Intra- and inter-specific competition between seedlings of *Acacia etbaica* and a perennial grass (*Hyparrenia hirta*)

Masresha Fetene*

Department of Biology, Faculty of Science, Addis Ababa University, P.O. Box 30193, Addis Ababa, Ethiopia

Received 8 June 2001; received in revised form 24 September 2001; accepted 10 October 2001

Abstract

Intra- and inter-specific competition between seedlings of *Acacia etbaica* Schweinf. and the grass *Hyparrenia hirta* (L.) Stapf. was studied to evaluate the influence of the perennial grass on the establishment of the tree seedlings. The experiment was conducted using a replacement series in which plants were grown in a greenhouse at an overall density of six individuals per pot, providing combinations of the two species from 0:6 and 6:0. Indices of intra- and inter-specific competition, relative crowding coefficients and relative yield totals (RYTs) were calculated from the dry weight data. For both shoots and roots, the crowding coefficient of *Hyparrenia* towards *Acacia* was five- to ten-fold that of *Acacia* towards *Hyparrenia*, which indicated a high competitive strength for the grass species. RYT values of the two species averaged 1.25, indicating some degree of resource complimentarity. Both species had comparable intra-specific competition based on shoot yield. However, based on the root yield, intra-specific competition of *Hyparrenia* was slightly lower than that of *Acacia*. Inter-specific competition of *Hyparrenia* on the root yield of *Acacia* was more than five times greater than vice versa. With more crowding, shoot/root ratio decreased more in *Hyparrenia* than in *Acacia* for pure stands as well as for mixtures which indicated that *Hyparrenia* could adjust biomass allocation. In general, the results indicated that *Hyparrenia* was competitively aggressive towards *Acacia* and may inhibit the growth of tree seedlings when the latter are planted within the grass community. Implications of the findings in terms of land reclamation efforts are discussed.

© 2003 Elsevier Science Ltd. All rights reserved.

Keywords: *Acacia etbaica*; *Hyparrenia hirta*; Inter-specific competition; Intra-specific competition
1. Introduction

The interaction of trees and grasses in the tropics has been widely discussed (Walker and Noy-Meir, 1982; Tainton and Walker, 1992; Scholes and Archer, 1997). The niche separation of grasses and trees, whereby grasses are superior competitors in the top soil layers while trees have exclusive access to the deeper soil layers, has been supported by several investigations (Belsky, 1990). Other studies have shown that, depending on particular situations, trees and grasses may compete for resources where their root systems overlap (Scholes and Walker, 1993; Belsky, 1994). A condition where this may always be true is when tree seedlings establish within a grass community. We observed such a case during a land reclamation effort in Ethiopia where the growth and establishment of seedlings of *Acacia etbaica* Schweinf. growing within a mature grass community of *Hyparrenia hirta* (L.) Stapf. was severely impeded.

*Acacia etbaica* has a wide occurrence, from semi-desert scrub to wooded grassland at altitudes that extend from 1200 to 2000 m. The tree is widely used to make the pillars and beams of earthen houses in Ethiopia (Thulin, 1989). *Hyparrenia hirta* is a drought-resistant perennial grass which occurs on dry hillsides and overgrazed areas at altitudes that extend from 1100 to 2600 m (Phillips, 1995). Both the tree and grass species are quite popular for their use in the construction of peasant huts and are also used to reclaim degraded areas. *Hyparrenia* is a tufted grass with a dense fibrous root system which may give the species a competitive edge when growing with other plants, especially seedlings (Bokhari et al., 1987). A question of interest was the competitive strength of seedlings of *Acacia* vis-a-vis the grass *Hyparrenia* when the two species are grown from seed. While the emergence and survival of tree seedlings in grass swards has been studied by several authors (Schmidt and Stubbendieck, 1993; O’Conner, 1995), few have addressed the relative competitive strengths of tropical tree seedlings and grasses grown from seeds. In this study, I present the results of a replacement series experiment whereby variable mixtures of a grass species and *Acacia* seedlings were grown alongside pure stands. The following questions were addressed: (1) what is the degree of intra- and inter-specific competition of *Hyparrenia* and *Acacia* when grown from seeds in mixtures of variable proportions and (2) how do the relative shoot and root competitive abilities of the two species compare?

2. Experimental design

2.1. Indices of competition

The overlap in the use of resources between *Acacia* and *Hyparrenia* was measured using a replacement series experiment (de Wit, 1960). In the experiment, plants of two species were grown together at the same overall density and the proportion of one species in the mixture was decreased as the proportion of the second species was increased. For comparison, pure stands of each species were also grown at the same
density as its occurrence in the mixed stands. The results were then analysed graphically using replacement diagrams following Harper (1977) and Snaydon (1991). It is assumed that when competition between two species is equal the contribution of each species to the total yield will be in direct ratio to its proportion in the mixture. Four indices were used in the present experiment: (i) the relative crowding coefficient \( K \), (ii) the relative yield total \( \text{RYT} \), (iii) index of intra-specific competition \( R_{ii} \), and (iv) index of inter-specific competition \( R_{ji} \) (de Wit and van den Bergh, 1965; Newman, 1983; Bi and Turvey, 1994; Jolliffe, 2000).

2.1.1. The relative crowding coefficient \( K \)

The relative crowding coefficient \( K \), a measure of the aggressiveness of one species towards another was calculated following Newman (1983) and Firbank and Watkinson (1985) as follows:

\[
K_{ij} = \frac{Y_{ij}F_j}{(Y_{ii} - Y_{ij})F_i}
\]

where \( K_{ij} \) is the relative crowding coefficient of species \( I \) towards species \( J \); \( Y_{ii} \) is the yield of species \( I \) in its pure stand and \( Y_{ij} \) is the yield of species \( I \) in mixture with species \( J \) and \( F_i \) and \( F_j \) are the relative frequencies of species \( I \) and \( J \), respectively.

2.1.2. The relative yield total \( \text{RYT} \)

\( \text{RYT} \), which is a measure of resource complementarity, was calculated as follows (de Wit and van den Bergh, 1965):

\[
\text{RYT} = \frac{Y_{ij}}{Y_{ii}} + \frac{Y_{ji}}{Y_{jj}}
\]

where \( Y_{ji} \) is the yield of species \( J \) in mixture with species \( I \) and \( Y_{jj} \) is the yield of species \( J \) in its pure stand. In two species mixtures, an RYT value close to 1.00 indicates that the two species make equal demands on the same limiting resources. RYT values greater than 1.00 indicate that species that still compete for the same resources may also make demands on different resources. RYT values less than 1.00 indicate mutual antagonism (Bi and Turvey, 1994).

2.1.3. Intra- and inter-specific competition \( R_{ii} \) and \( R_{ji} \)

The relative importance of intra-specific \( R_{ii} \) and inter-specific \( R_{ji} \) competition were assessed following Jolliffe et al. (1984):

\[
R_{ii} = \frac{Y_{ip} - Y_{ii}}{Y_{ip}} \quad \text{and} \quad R_{ji} = \frac{Y_{ii} - Y_{ij}}{Y_{ii}}
\]

where \( R_{ii} \) is the relative effect of intra-specific competition on plants of species \( I \) and \( R_{ji} \) is the relative effect of inter-specific competition from species \( J \) on the yield of species \( I \). \( Y_{ip} \) is the “projected yield” of species \( I \), which is the expected yield of that species at a given density in the absence of intra- and inter-specific competition. \( Y_{ip} \) is calculated as the product of the density of the species and the yield of the species when grown as single plants.
2.2. Plant growth conditions and harvesting

Seeds of both Acacia and Hyparrenia were collected from the field in Haiq (north central Ethiopia, 11°30’N and 39°35’E), at 1800 m a.s.l. The seeds were germinated in Petri dishes on wet filter paper in the dark in an incubator set at 25°C. Seeds of A. ethbaica were mechanically scarified using sand paper to hasten germination. Germinated seeds were transplanted into a soil, sand and compost mixture (2:1:1) in polyethylene pots of 20 cm diameter and 30 cm depth. The seeds of the two species were sown to obtain an overall density of six plants per pot for each species combination, providing combinations of the two species from 0:6 to 6:0. Pots containing pure stands of the two species from one to six plants per pot were also maintained. Plants were watered with 200 ml of water per day and 100 ml of Ingstad nutrient solution (Ingstad, 1970) once a week. The experiment was conducted in three replicates in a greenhouse. The daily temperatures and humidity of the greenhouse averaged 24°C and 56%, respectively.

Plants were harvested 180 days after sowing. Shoots and roots were separated and put in paper bags. Roots of different species were separated whereas roots of the same species within a pot were left intact due to difficulty of separation. Harvested plant parts were then dried in an oven at 80°C for 48 h. From the yield data, the relative crowding coefficients of the species towards each other, RYT of each species combination, and the relative effects of intra- and inter-specific competition on the yield of each species were computed.

2.3. Statistics

Data were analysed by analysis of variance (ANOVA) according to the generalized linear model (GLM) procedure of Sigma-stat. Test for normality was performed with the Kolmogorov–Smirnov test of the program. The difference between the treatment means were considered significant when $p \leq 0.05$.

3. Results

3.1. Crowding coefficients and relative total yields

Data on the crowding coefficients and the RYT values of the two species are presented in Table 1. Both in root and shoot yield, the relative crowding coefficient of Hyparrenia towards Acacia ($K_{ha}$) was significantly greater than converse ($K_{ah}$). The crowding coefficient of Hyparrenia at the root level was much greater than that at the shoot level. In most cases, the crowding coefficients of Hyparrenia towards Acacia were between five to ten times greater than that of Acacia towards Hyparrenia. The RYT values of the two species averaged 1.24 for the shoots and 1.26 for roots. Except in two cases (one each for shoot and roots) RYT was always higher than 1.0 (Table 1).
3.2. Intra-specific competition

Fig. 1 shows the relative effect of intra-specific competition on the yield of Hyparrenia and Acacia. The intra-specific competition of both species increased with number of plants per pot. The increase was linear until three plants per pot but plateaued with further increase in number of plants per pot. Intra-specific competition in shoot yield was similar in both species. There was no difference in intra-specific competition of shoot and root of Acacia. However, roots had significantly lower intra-specific competition than shoots in Hyparrenia.

3.3. Inter-specific competition and replacement diagrams

Inter-specific competition between the shoot and roots of Acacia and Hyparrenia is shown in Fig. 2. In general, the relative effect of inter-specific competition from Hyparrenia on Acacia was greater than that of Acacia towards Hyparrenia. The effect was more pronounced in roots than in shoots. Inter-specific competition from Hyparrenia on Acacia showed a general increasing trend with increase in the frequency of Hyparrenia in the mixture, especially in roots. Hyparrenia contributed significantly higher biomass to the total yield in both shoot and roots when the two species were grown in mixtures (Fig. 3). However, the yield of Hyparrenia decreased as its proportion increased in the mixture. With Acacia there was a slight increase in
yield with an increase in its proportion in the mixture. The increase was pronounced more in shoot yield than in root yield (Fig. 3).

3.4. Shoot/root ratio

Both in pure stands and in mixtures shoot/root ratio of *Acacia* did not vary significantly with increase in the number of plants per pot, but was mostly higher than in *Hyparrenia*. Shoot/root ratio in *Hyparrenia* decreased significantly with an increase in the number of plants per pot both in pure stands and mixtures. Mixed stands had higher shoot/root ratio in *Acacia* than pure stands, while in *Hyparrenia* the reverse was true. However, for both species the differences were not statistically significant (see Fig. 4).

Fig. 1. The relative effects of intra-specific competition on the shoot and root yields of *Acacia etbaica* and *Hyparrenia hirta*. Vertical lines are standard errors.
4. Discussion

Hyparrenia had larger relative crowding coefficient values towards Acacia both in root and shoot competition, which indicated that the grass species was more aggressive towards the acacia seedlings. The RYT of the mixtures of the two species averaged 1.25. Such values (i.e. >1.00) indicate that while the two species compete for resources, there is also some degree of resource complementarity between them. Similar studies on legume and non-legume mixtures have attributed high values of RYT to the use of different nitrogen sources in addition to differences in root and shoot characteristics (Martin and Field, 1984; Tofinga et al., 1993; Semere and Froud-williams, 2001). Slightly higher values of the crowding coefficient of Hyparrenia based on the root yield compared to the shoot yield, indicated that its
root competitive abilities were relatively higher than its shoot competitive abilities. In part, this could be attributed to the fact that root competition starts as soon as the root system of one plant intermingles with that of the other, which usually occurs long before leaf canopies are sufficiently developed to allow competition for light (Aspinall, 1960). In the present study, since crowding coefficient values of the shoot of *Hyparrenia* were also high, it may be concluded that the aggressiveness of *Hyparrenia* depended on the combined effects of root and shoot competition.

Both species had comparable intra-specific competition for shoots. Intra-specific competition on the yield of *Hyparrenia* based on the roots was significantly lower than that based on the shoot. A lower intra-specific root competition might be an advantage in mixtures and this may contribute to the higher root competition abilities of *Hyparrenia* (Bi and Turvey, 1994). This is further supported by the data.

Fig. 3. Dry weights of shoots and roots of *Acacia etbaica* and *Hyparrenia hirta* in their various proportions within the replacement series, and the combined total yields of the two species. Vertical lines are standard errors.
on the effect of inter-specific competition of Hyparrenia on the root yield of Acacia, which was in most cases five to six times higher than that of Acacia on Hyparrenia.

Decrease in shoot/root ratio with more crowding was observed in Hyparrenia but not for Acacia both for the pure stands as well as for the mixtures. This indicates that Hyparrenia invested more on roots with progressive crowding, which further shows that the species was capable of adjusting biomass allocation, depending on the conditions. The results indicate that Hyparrenia is competitively aggressive towards Acacia and may inhibit the growth of the latter when growing near each other. As related to the aggressiveness of Hyparrenia, it may be said that the pot environment may have slightly intensified inter-specific competition. Also, as the experiment was performed under well-watered conditions in a glasshouse, extrapolation of the

Fig. 4. Shoot/root ratios of Acacia etbaica and Hyparrenia hirta in the replacement series both pure stands and mixed stands. Vertical lines are standard errors.
results under field conditions may be limited. The case in a dry environment with mature trees that have extended root systems may also be different. Nevertheless, results of the experiment are consistent with field observations that the growth of *Acacia* seedlings is severely limited by competition from grasses.

*Acacia* is a hardy tree species of dry savannas and degraded hills much preferred for its hard wood, especially in northern Ethiopia. The tree has a capacity to recover degraded hills following enclosures of a few years (Pausewang and Zegeye, 1994). However, such lands protected for reclamation are frequently colonized by several grass species among which *Hyparrhenia* is the most prominent one. Protecting seedlings of *Acacia* from the intense competition of *Hyparrhenia* especially at the early stages as shown in the present study, becomes imperative for successful land reclamation.

**Acknowledgements**

Financial support from the African Academy of Sciences is gratefully acknowledge. I thank Yonas Feleke for his excellent technical assistance and Zerihun Woldu for insightful discussions.

**References**


