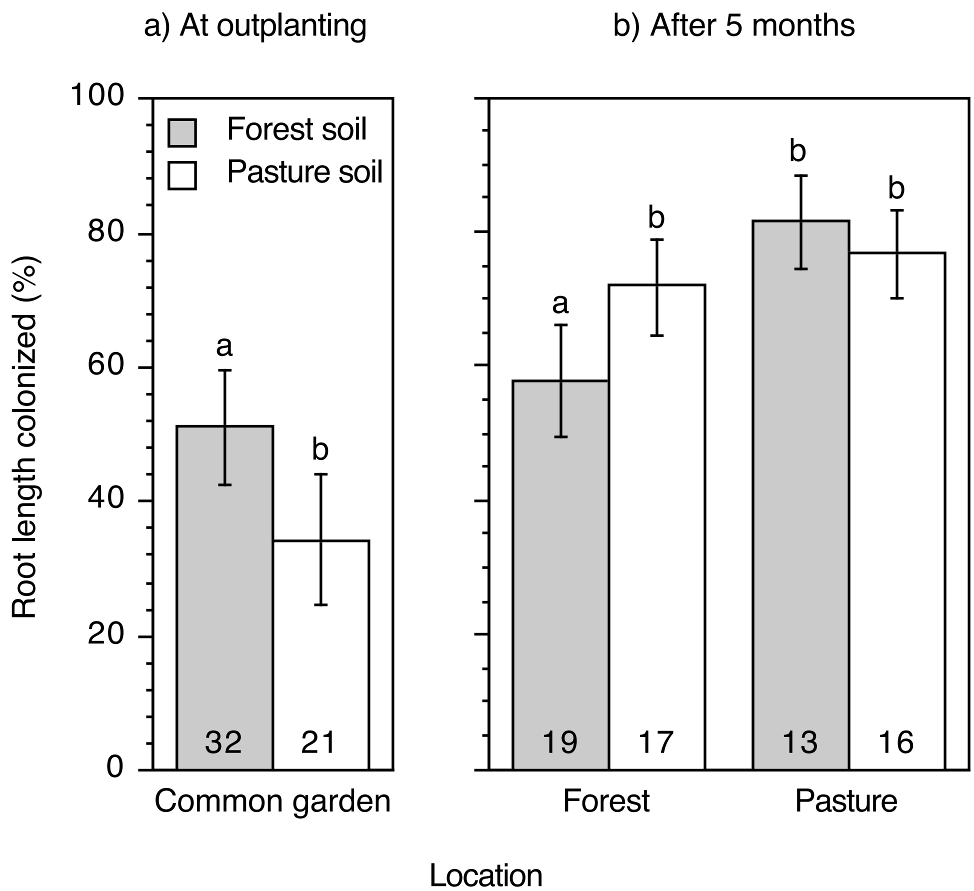

Figure 2.7 Root colonization of *Terminalia amazonia* seedlings by arbuscular mycorrhizal fungi a) ten days prior to outplanting and b) after 5 months of growth in forest or pasture at field sites in Siete Colinas, Coto Brus, Costa Rica. Sample size is shown at base of each bar. Error bars indicate 95% confidence intervals. Means that share a letter do not differ at $\alpha = 0.05$.

DISCUSSION

Pastures as safe sites

Both survival and growth of *T. amazonia* seedlings were much higher in pasture than in forest in this study. Once the barriers of seed dispersal, germination and cattle grazing are removed, and competition with pasture grasses is reduced, the pasture environment is more conducive to seedling establishment than adjacent forest sites for this tree species.

The difference in seedling establishment between forest and pasture is likely due in large part to light. Seedlings in full sun in the pasture and seedlings in high light in the forest understory suffered lower mortality than seedlings in the shade. Light almost certainly benefits plants both directly through increased photosynthesis and indirectly, by lowering abundance of, and susceptibility to, pathogens (Augspurger 1984) and increasing colonization by mycorrhizal symbionts (Gehring 2003).

Terminalia has been classified as a genus with seedlings requiring light gaps to survive (Whitmore 1998, p. 120). Seeds of *T. amazonia* (*personal observation*) and *T. oblonga* (Augspurger 1984) found germinating in the forest understory quickly succumb to damping off. While seeds are dispersed broadly across the forest floor, seedlings are found in clumps, suggesting establishment in former light gaps and persistence as a seedling bank in the understory (*personal observation*). The light compensation point of *T. amazonia* is not known. Mortality in the understory may result from attack by pathogens; it may also result from a respiratory rate (Walters and Reich 1996, Davies 1998) or carbohydrate transfer rate to mycorrhizal symbionts (Smith and Read 1997) that exceeds the rate of carbon fixation.

The ability of *T. amazonia* seedlings to respond to increases in light availability by increasing photosynthetic rate is typical of many 'light-demanding' tropical tree species (Whitmore 1998). Such a response does not necessarily preclude an ability to maintain carbon balance under low light (Bloor and Grubb 2003). This study suggests that other tree species which require light gaps for seedling establishment are likely to exhibit improved establishment in pastures relative to forest.

Light has both direct and indirect effects on disease incidence: by increasing ultraviolet radiation, which reduces spore viability; by decreasing relative humidity, which increases spore desiccation and reduces spore germination (Dix and Webster 1995); and by improving a seedling's carbon balance, so it is less likely to be detrimentally affected by pathogen infection (Augspurger 1984). During the wet season, when *T. amazonia* seeds are germinating, relative humidity in the pasture dips low enough each day to inhibit spore germination of a variety of pathogens (Dix and Webster 1995). In contrast, relative humidity in forest remains high enough throughout the day year-long to promote spore germination.

Forest soil inoculum benefit

Forest soil inoculum facilitated seedling establishment of *T. amazonia* in both forest and pasture, and the benefit of forest soil inoculum to seedlings was derived almost entirely from an improvement in survival rather than an increase in growth. In semi-arid sites in Kenya, (Wilson et al. 1991) found that inoculation of *T. prunioides* with forest soil increased survival but not growth relative to controls. Differences in both the abiotic and biotic characteristics of forest and pasture soil could play a role in observed differences in seedling survival. Seedlings inoculated with forest soil may have experienced a slight fertilization effect from the higher availability of inorganic N (and possibly P) in forest than pasture soil. However, light, rather than nutrients, is likely to limit plant growth in the forest understory (Denslow et al. 1987), so higher nutrient availability in forest soil could likely only explain the soil inoculum effect for seedlings grown in pasture. Another explanation is that micro-organisms (or their products) that benefit or protect forest seedlings are more prevalent in forest soil.

Colonization of roots by AM fungi was higher at outplanting for seedlings inoculated with forest soil than those inoculated with pasture soil. Previous work with these soils suggests that species composition of AM fungi differs between forest and pasture (Chapter One). Consequently, the observed difference in colonization may be the result of different species colonizing seedlings in pasture and forest soils (Hart and Reader 2002b). Alternatively, the slighter higher nutrient status or lower pH of forest soil relative to pasture soil may have had a positive effect on root colonization. Increases in root colonization between treatments are usually associated with increased host growth (Smith and Read 1997). Other soil biota beneficial to forest tree seedlings may also have been present in forest soil inoculum and absent from pasture soil inoculum (Setala and Huhta 1991).

Additionally, the use of mixed soil inoculum may have biased the AM fungi colonizing roots toward those species which can tolerate disturbance (Klironomos and Hart 2002). In that case, the higher levels of root colonization on seedlings inoculated with forest inoculum might be due to greater resilience of AM fungi in forest soils to disturbance. This seems unlikely, since previous studies have found that AM fungi of forest soils are less resilient to disturbance than AM fungi of pasture or grassland soils (Jasper et al. 1991, Fischer et al. 1994).

After outplanting, the higher levels of root colonization in seedlings inoculated with forest soil did not persist. However, there was a difference between the soil inocula in how root colonization by AM fungi changed with habitat. For seedlings inoculated with forest soil, root colonization in the forest environment was lower than root colonization in the pasture environment. For seedlings inoculated with pasture soil, there was no difference in root colonization between habitats. Consequently, seedlings inoculated with pasture soil and planted in forest should have contributed a greater proportion of their carbon to AM fungal symbionts than seedlings inoculated with forest soil. Such a carbon drain could explain lower survival of seedlings inoculated with pasture soil in forest relative to seedlings inoculated with forest soil.

AM fungi in seedlings inoculated with forest soil appeared to exhibit a response to differences in the light environment, while AM fungi in seedlings inoculated with pasture soil did not. In low light, AM fungi found in forest colonized seedlings to a lesser extent than pasture AM fungi. Pasture fungi colonized seedlings to the same extent in high and low light environments. If colonization levels reflect carbon transfer from plants to AM fungi, pasture AM fungi may result in a negative carbon balance for seedlings grown in the shade, resulting in higher mortality.

Previous work on factors influencing seedling establishment has usually compared recruitment in the understory with recruitment in light gaps, or compared seedling establishment in pastures with or without ameliorating conditions (Zimmerman et al. 2000, Holl 2002). There has been little research that contrasts seedling establishment between forest understory and pasture

(Gerhardt 1996). Research in pastures has emphasized the difficulty of establishing seedlings in pasture (Aide and Cavelier 1994). Yet, seedling establishment in pastures may actually be considerably higher than that observed in forest (Gerhardt 1993).

Contrary to expectation, there was no interaction of habitat with soil inoculum. This study found no evidence that inoculation of forest seedlings with pasture soil might benefit seedlings by reducing early mortality due to soil pathogens (such as those causing damping off). It is possible that the amount of soil used during outplanting and the length of time for which forest seedlings were exposed to pasture soil were insufficient to provide a measurable reduction in soil pathogen inoculum.

Although the benefit of forest soil inoculum did not differ across habitats, the mechanism whereby forest soil inoculum benefits tree seedlings may differ between low and high light environments. This study was designed to assess whether there is a benefit to inoculating seedlings with forest soil. Future work is needed to ascertain the mechanisms by which inoculation with forest soil benefits seedlings