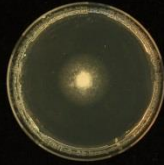
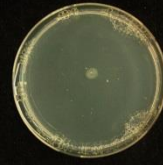
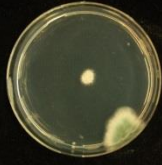

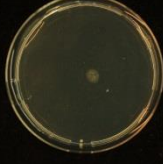
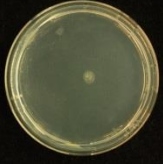

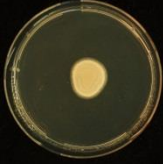
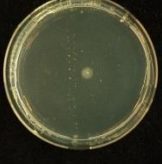
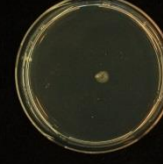
					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose
					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum
					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin
					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
31. Alfalfameal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin



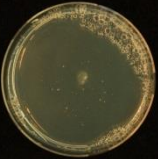
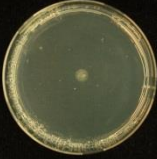
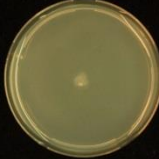
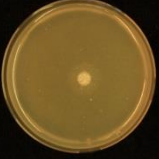
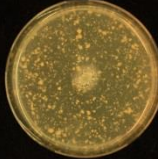
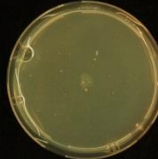
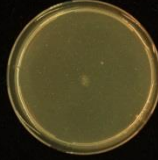
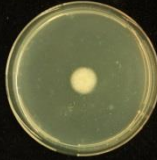
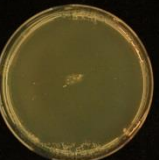
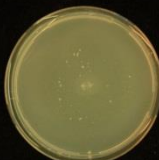
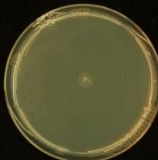
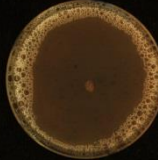


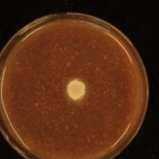


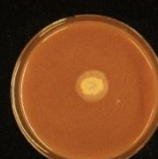

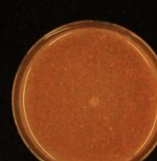



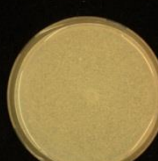
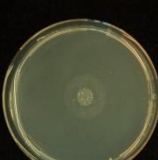


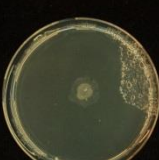
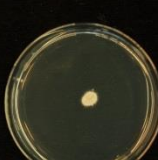

					
T 82					
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose
					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose
					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum
					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin

					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose
					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose
					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum

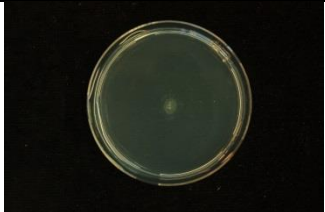
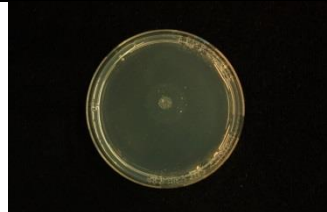


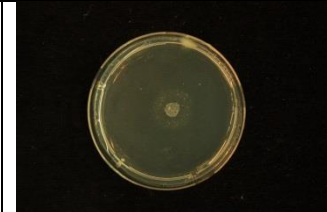
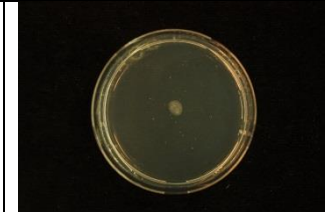

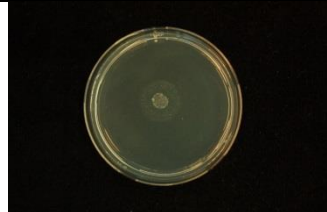
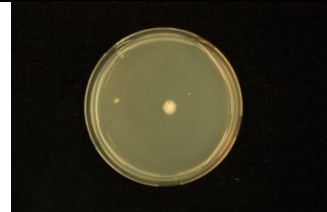


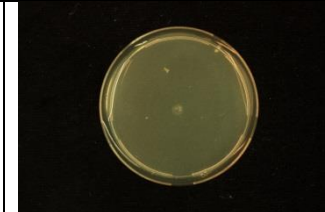






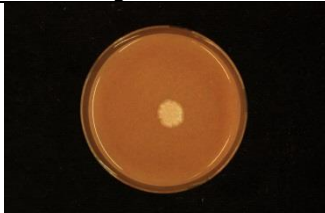

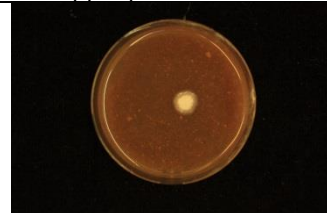
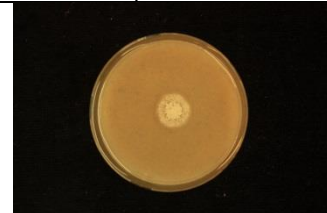
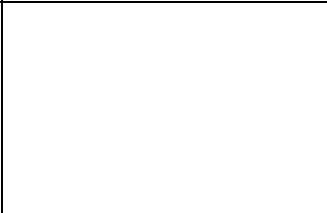
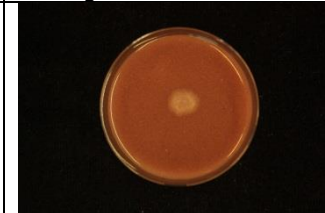
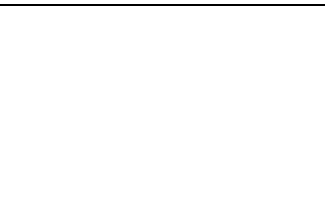
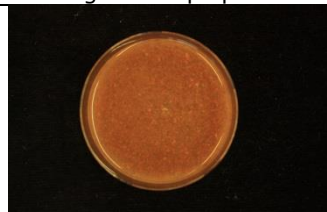
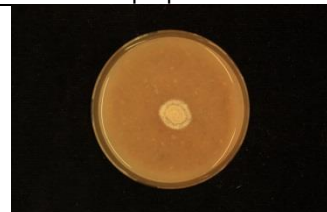
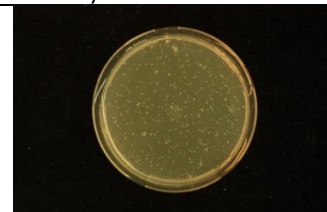
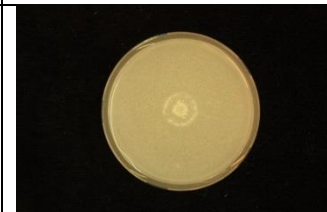
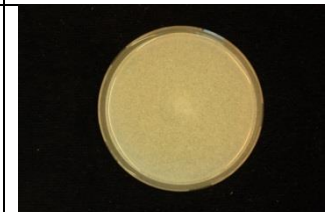
T 70 *Odontotermes*-symbiont


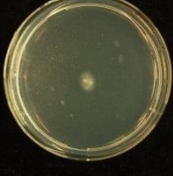
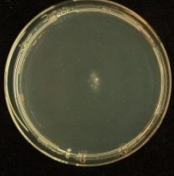
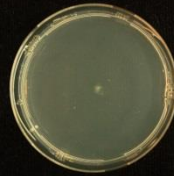
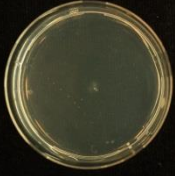
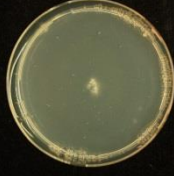
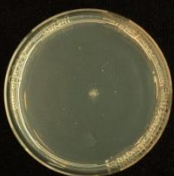
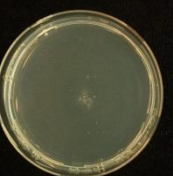
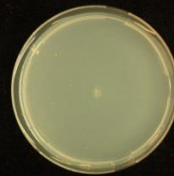


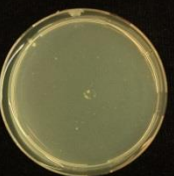












					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin
					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose
					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose

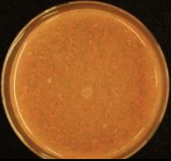


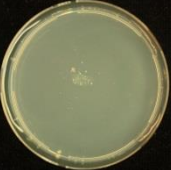
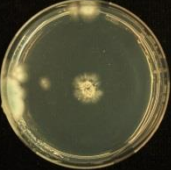
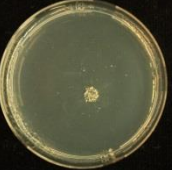
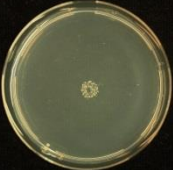
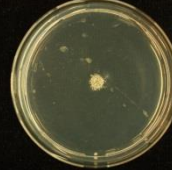
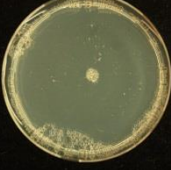
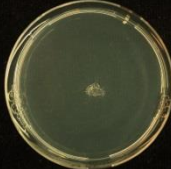
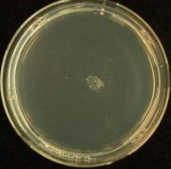
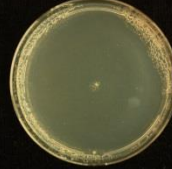
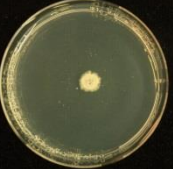
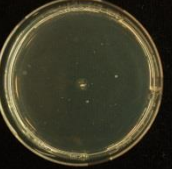
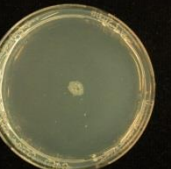
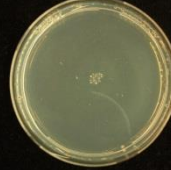
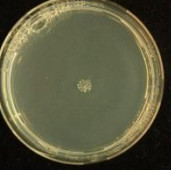

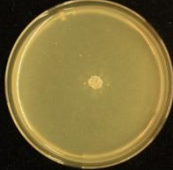
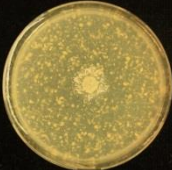
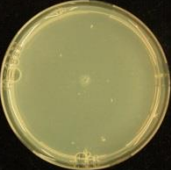
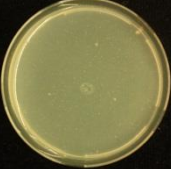

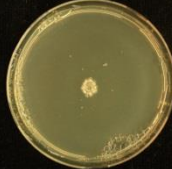
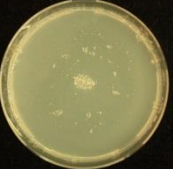
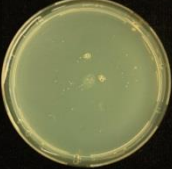
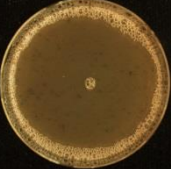
T 71 *Odontotermes-symbiont*



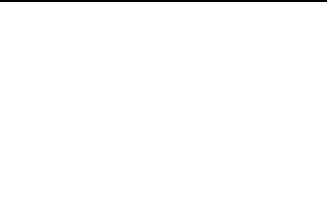
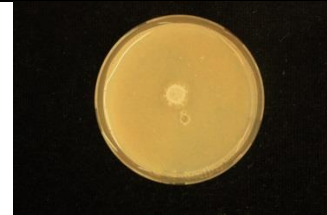
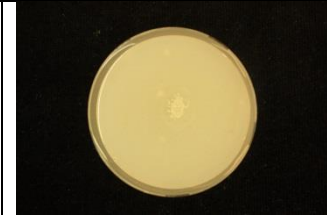




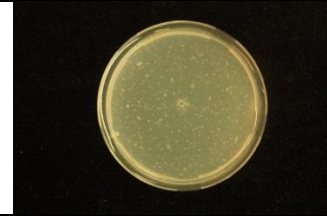


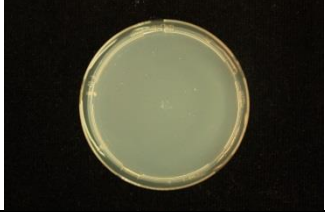

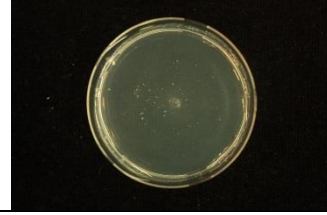
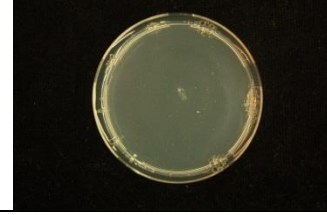
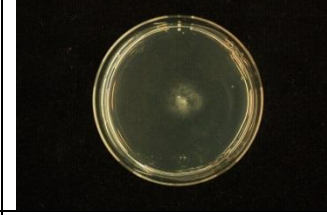
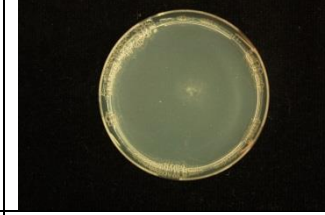
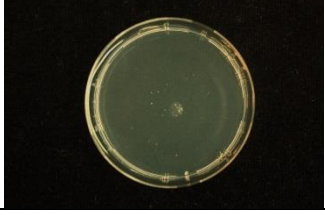
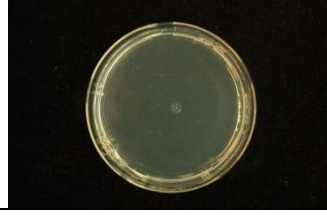
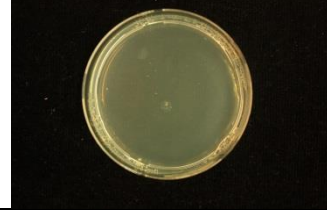
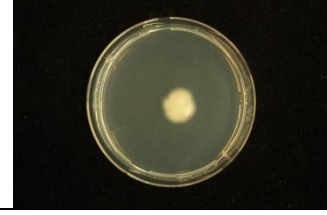
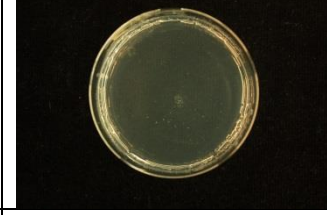
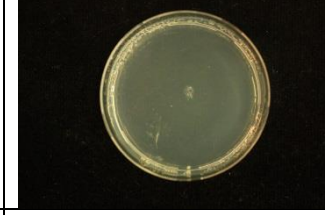

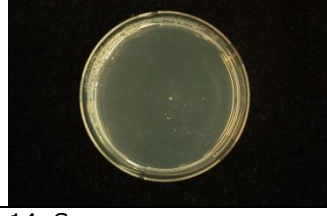
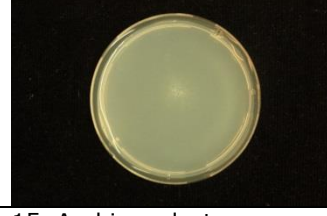
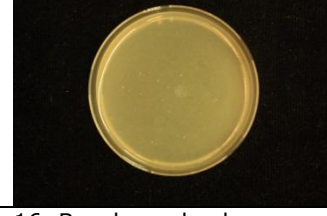
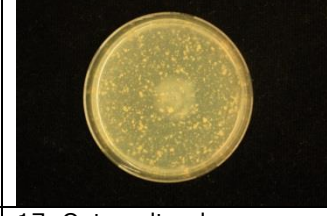
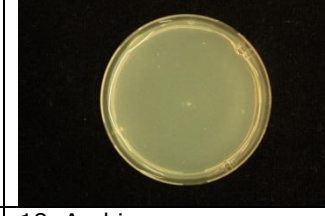
					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum
					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin
					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose


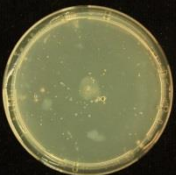
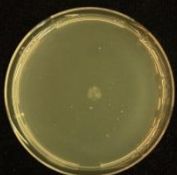

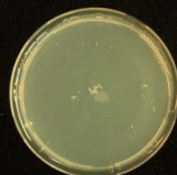










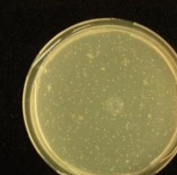

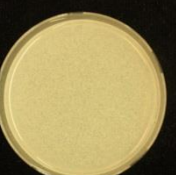
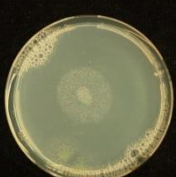

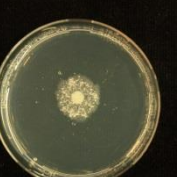
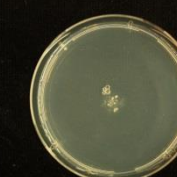


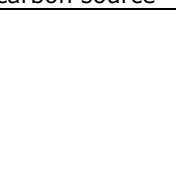
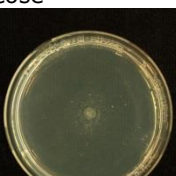



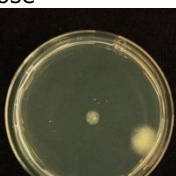
T 72 *Odontotermes*-symbiont

					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose
					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum
					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin
					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
31. Alfalfameal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin

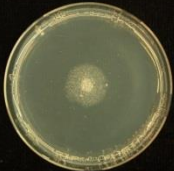

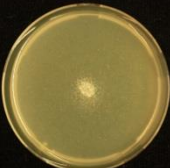
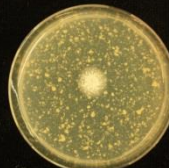


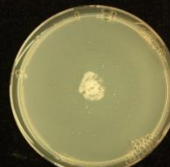





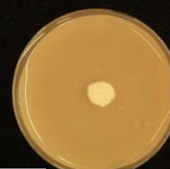
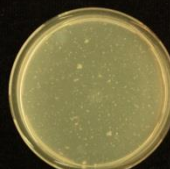

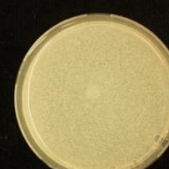
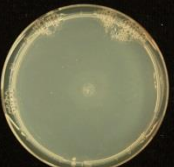

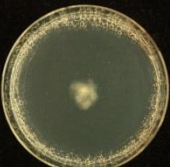
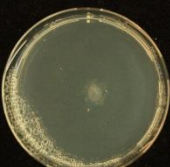
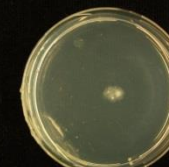
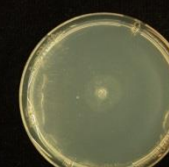
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose
					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose
					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum
					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal

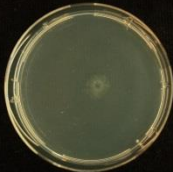
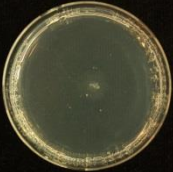


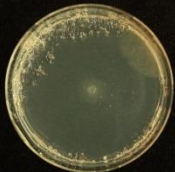
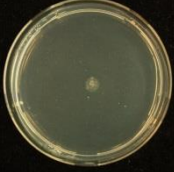
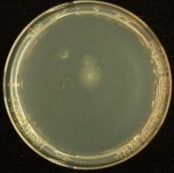
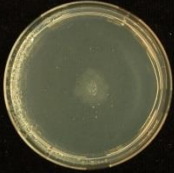
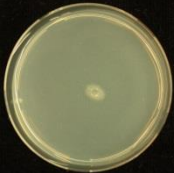

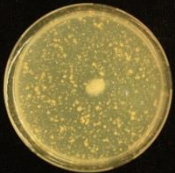
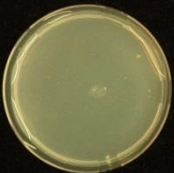
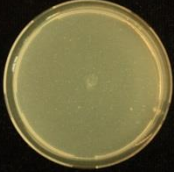

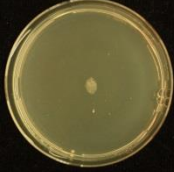
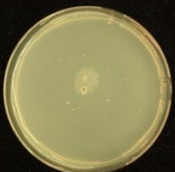
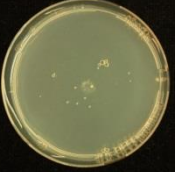
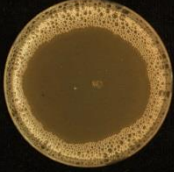


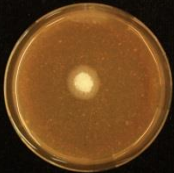
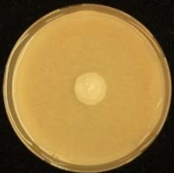





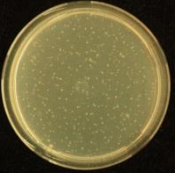

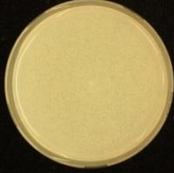
					
T 52 <i>Microtermes</i> -symbiont					
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose
					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose
					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum
					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin

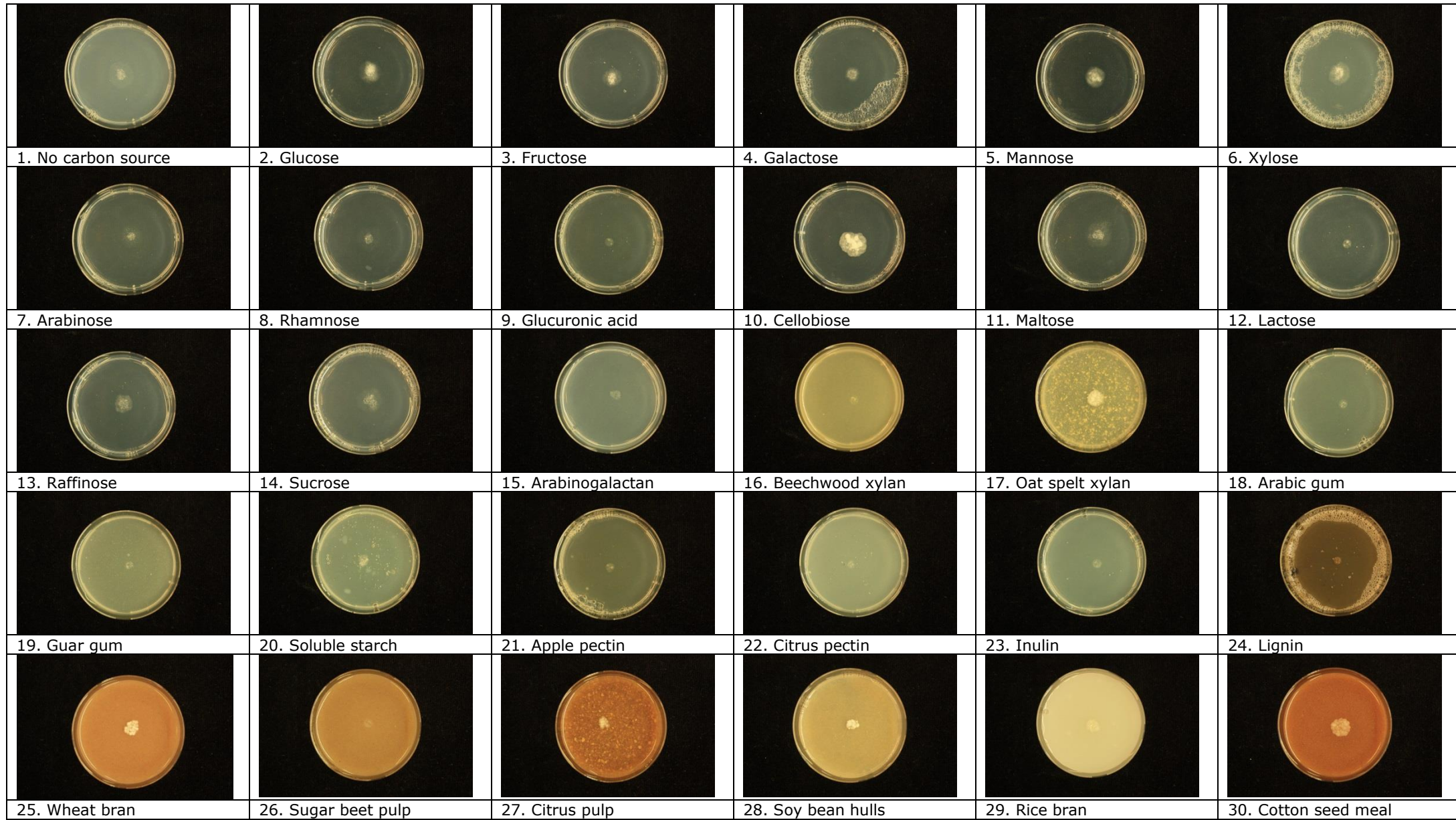
					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
T 54 <i>Microtermes</i> -symbiont					
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose
					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose
					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum

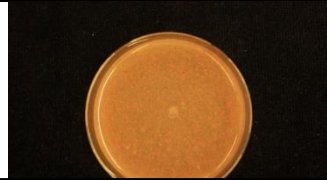



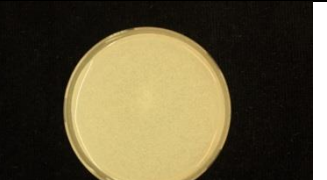
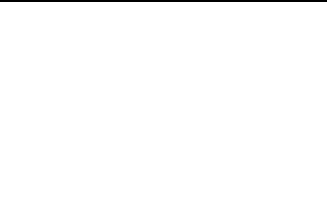
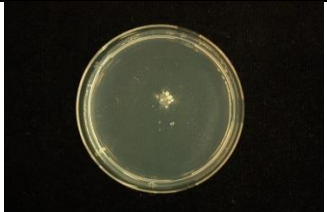


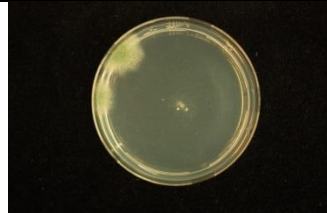
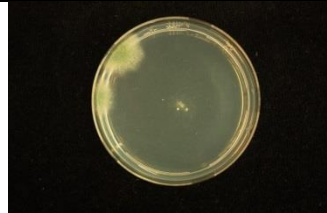
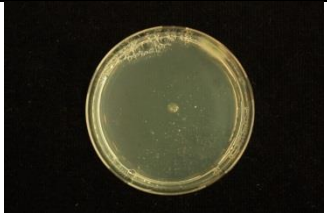

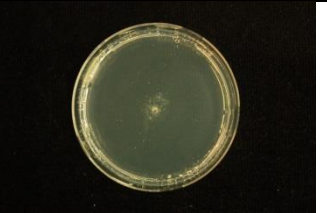
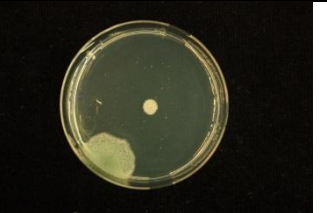
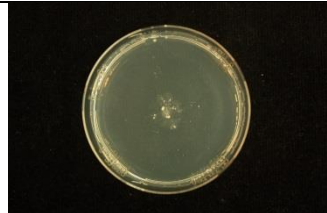
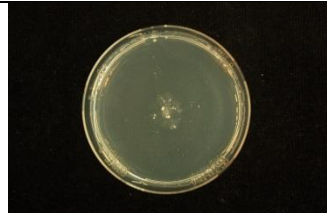
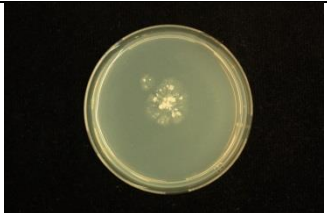
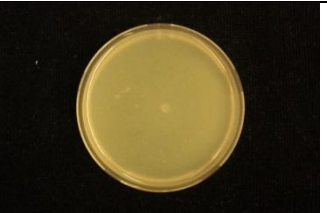

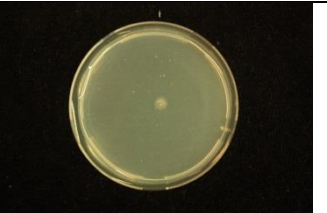





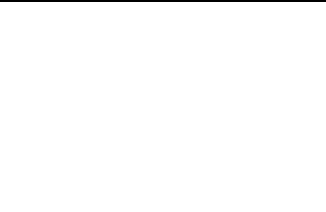
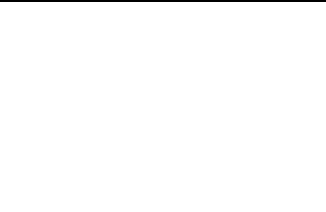
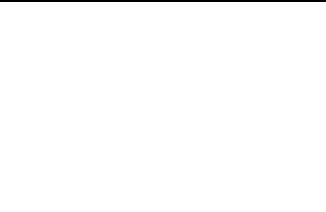
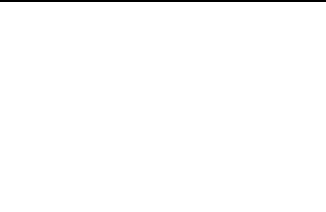
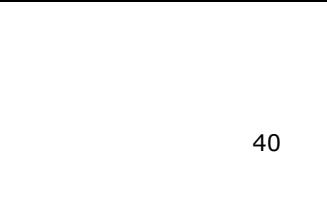
					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin
					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose
					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose

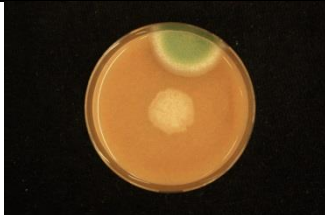


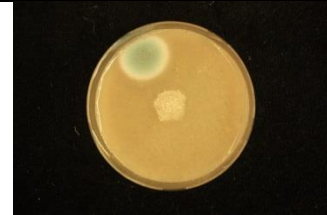
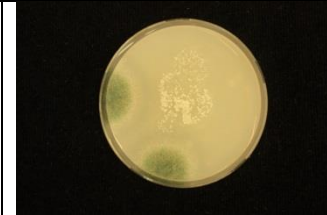
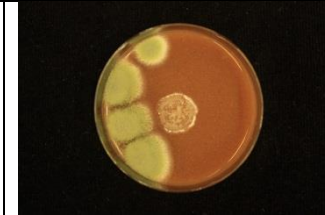


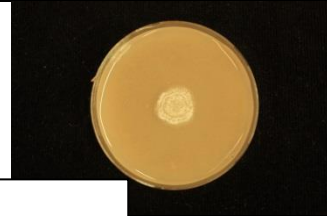





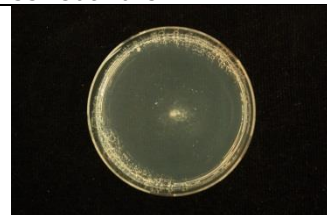
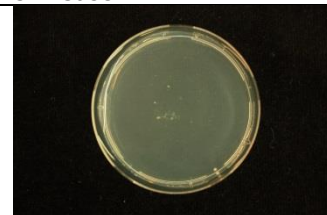
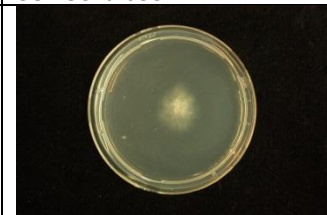
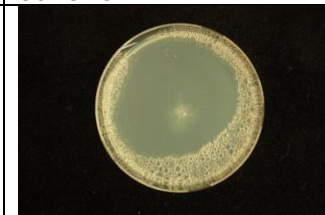
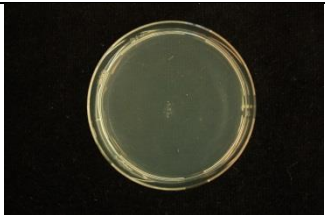
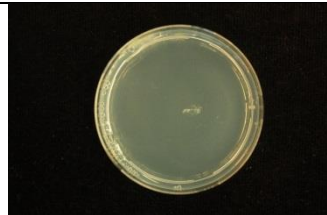
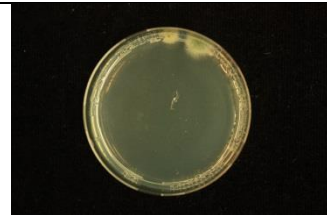
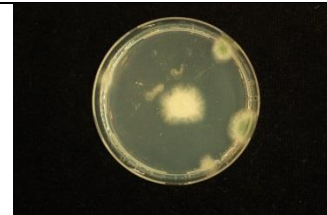
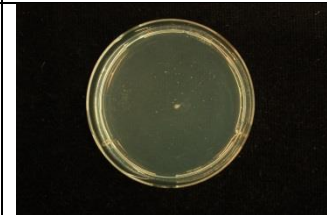
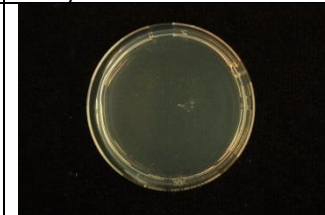
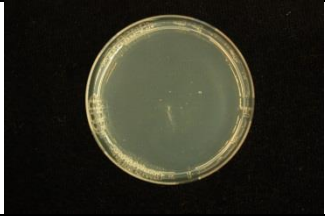
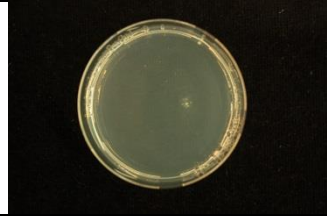


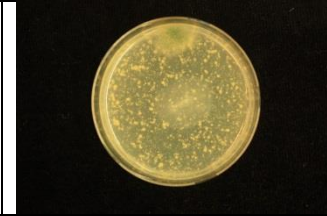
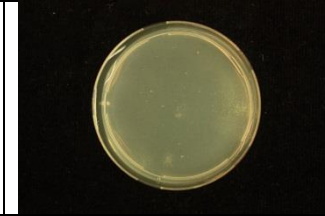
T 73 *Odontotermes-symbiont*


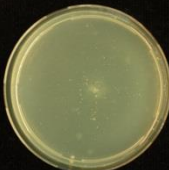
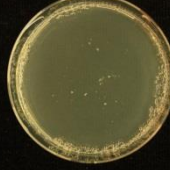

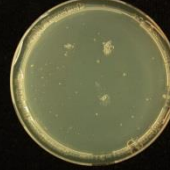
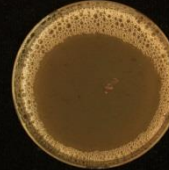
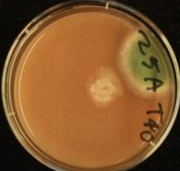
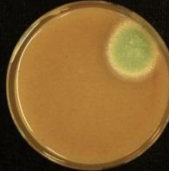





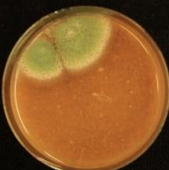



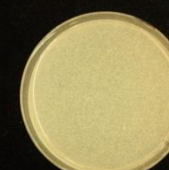
					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum
					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin
					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
T 74 <i>Odontotermes</i> -symbiont					
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose

					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose
					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum
					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin
					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
31. Alfalfameal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin



					
T 64 <i>Macrotermes</i> -symbiont					
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose
					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose
					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum
					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin
					

					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
T 40 <i>Microtermes</i> -symbiont					
31. Alfalfa meal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin
					
1. No carbon source	2. Glucose	3. Fructose	4. Galactose	5. Mannose	6. Xylose
					
7. Arabinose	8. Rhamnose	9. Glucuronic acid	10. Cellobiose	11. Maltose	12. Lactose
					
13. Raffinose	14. Sucrose	15. Arabinogalactan	16. Beechwood xylan	17. Oat spelt xylan	18. Arabic gum

					
19. Guar gum	20. Soluble starch	21. Apple pectin	22. Citrus pectin	23. Inulin	24. Lignin
					
25. Wheat bran	26. Sugar beet pulp	27. Citrus pulp	28. Soy bean hulls	29. Rice bran	30. Cotton seed meal
					
31. Alfalfameal	32. Corn gluten	33. Oat hulls	34. Casein	35. Cellulose	36. Chitin