THE EFFECT OF OZONE AIR POLLUTION

ON

PLANT COMPETITION

by

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ABSTRACT

Low levels of ozone air pollution have been shown to cause reductions in plant growth. It has been proposed that these reductions could translate into effects on a plant's competitive ability, and hence, on the inter-relationships of plants in a community.

Experiments were carried out to determine if there was an effect of low levels of ozone on intra- and inter-specific competition of barnyardgrass (BYG), redroot pigweed (RPW) and green foxtail (GFT). Three ozone treatments (a filtered air control, and 75 ppb/7 hr and 150 ppb/3.5 hr daily) were applied to monocultures and binary mixtures in replacement and additive series. The two ozone treatments represent the same ambient dose. The effects of each on the plants studied were compared and contrasted.

The order of competitive ability of the three species was found to be BYG > RPW > GFT. There were significant differences in the interaction of the species between the three ozone treatments. BYG experienced significant intra-specific competition only in the two ozone-added treatments; GFT was significantly affected by its own density only in the control. In contrast, RPW experienced significant intra-specific competition effects in all treatments.

BYG benefitted significantly from the presence of GFT in the control. A similar positive effect of GFT density on BYG yield is seen in the 150 ppb/3.5 hr treatment. It is suggested that this localized positive allelopathic effect may be due to the upward transport of a volatile compound released by GFT, or disseminated through the soil. All inter-specific competitive relations of GFT and RPW were significant in all ozone treatments.

RPW appeared to experience the most ozone effects of the three species studied. RPW and GFT in replacement series mixtures showed over-yielding in the control treatment, equal replacement in the 75 ppb/7 hr treatment and under-yielding in the 150 ppb/3.5 hr treatment. This interaction of ozone and competition treatments between RPW and GFT was significant for root dry weight per pot.

BYG yield was significantly enhanced in the 75 ppb/7 hr ozone treatment over the control and 150 ppb/3.5 hr treatments. This may reflect an acclimation of BYG plants to the low (0.01-0.04 ppm) ambient background levels of ozone. The concept of an appropriate control treatment is discussed.

Although the 75 ppb/7 hr and 150 ppb/3.5 hr treatments represent the same ambient dose, the species used in this study reacted quite differently to the two treatments. Overall, the more acute 150 ppb/3.5 hr dose had a more detrimental effect on the yield variables measured for RPW and GFT, and the 75 ppb/7 hr treatment had a significant enhancing effect on BYG yield over that of the control and the 150 ppb/3.5 hr dose.

An examination of the size frequency distributions of the three species confirms that BYG is competitively dominant, whereas the GFT size distributions do not appear to be sensitive to competitive suppression. RPW displays a very skewed size frequency distribution under all treatments. It is suggested that RPW has inherent genetic variability for a wide size distribution in the populations studied. There were no ozone effects on the size frequency distributions of any species studied.

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ABBREVIATIONS

ANOVA	analysis of variance
BYG	barnyardgrass, *Echinochloa crus-galli* (L.) Beauv.
GFT	green foxtail, *Setaria viridis* (L.) Beauv.
hr	hours
NO_x	oxides of nitrogen
MLR	multiple linear regression
O_3	ozone
ppb	parts per billion
ppm	parts per million
RPW	redroot pigweed, *Amaranthus retroflexus* L.
SSR	sequential simple regression

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1. INTRODUCTION

Plants are rarely found growing in isolation. In natural ecosystems and agricultural systems, plants usually share their immediate environment with individuals either of the same species in monocultures or of a different species in mixtures. The presence of other plants changes the environment of their neighbours and may alter their growth rate and form (Harper, 1977). Specifically, there is an interaction between the proximity of neighbours and resource availability in defining neighbour relations. The detrimental interference in growth due to the unequal allocation of resources is competition (Harper, 1961). Both the immediate and evolutionary success of a plant depends on its ability to compete.

The competitive ability of a plant depends on its integral physiological condition. Any factor that will affect plant growth will have a subsequent effect on that plant's competitive ability. Air pollutants are recognized as a source of stress for plants and it has been suggested that this stress could alter the competitive ability of certain species, or modify their physiology, thereby altering their survival potential (Smith, 1974).

Growing plants are very susceptible to air pollutants, with reductions in photosynthesis and growth often occurring before visible symptoms are noted (Bennett and Hill, 1974). Ozone, a strong oxidant component of photochemical smog, has been shown to both stimulate (Bennett *et al.*, 1974) and depress (Manning and Feder, 1975) plant growth at low concentrations. Ozone is rapidly being recognized as a serious pollutant problem both in urban and rural areas (Heck *et al.*, 1983).

Bennett and Runeckles (1977) studied the effects of low levels of ozone on competition in binary mixtures of annual ryegrass and crimson clover. Using the de Wit (1960) replacement series, they found that those components of yield which were measured were less depressed by ozone when in species mixtures than in monocultures.

The present study was undertaken to extend these results by examining the competitive relationships of three annual species exposed to ozone. The competitive relations of barnyardgrass, redroot pigweed and green foxtail have been well documented in the field (Minjas, 1982), allowing a comparison of the ozone effects in controlled environment chambers to those of natural conditions.

One objective of this study was to determine experimentally the effects of low levels of ozone on inter- and intra-specific competition, and compare it to the species' response to ozone in monocultures. The second objective of this study was to examine the differences, if any, between the responses to two ozone exposure regimes which represent the same ambient dose, but differ in concentration and duration.

2. LITERATURE REVIEW

2.1 OZONE EFFECTS ON PLANTS

The growth of urban areas, accompanied by high-density automotive traffic, industrial activity and a rising need for power generation, has led to increased levels of air pollutant emissions. These high concentrations of combustion products, particularly the oxides of nitrogen, and volatile organic components, participate in a complex series of chemical reactions driven by sunlight, producing photochemical smog (Demerjian, 1986). Ozone (O_3) is a secondary reaction product of this process on which a great deal of attention has been focused recently. Ozone and its precursors can be transported for hundreds of kilometers, and because non-urban air contains few compounds which react with ozone, it can persist for longer periods in rural areas (Jacobson, 1982). A great deal of research has been done on the effects of ozone on vegetation, particularly with agricultural plants.

In order to allow a prediction of a plant's response to air pollutants, many dose response models have been tested. The classic description of pollutant exposure uses the term "dose", which is the product of concentration and time. However, the necessary existence for many species of a threshold concentration below which there is no response, has led to the conclusion that the relative importance of duration of exposure is much less than that of concentration. As well, because the movement of gaseous pollutants is passive (Heath, 1980), many other factors control the availability of the gas to the plant. The velocity of deposition, $\mathbf{v_g}$, to the plant can be described by the equation

$$\mathbf{v_g = F/X}$$

where **F** is the flux and **X** the concentration at some reference height (Chamberlain, 1986). The resistance to transfer ($\mathbf{r_{total}}$), the reciprocal of $\mathbf{v_g}$, is the sum of three resistances

$$\mathbf{r_{total} = r_a + r_s + r_m}$$

where $\mathbf{r_a}$ is the resistance of the boundary layer near the stomata; $\mathbf{r_s}$ is the stomatal resistance; and $\mathbf{r_m}$ is the resistance encountered from the substomatal chamber to the cellular interior, including cell walls and membranes. The turbulence of the air above a plant, the presence of a canopy, the thickness of the boundary layer and the water relations of the plant all affect the deposition of the gas to the plant. It is important to recognize that the dose expressed in terms of the ambient concentration above a plant is not necessarily the dose received by the plant. The true dose or effective dose, determined as uptake, or flux, is a better approximation of the dose actually received by the plant (Runeckles, 1974).

Membranes are the primary site of ozone attack within a plant (Tingey and Taylor, 1982; Evans and Ting, 1983). The phytotoxicity of ozone involves molecular events which result in a perturbed cellular structure and function and culminates in an altered membrane permeability. Whether or not this translates into injury depends on the ability of the plant to repair or compensate for the altered membrane permeability.

Low levels of ozone can stunt growth (Feder, 1971) and cause reductions in photosynthesis (Bennet and Hill, 1974) without producing visible injury. Yang *et al.*(1983) described decreases in net photosynthesis and dark respiratory rates in Eastern White Pine at ozone concentrations of 0.10 ppm. *Lolium multiflorum* and *Trifolium incarnatum* were shown to have less growth and yield than controls when treated daily with 0.03 or 0.09 ppm ozone (Bennett and Runeckles, 1977). Reich and Amundson (1985) carried out experiments in which *Acer saccharum*, *Glycine max* cv. Hodgson, *Pinus strobus*, *Populus deltoides*, *Quercus rubra*, *Trifolium repens* cv. Arlington and *Triticum aestivum* cv. Vona were exposed to ozone concentrations ranging from 0.01 to 0.125 ppm. In all species, exposure to any increase in ozone reduced net photosynthesis. These ozone-induced reductions in photosynthesis were related to subsequent declines in growth and yield. Hybrid poplar, *Populus deltoides* x *tricarpa*, exposed to 0.025, 0.05, 0.085 and 0.125 ppm ozone showed inverse linear reductions in leaf, stem, root and total dry mass per plant (Reich and Lassoie,1985).

A great deal of research on the effects of ozone on agricultural species has been undertaken recently in the United States, in the form of a nation-wide study called the National Crop Loss Assessment Network (NCLAN) (Heck *et al.*, 1982; Heck *et al.*, 1983; Heck *et al.* 1984a, 1984b). Based upon these studies, preliminary estimates suggest that about $3 billion of direct agricultural crop losses would result if the USA experienced a seasonal 7-hour/day mean ozone concentration of 0.06 ppm (Heck *et al.*, 1983). The exposure regimes in the studies carried out under the NCLAN program were applied in open top chambers to field grown plants. Winter wheat, *Triticum aestivum* cv. Abe, Arthur-71 and Roland exposed to 0.023, 0.041, 0.068, 0.095 and 0.122 ppm 7-hr/day seasonal means of ozone showed a general decrease in all yield variables in one season, and in the weight yield variables in the second season (Kress *et al.*, 1985). The ozone effects and cultivar effects were significant in both years.

Hordeum vulgare L. cv. Poco and CM-72, exposed under the same treatment regime to 0.03-0.09 ppm ozone showed no ozone effects on yield or growth (Temple *et al.*, 1985). The authors suggest that the threshold for an ozone effect on yield of these barley cultivars is above a seasonal 7-hour mean of 0.06 ppm.

Lactuca sativa L. cv. Empire, under similar exposure conditions, showed severe foliar injury at 0.104 and 0.128 ppm ozone (Temple *et al.*, 1986). Total head weight was reduced 13 and 35 percent respectively compared to growth in fully charcoal-filtered air. As well, plants in the 0.104 and 0.128 ppm treatments matured 2-3 weeks later than plants in low ozone chambers.

Predicted percent root weight losses for four cultivars of *Brassica rapa* L. exposed to ambient air in which 0.04, 0.06 or 0.08 ppm ozone were added were 7, 24 and 47 percent, respectively (Heagle *et al.*, 1985). Foliar necrosis was seen on all expanded leaves of all cultivars after a 3.5 hour exposure to 0.09 or 0.11 ppm ozone.

In field studies of *Glycine max* L. Merr. cv. Davis, the radiation intercepted by the canopy during the season decreased as the ozone concentration was increased (Unsworth *et* *al.*, 1984). A lowered efficiency of dry matter production early in the season, and an altered seed and pod development, restricted yield.

In direct contrast to all the reports of linearly decreasing yield variables with increasing ozone concentrations, apparent stimulations of plant growth by low levels of ozone have been reported (Bennett *et al.*, 1974). Concentrations of ozone less than 0.1 ppm appear to have a stimulatory effect on various growth parameters of *Phaseolus vulgaris, Hordeum vulgare* and *Polygonum lapathifolium.* The authors suggest that the similarity between reported ambient levels of ozone in many locations and those which stimulate plant growth reflects the fact that plants exhibiting such stimulations are adapted to low levels of air pollution. This brings into question the use of a no-ozone control, which would put plants adapted to low levels at a disadvantage.

When plant yields are reduced, it is not necessarily a consistent loss over the whole of the plant. When photosynthesis is inhibited, the supply of assimilates is reduced, and because shoots have priority in the utilization of assimilates, root development is often one of the initial sites of inhibition in response to ozone exposure (Oshima *et al.*, 1978). As the storage capacity of the plant is reduced, transport of nutrients and water to developing fruit decreases (Jacobson, 1982). The root dry weight of *Trifolium repens* L. cv. Tillman exposed to 0.0, 0.05, 0.10 and 0.15 ppm ozone for six days, four hours daily, was reduced more than shoot dry weight as a response to reduced net photosynthesis over the ozone treatments (Blum *et al.*, 1983). Proportionally, the carbon allocated to the roots increased gradually from 35 to 52 percent with increasing ozone levels up to 0.10 ppm, and then rapidly decreased to 21 percent at 0.15 ppm. Carbon allocation to developing leaves decreased from 64 to 48 percent with increasing ozone levels up to 0.10 ppm, and then increased to 79 percent at 0.15 ppm.

The amount of labelled ^{13}C-assimilates of *Phaseolus vulgaris,* exposed continuously for four days to 0.20 ppm ozone, translocated to the non-photosynthetic organs (stem and root) decreased by 53%, while that translocated to the photosynthetic organs (leaves) was reduced by only 28% (Okano *et al*, 1984). Whereas the primary leaf, which is the main source of photosynthates for growth of roots, showed a considerable reduction in $^{13}CO_2$ fixation (62%) and an inhibition of translocation, the first trifoliate leaf, which mainly nourished the immature growing leaves, did not show such a decrease in exported labelled assimilates because a smaller reduction in $^{13}CO_2$ fixation was almost compensated by an acceleration of translocation. The authors suggest that the plants had adapted themselves to a polluted environment so that the reduction of growth efficiency caused by ozone could be minimized. In contrast, a study by Reich and Lassoie (1985) showed no effect of ozone treatment on partitioning of dry matter in *Populus deltoides* x *trichocarpa*.

Climatic, edaphic and genetic factors all influence the expression of oxidant damage in plants, as do the pathogen interactions of the plant, the time of exposure and the age of the plant (Heck *et al.*, 1965; Heck, 1968). Haas(1970) suggested that crop maturity regulates the time of symptom expression and crop vigor its severity. Plant foliage appears to be generally most sensitive to ozone at the time of full expansion (Haas, 1970; Blum and Heck, 1980). As new leaves appear on older plants, they become progressively less sensitive to ozone (Ting and Dugger, 1968).

Ozone has been shown to cause partial stomatal closure after several hours exposure (Hill and Littlefield, 1969). Relative humidity has a large effect on the expression of ozone damage, and it appears to be due to the interaction of humidity and stomatal closure (Dunning and Heck, 1977; Leone and Brennan, 1969; Otto and Daines, 1969; Rich and Turner, 1972) although McLaughlin and Taylor (1981) suggest that it is not stomatal regulation but altered internal leaf resistance to uptake that is important. In contrast, Tingey and Hogsett (1985) showed that drought stress reduces ozone injury and suggested that the effect is the result of the influence of water stress on stomatal aperture rather than through biochemical or anatomical changes. Further to this, Heggestad *et al.* (1985) found that exposure to enhanced ambient ozone levels caused *Glycine max* L. plants to lose tolerance to drought stress. In contrast, Reich *et al.* (1985) found that although drought stress and increasing ozone concentrations, up to 0.13 ppm, decreased leaf conductance in *Glycine max* L., there was no interaction between these factors.

The effect of air velocity on plant injury due to ozone was found to be significant in *Phaseolus vulgare* L. cv. Ashley (Heagle *et al.*, 1971). The authors suggest that increased ambient air velocity through dense plant stands could be increasing injury by interrupting the boundary layer, and by continually replacing pollutants absorbed by the plants. An increase in growth temperature was shown to increase sensitivity of *Phaseolus vulgaris* L. and *Nicotiana tabacum* L. cv. Bel W_3 to ozone injury (Dunning and Heck, 1977). In contrast, Miller and Davis (1981) found that *Phaseolus vulgaris* L. cv. Pinto III was more sensitive to ozone foliar injury at 15^{o}C and 32^{o}C than at 24^{o}C, an effect which was not related to stomatal conductance of the exposed leaves. Dunning and Heck (1973) demonstrated that ozone injury to *Phaseolus vulgaris* and *Nicotiana tabacum* was increased by an increased light intensity before ozone exposure. This response is species-specific (Dunning and Heck, 1977).

The translation of chamber or greenhouse studies to actual field conditions is not entirely straightforward. Lewis and Brennan (1977) compared the greenhouse and growth chamber responses of *Phaseolus vulgaris* to ozone to that in open top chambers. Both the expression and severity of ozone effects varied depending on the exposure apparatus. The severity of ozone injury was greatest in the greenhouse and least in the open top chambers. De Vos *et al.* (1983) found that 26 *Solanum tuberosum* cultivars and genotypes responded differently to ozone stress in controlled environment chambers than in the field. Genotypes that were susceptible to ozone in laboratory tests appeared to be resistant to oxidant injury in the field, but susceptible genotypes in the field were also susceptible in the laboratory. Heagle *et al.* (1983) compared the ozone response of *Glycine max* cv. Davis in soil, sand and a mixture of perlite, peat moss and vermiculite. Their results suggest that the response to ozone is fairly uniform over the range of substrate types. Soil is a major sink for ozone (Turner *et al.*, 1974) and compaction and additional soil moisture increases the resistance to ozone removal, whereas autoclaving decreases the resistance (Turner *et al.*, 1973).

2.2 OZONE EFFECTS ON COMMUNITIES

Although the effects of ozone on plants have been well researched, the subsequent effects on plant populations, communities and ecosystems have not received as much attention (Runeckles, 1986). Most of the reports dealing with ozone effects on ecosystems are descriptions of the ecological changes in an area where elevated oxidant levels occur. Many of these studies involve forest ecosystems, where the effects of pollutants on major tree species threaten to have far-reaching successional impact (Skelly, 1980; Smith, 1980; McLaughlin, 1985).

One such area is the San Bernadino Mountains of Southern California, where the decline of the ponderosa pine, *Pinus ponderosa* Laws., population has been well documented. This forest ecosystem has been subject to oxidants from the Los Angeles Metropolitan complex for thirty years (Smith, 1980). Cobb and Stark (1970) predicted that if the pollutant levels continued to rise, there would be a conversion from the then well-stocked forest dominated by ponderosa pine to poorly stocked stands of less susceptible species. They attributed the mortality of ponderosa pine to subsequent bark beetle infestation of air pollutant-stressed trees.

Miller(1973) reported that ponderosa pine mortality in the area ranged from 8-10 percent during 1968-1972. An intensive inventory of vegetation present in a 233 ha study block in the San Bernadino National Forest lead the author to conclude that the lower two-thirds of the area will probably shift to a greater proportion of white fir. The rate of community composition change was deemed dependent on the rate of ponderosa pine mortality.

McClenahen (1978) quantified community changes in a deciduous forest in the upper Ohio River Valley situated along a gradient of polluted air containing elevated concentrations of chloride, sulfur dioxide and fluoride. Species richness, evenness and diversity were reduced within the overstory, subcanopy and herb strata near point sources. The importance of sugar maple, *Acer saccharum* Marsh., was reduced in all strata with increasing pollutant dose, whereas the importance of spicebrush, *Lindera benzoin* L., increased in the understory strata with an increasing pollutant exposure.

Plant communities experience two retrogressive processes when under the influence of air pollutants (Guderian and Kueppers, 1980). The first, a change in structure and function of the community, occurs through a series of direct and indirect effects, and can lead to total destruction. The nature of the pollutant load and the condition of the community govern the severity of the response. The second process occurs parallel to this degradation and involves a spontaneous or human-initiated process during which the original adaptive resistant members of the existing community as well as new arrivals or introductions undergo secondary succession. This secondary succession which begins as soon as the original vegetation begins to change leads in time, under constant loading, to the formation of new, less complex stable structures. Typically, this process leads to a change in species composition toward a simplification of the system. The authors differentiated between the effects of high, intermediate and low pollution dosage. Essentially, the difference is the severity of the immediate reaction to the loading, and the time in which the community has to adjust to the stress.

Air pollutants may modify community composition even though only a few species are sensitive (Treshow, 1968). Often the community structure and stability depends on relatively few species. Any effect on these dominant species would have dramatic consequences.

Two studies have been carried out to quantify the impact of pollutants on entire vegetative communities. In the first, 70 common species indigenous to intermontaine grassland, oak, aspen and conifer communities were exposed to ozone with the use of portable fumigation chambers (Treshow and Stewart, 1973). Injury thresholds were determined, and species found to be most sensitive to ozone in the grassland and aspen communities investigated included some dominants which were considered key to community integrity, including aspen, *Populus tremuloides* Michx.. Concentrations greater that 0.150 ppm produced injury in most species.

The aspen community was further investigated in the second study (Harward and Treshow, 1975). Fourteen understory species were fumigated in greenhouse chambers throughout their growing seasons. Plant sensitivities varied sufficiently to cause the authors to speculate that a year or two of exposures to ozone above 0.07-0.150 ppm would cause major shifts in composition in the aspen community.

The response of any given ecosystem to ozone air pollution is as a result of the expression of direct effects to the individual component species within that ecosystem (Skelly, 1980). As an individual plant or species reacts to the pollutant, its inter-relations with other plants may be affected.

The effects of ozone on a mixture of tall fescue, *Festuca arundinaceae* Schreb. cv. Kentucky 31, and ladino clover, *Trifolium repens* L. cv. Tillman, have been studied in detail. Exposures were carried out in open top chambers in the field, and concentrations were low (0.03 -0.08 ppm). Growth was greater for both species in mixture than in monocultures (Montes *et al.*, 1982), which the authors interpreted as either protocooperation or the escape by both species of some measure of intra-specific interference. The relative yield data suggested that the ozone effects on clover were greater in mixture than in monocultures. The authors suggest that this may be due to a denser monoculture canopy, which would provide more mutual protection against ozone than the canopy associated with the mixture.

Ozone concentrations ranging from 0.02 to 0.10 ppm applied to clover-fescue mixtures in open top chambers reduced the yield of clover substantially more than the yield of fescue (Blum *et al.*, 1983). The magnitude of these ozone effects appeared to be determined to a large extent by water availability. The authors suggest that the stability of the fescue-clover forage system would be reduced by the presence of ozone air pollution. They do, however, report that clover is often lost from such forage mixtures after several years due to diseases, insects, competition, drought and poor management. It is possible that the ozone load would accelerate that process and further reduce the quality of the forage.

Similar ozone effects on clover were found in a study of the effects of low levels of ozone, 0.03-0.09 ppm, on mixtures of annual ryegrass, *Lolium multiflorum* Lam., and crimson clover, *Trifolium incarnatum* L. (Bennett and Runeckles, 1977). The yield and leaf area of clover were more affected by ozone than that of the ryegrass so that the proportion of ryegrass in the mixtures was greater at 0.09 ppm. The total dry weight, leaf area and tiller number were less depressed in species mixtures by ozone than in monocultures. Tillering of ryegrass in mixture was 26% greater in the 0.09 ppm ozone treatment than in the no-ozone control. The crowding coefficient (De Wit, 1960) of ryegrass relative to clover was less than unity in filtered air, but greater than unity in the 0.09 ppm ozone treatment. The authors suggested that this implied that 0.09 ppm ozone impaired clover's ability to compete with ryegrass in mixture.

Similar reductions in yield of clover, *Trifolium subterraneum* L., and perennial ryegrass, *Lolium perenne* L., in mixtures in the presence of sulfur dioxide were reported (Murray,1984). The author suggested that the inability of SO_2-sensitive clover plants to compete with grasses would be further aggravated by the presence of other pollutants, namely ozone. The shift of pasture dominance towards grasses would be enhanced by the loading of two pollutant stresses.

Controlled SO_2 exposure of a native grassland dominated by *Agropyron smithii* Rydb. revealed that at low concentrations and with the addition of nitrogen, plant growth was increased (Lauenroth *et al.*, 1983). As decomposition processes are slowed by SO_2 exposure, the authors suggested that on a long term basis, the decreased decomposition rates and a decreased nutrient availability to the plants may produce detrimental effects on nutrient cycling and the productivity of the system would be negatively affected.

2.3 COMPETITION

Competition is a word which has been overused and often misunderstood. In defining the competitive relations between plants it is important to clearly define the use of the word. It is essential to recognize the way in which the words competition and interference are often interchanged. Interference was defined by Harper (1961) as "all responses of an individual plant or plant species to its environment as this is modified by the presence and/or growth of another". Bleasdale (1960) defined competition between two plants as when "the growth of either or both of them is reduced or modified as compared with their growth or form in isolation". Silvertown (1982) used Harper's 1961 definition of interference for all interactions between species in mixtures which lead to a reduction in plastic growth or survival in one or both species, while he defined competition as acting in those situations where interference is expressed as a reduction in the number of plants or in the number or their surviving offspring in both or all species in a mixture. In this thesis the word competition will be used as interference was defined by Harper (1961).

Competition only occurs when there is a limited supply of a resource, such as light, water or nutrients, which is necessary to the competitors (Trenbath, 1976). In a stand of young, simultaneously-established plants, the leaf area index and root density are low enough to permit all plants to grow as they would in isolation under the same conditions. However, as growth proceeds, the demands of expanding shoot and root systems on the available resources leads to mutual interference in the acquisition of those resources. The plant's growth in the stand falls below that which it would be under an isolated, but similar situation. There is a marked plastic response of many plants to an increasing density of either plants of the same species or different species (Marshall and Jain, 1969; Pemadasa and Lovell, 1974).

The degree of interference depends on the density of planting, the availability of the resources and the plant's ability to intercept and absorb these resources in the face of the interference. This competitive ability of a plant is the character which most competition studies seek to measure.

Whereas many authors have emphasized competition for either nutrients, light or water, Bleasdale (1960) pointed out that plants can compete for a supply of growth factors either simultaneously or in rapid succession, thereby integrating the situation. He suggested using plant weights as an index of competition. Although plants may start out with inherent genetic differences in plant size, the varying growth response to an uneven distribution of growth factors amplifies the earlier differences, and final differences in plant size will be predominantly the result of competition (Trenbath, 1976).

Two forms of competition are defined; that between plants of the same species, intra-specific competition, and that between individuals of different species, inter-specific competition. Monocultures, or stands of the same species, at varying densities, are used to determine the degree of intra-specific interference. Replacement and additive series designs have been used for the determination of inter-specific competition effects.

Many competition studies are of an agricultural nature, dealing with the effect of a weed species on a crop's yield, or the yields of intercropped species. The additive series design is often used to study the former type of interaction; the crop, planted at a fixed density, is sown with a weed species planted at a range of densities. Although this design accurately simulates the real situation of a crop invaded by a weed species, it has certain limitations in its interpretation. The effects of total plant density and of weed density on the weed or crop are confounded in that, at high weed density, the total density is also high.

Dew (1972) derived a competition index for wild oats in barley, wheat and flax which was based on the additive series approach. He found that the yield of the indicator (crop) species was a simple function of the square root of the density of the accompanying (weed) species:

$$\mathbf{Y = a - b\sqrt{x}} \quad \ldots\ldots\ldots\ldots\ldots (1)$$

where **Y** is the yield of the indicator species, **x** is the density of the accompanying species and **a** and **b** are constants. The index of competition (CI) was then calculated by using the regression coefficient (**b**) and the intercept (**a**).

$$\mathbf{CI = b / a}$$

This index was used to estimate crop loss due to the presence of a weed species.

Cousens (1985a) also developed a model to describe crop yield loss as a function of weed density. The model was of the form of a rectangular hyperbola ;

$$\mathbf{Y_L = Id /(1 + Id/A),}$$

where $\mathbf{Y_L}$ is the percentage yield lost because of weed competition, **I** is the percentage yield lost per unit weed density as **d** tends towards zero, **d** is the weed density and **A** is the percentage yield loss as **d** tends towards infinity. From this equation, the author was able to generalize and predict that the rate at which yield loss increases with increasing density is proportional to the square of the yield loss per weed plant. The model was extended to include the crop density as a further variable (Cousens, 1985b):

$$\mathbf{Y = aC /(1 + bC + fD),}$$

where **Y** is yield, **C** is the crop density, **D** is the weed density and **a,b** and **f** are arbitrary parameters. The author cautioned against interpreting the parameters in terms of an individual plant's occupation of space.

The replacement series design in which the total density is kept constant and the proportions of the two species are varied (de Wit, 1960) has been widely used in the study of intercropped mixtures. However, it does not accurately imitate the crop-weed situation in which the proportion of the weed rarely surpasses that of the crop. The design allows an interpretation of the relative yield total (RYT, the sum of the relative yields of each species), which can help identify an overyielding or underyielding situation in multicropping situations.

Connolly (1986) has pointed out some fundamental difficulties in the interpretation of the replacement series method. Although mixtures are two-dimensional, the replacement series consists of points on a one-dimensional line. The arbitrary selection of a particular replacement line, including both the pure stand densities and mixture proportions, carries the risk of confounding effects of the two densities. As well, the replacement method is particularly prone to problems when species of different sizes are mixed.

Thomas (1970) derived a mathematical model to complement the competition model of de Wit (1960) which tests the hypothesis that two species are crowding for the same "space" (*sensu* De Wit, 1960). The model can be represented by the equation

$$\mathbf{y_1} = \mathbf{u_1 k_{12} z_1 / (k_{12} z_1 + z_2)} \quad \ldots\ldots \quad (2)$$

where $\mathbf{y_1}$ is the yield, $\mathbf{u_1}$ is a constant, and $\mathbf{z_1}$ and $\mathbf{z_2}$ are the densities of species one and two respectively. The parameter $\mathbf{k_{12}}$ is called the relative crowding coefficient of species one with respect to species two. Thomas's four-parameter model tests whether the standard deviations of the two populations are equal. If this test is not significant, a three-parameter model in which the relative crowding coefficients of the two species on each other are reciprocally related can be tested. If the three-parameter model proves to be significant, the species are interpreted to be crowding for "different space", i.e. are not competing for the same resources. A value of the product of $\mathbf{k_{12}}$ and $\mathbf{k_{21}}$ (derived from the 4-parameter model) greater than one indicates the species are operating for mutual benefit, whereas if the product is less than one, an inhibitory mechanism is in operation.

Based on the spacing formulae first described by de Wit (1960), Khan *et al.*(1975) proposed models of interaction between two genotypes in mixture. Equations were formulated describing crowding for the same space

$$\mathbf{O_1 = k_{12}\, z_1\, M_1 / (k_{12} - 1) z_1 + 1}$$

and crowding for partly the same space

$$O_1 = k_{1(2e)} z_1 M_1 / (k_{1(2e)} - 1) z_1 + 1$$

where O_1 is the yield of the genotype in mixture, z_1 is the relative input frequency, M_1 is the yield per unit area of each genotype and $k_{1(2e)}$ represents the relative crowding coefficient where a genotype crowds for space with the other genotype and also crowds for "empty space"..

The interpretation of the classic replacement series was questioned by Jolliffe *et al.* (1984) for its use of expected yields for comparative purposes. The authors pointed out that the actual monoculture yields would be better used as a comparison in order to illustrate the effects of inter-specific competition. Two indices were proposed as measures of plant interference in monoculture and mixtures, the relative monoculture response:

$$R_m = Y_p - Y_m / Y_p$$

where Y_p is the projected yield of a species and Y_m is the actual monoculture yield, and the relative mixture response

$$R_x = Y_m - Y_x / Y_m$$

where Y_x is the actual mixture yield. The predicted yield is that which would occur were there no interference, that is the projection from the initial slope of the monoculture yield density curve.

The predictive ability of a competition study is of great value in an agricultural situation. If a model were able to predict the interaction of two species accurately, the yield of a crop might, theoretically, be increased by maintaining the density of a second species at a level where the yield of the crop was highest, or in multicropping, by maintaining the component densities in such a proportion that the total yield was at a maximum. To this end, many authors have introduced models they deem as best able to predict the competitive interactions of plants of the same or different species.

The relationship between yield and density can be defined mathematically in two ways; as an asymptotic one where yield rises to a maximum and is then relatively constant at high density or as a parabolic one where yield rises to a maximum and then declines at high densities. As Wiley and Heath (1969) suggest, these two relationships are merely different degrees of expression of a single relationship.

Bleasdale and Nelder (1960) introduced a power function equation to describe the relationship between yield and density in crop plants:

$$\mathbf{w}^{-\Theta} = \mathbf{A}\mathbf{p}^{\phi} + \mathbf{B}$$

where **w** is the yield per plant, **p** is the number of plants per unit area and **A**, **B**, Θ and ϕ are constants. The authors suggested that the use of Θ, a positive quantity usually less than unity, gave a much better fit to data from spacing experiments. When $\Theta = 1$, the equation describes the special case where total yield per unit area is reciprocally related to density (Bleasdale, 1966a). This is the form of the yield density relationship previously described by Shinozaki and Kira (1956). Bleasdale (1966b) reported that in practice, it is the ratio of Θ to ϕ which is important, and suggested using $\phi = 1$ in fitting the equation.

Watkinson (1980) reparamaterized Bleasdale's equation to describe the relationship between individual plant weight and surviving plant density:

$$\mathbf{w} = \mathbf{w}_{\mathbf{m}} (1 + \mathbf{aN})^{-\mathbf{b}},$$

where $\mathbf{w}_{\mathbf{m}}$ is the dry matter production of the isolated plant, **w** is the mean weight per plant, **N** is plant density and **a** and **b** are constants. He interpreted **a** as the area required to achieve a yield of $\mathbf{w}_{\mathbf{m}}$ and **b** as the effectiveness with which resources are taken up from that area. Another equation describing mortality during self-thinning was used in conjunction with the first equation in order to assess the relation between total plant yield and the sowing density. Consideration of allometry then enabled the author to create a model of the population dynamics of annual plants with effectively discrete generations. The original model was then extended to a two species interaction in order to determine the effect of a second species on the reproductive performance of the other (Watkinson, 1981). Further manipulation of the model provided Watkinson (1982) with a method to determine the magnitude of the effect of the time of thinning during the vegetative phase of the life cycle on population density and compare it with the effect during the seed phase of the life cycle. Using the constants **a** and **b** from the model, Watkinson (1984) devised an equation which related the effects and intensity of crowding to the addition of nutrients.

Although the models of Watkinson are very perceptive in that they consider plant survival and seed yield, and hence, the evolutionary consequences of competition, they are very complicated in their interpretation due to the degree of manipulation of the original data and the number of constants which are produced.

Silander and Pacala (1985) proposed a much simpler model to predict the effect the inter-individual interference on fecundity of individuals in populations . The equation

$$S = M (1 + CW)$$

includes a variable **W** defined as the index of crowding, where **S** is the number of seeds produced per plant, **M** is the maximum number of seeds produced by a plant with no neighbours and **C** is a decay constant. Modeling the performance of *Arabidopsis thaliana*, they found that fecundity predictors were better based on adult plants rather than seedlings.

Vandermeer (1984) proposed a yield density model for monocultures based upon a similar approach to that developed by Bleasdale and Nelder (1960) and Watkinson (1980) and claimed a simpler biological interpretation of the parameters:

$$w = W_m / (1 + qD^b),$$

where **D** is the density, W_m is the biomass of a plant in isolation, **w** the average biomass of a plant in the population, **q** is a measure of competition including its intensity and operational area and **b** is a measure of the rate at which competition decays as a function of distance between plants. The index W_mD could be used to describe the carrying capacity of the population.

Firbank and Watkinson (1985) presented a model to describe competiton in two-species mixtures, based on the model of Watkinson (1980):

$$w_A = w_{mA} (1 + a_A (N_A + \alpha N_B))^{-b_A}$$

where w_A is the mean yield per plant of species A, w_{mA} is the mean yield of isolated plants of species A, a_A is a parameter representing the area required by a plant to achieve a yield of w_m, N_A and N_B are the density of species A and B, respectively, b_A describes the efficiency of resource utilization by the population and α is the competition coefficient. The authors further manipulated this equation to obtain other equations which could be used to estimate survival and the yield per unit area for each species in a mixture.

Wright (1981) extended the simple reciprocal relationship used in the analysis of plant yield-density relationships in monoculture to binary mixture situations

$$w_a^{-1} = A_a + B_{aa} p_a + B_{ab} p_b$$

where w_a is the plant weight of component **a** in mixture with component **b**, p_a and p_b are the densities of species **a** and **b** respectively. The author defined B_{ab} as the coefficient of the effect of increasing density of plants of type **b** on the weights of plants of type **a**. The reciprocal of B_{aa} is the yield that the monoculture of **a** at high densities would tend toward. The ratio of B_{ab}/B_{aa} is representative of the between species to within species component sources.

Spitters (1983a) produced an almost identical model using a multiple linear regression (MLR) of yield on density:

$$w^{-1} = b_{1,0} + b_{1,1}N_1 + b_{1,2}N_2, \ldots \quad (3)$$

where **w** is the average weight per plant, N_1 and N_2 are the densities of species one and two, respectively, in the mixture and $b_{1,0}$, $b_{1,1}$ and $b_{1,2}$ are constants. He more clearly interpreted all the constants in the model; $b_{1,1}$ measures the effect of intra-specific competition and $b_{1,2}$ measures the effect of inter-specific competition on the yield of species one. The constant $b_{1,0}$ represents the virtual biomass of an isolated plant . Like Wright (1981), Spitters manipulated the coefficients to produce an index of competition:

$$b_{1,1} / b_{1,2} .$$

He interpreted this index as follows: the addition of one plant of species one has an effect on w^{-1} equal to adding $b_{1,1} / b_{1,2}$ plants of species two. He derived an index of niche differentiation from the coefficients as well:

$$(b_{1,1} / b_{1,2}) \times (b_{2,2} / b_{2,1}).$$

When this index exceeds unity, there is niche differentiation. He further extended the model to study the effects of competition on marketable yield (Spitters, 1983b). The competitive effects and the advantage of mixed cropping could be estimated from the market yield data.

Although the Spitters (1983a) multiple linear regression (MLR) approach to analyzing the effects of density on yield is simple, the coefficients representing intra- and inter-specific competition are not entirely independent of one another. A more intuitively correct way of examining the data has been proposed (Jolliffe, personal communication) which has its origins in the work of Jolliffe *et al.* (1984). The monoculture densities and yields are analyzed in a simple regression according to the equation

$$w_1^{-\Theta} = B_{1,0} + B_{1,1} N_1, \ldots\ldots\ldots (4)$$

where w_1 is the yield of species one at density N_1, Θ is a constant and $B_{1,0}$ and $B_{1,1}$ are coefficients which represent the virtual biomass of an isolated plant and the effect of the addition of a plant of species one on the yield of species one (intra-specific competition), respectively. The variation from the monoculture yields caused by the addition of a second species is then regressed against the density of the second species, with the regression forced through the origin, i.e.

$$w_d^{-\Theta} = 0 + B_{1,2} N_2, \ldots\ldots\ldots (5)$$

where w_d is the deviation from the monoculture yield, N_2 is the density of the second species and $B_{1,2}$ is a coefficient representing the effect on the yield of species one caused by the addition of one plant of species two. The coefficients from these sequential simple regressions (SSR) can be combined to give an expression incorporating both the intra- and inter-specific competition:

$$w_1^{-\Theta} = B_{1,0} + B_{1,1}N_1 + B_{1,2}N_2.$$

In this way, the intra- and inter-specific competition effects are effectively compartmentalized. Competitive indices can be computed as in the Spitters (1983a) multiple linear regression analysis, i.e. $B_{1,1}/B_{1,2}$, and an index of niche differentiation can again be calculated, i.e. $(B_{1,1}/B_{1,2}) \times (B_{2,2}/B_{2,1})$. The interpretation of these indices follows Spitters (1983a) original interpretation.

Mithen *et al.* (1984) did a simple, but elegant, study of the growth and mortality of individual plants as a function of the area available to each plant. The area around even aged *Lapsana communis* L. plants, as defined by Thiessen polygons, was a good predictor of plant weight. Plants in small polygons were much more likely to die than those in larger areas. The seedling stage appeared to be the most susceptible to available area effects, implying that some of the reduction in growth of survivors due to interference at an earlier age has an effect which persists after those neighbours have died. There was a hierarchy in plant sizes, i.e. many small plants and a few large ones, which developed before self-thinning began and was maintained as thinning occurred. The authors suggest that this hierarchy is continually generated by growth and interference and reduced by mortality of the smallest individuals.

Size hierarchies exist in most plant populations, where much of the population's biomass is contained by a few large individuals (Weiner, 1984). Size hierarchies have great ecological and evolutionary significance in that the smallest plants are more often those which suffer density-dependent mortality and are often less fit than larger plants. There are many causes of size inequality caused by differential growth rates, including age differences, genetic variation, heterogeneity of resources, environmental factors and herbivore activity. Many authors have suggested that competition may cause or exaggerate size differences (White and Harper, 1970; Weiner, 1985). A pattern of dominance and suppression is envisaged, where differences in size are exacerbated as large plants monopolize resources at the expense of the growth of smaller plants. Weiner (1985) demonstrated that size inequality always increased with increasing density in a study of the effects of intra- and inter-specific interference in populations of *Trifolium incarnatum* and *Lolium multiflorum*. As well, size inequality was increased by the addition of nutrients when interference was occurring. The dominant species, *L. multiflorium*, showed less size inequality in mixtures than in monocultures, while *T. incarnatum*, the suppressed species, displayed more inequality in mixture than in monoculture. These results agreed with the author's interpretation of the dominance and suppression model of size hierarchy; that is, a competitive dominant species would have a more equal size distribution in mixture than in monoculture, while a suppressed species would have a more unequal distribution in mixture than in monoculture.

In contrast, Turner and Rabinowitz (1983) attributed shifts in size distribution in even-aged populations of *Festuca paradoxa* to variance in the exponential growth rates. They found that competition (intra-specific) retarded the appearance of skewing. Based on many studies, the authors point out that where skewness increased with density, the plants were dicots and conifers, whereas in cases where skewness did not increase with increasing density, the populations were grasses. They suggest that plant architecture influences how plants compete and that the vertical, erect form of grass seedlings renders light competition less crucial than belowground resource depletion, whereas the simplest view of dominance and suppression is that light competition is critical.

Huston (1986) suggested that increasing plant densities in a randomly spaced population, as compared to a regular distribution of adult plants which occurs more frequently in natural plant populations (Harper, 1977), may produce symmetric competition. This would result in deviations from the dominance and suppression theory of size inequality, where assymetric, or one-sided competition occurs.

A study of the competitiveness and growth of *Amaranthus retroflexus* L., *Chenopodium album* L., *Echinochloa crus-galli* L. and *Solanum nodiflorum* Jacq. under field conditions in a replacement series design showed that *E. crus-galli* was always the superior competitor when grown in mixture with the other three species (Roush and Radosevich, 1985). *E. crus-galli* maintained a low canopy area index but had a greater root volume relative to shoot growth early in the season. McGraw (1985) reported that root competition often develops before shoot competition in depressing the growth of less competitive plants. Roush and Radoseveich (1985) suggest that under similar environmental conditions, *E. crus-galli* would displace the other species from mixtures over time.

In a study of competition between *E. crus-galli* and *A. retroflexus*, Siriwardana and Zimdahl (1984) reported that *E. crus-galli* was more competitive than *A. retroflexus* at all densities, and experienced more intra-specific competition than inter-specific. In replacement series, as the proportion of *E. crus-galli* was reduced, the proportion of fresh weight of *E. crus-galli* increased relative to *A. retroflexus*, and the authors suggested this was due to reduced intra-specific competition.

Competition studies on *E. crus-galli* (BYG), *A. retroflexus* (RPW) and *Setaria viridis* (GFT) in the field showed that BYG was a strong competitor against both RPW and GFT, and RPW strongly competed against GFT (Minjas and Runeckles, 1984). RPW responded more to its own increasing density than to the presence of GFT (Minjas, 1983). The relative yield totals of RPW and BYG were consistently greater than one, indicating that the species were not exclusively competing for the same space. Similar non-competitive interactions between BYG and GFT existed in one season although an increasing proportion of BYG depressed the crowding coefficients of GFT. In the following season, the mixture yield of RPW-GFT in replacement series was consistently greater than the monoculture yield of RPW, with RPW contributing proportionately more. There was a substantial non-competitive component to their interaction, and the author suggested that the tap root system of RPW exploited a different soil layer than the fibrous root system of GFT which occupies the top soil horizons.

3. MATERIALS AND METHODS

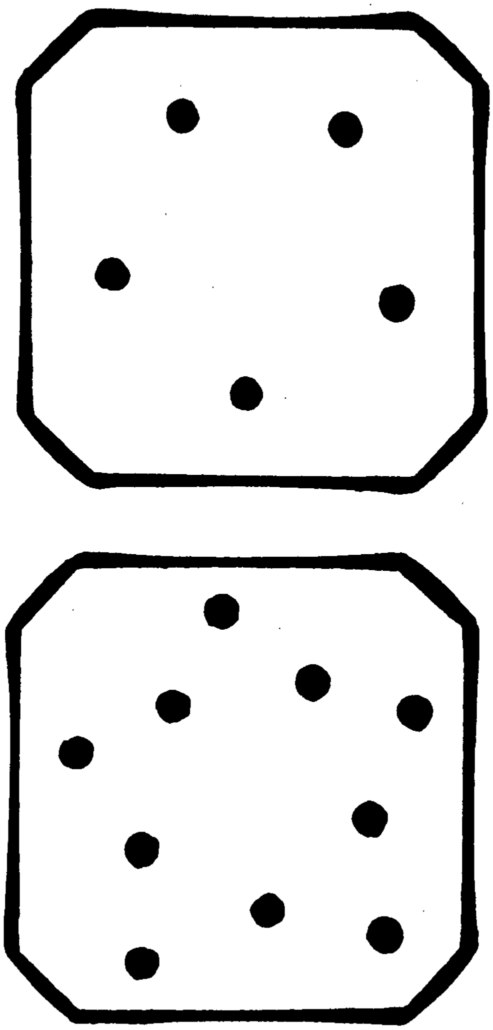
3.1 Plant Materials

The three plant species used in this study were *Echinochloa crus-galli* (L.) Beauv., barnyardgrass (BYG), *Setaria viridis* (L.) Beauv., green foxtail (GFT) and *Amaranthus retroflexus* L., redroot pigweed (RPW). The seeds used were collected in 1982 from plants used in competition studies in the field at the University of British Columbia (Minjas, 1982). Original seeds of BYG and RPW were collected from agricultural fields at Agassiz Research Station, Agriculture Canada, Agassiz, B.C. in the summer of 1979. Those of GFT were obtained from grain screenings.

Seeds were germinated in the greenhouse in flats containing finely sieved (5 mm) soil and an appropriate layer of Redi-Earth professional horticultural growing medium. Flats of RPW and GFT were covered with plastic to increase soil temperatures and promote germination. All flats were drenched with No-Damp (2.5 % oxine benzoate) to prevent damping off. Sowing was staggered to obtain seedlings of approximately the same size for pricking out, immediately after the development of RPW's first true leaves. This was approximately 10-11 days after sowing for RPW, 9-10 days after sowing for GFT and 7-8 days after sowing for BYG.

The seedlings were pricked out into 5 inch round pots in experiment 3 and into 4 inch square pots in all other experiments (see Table 1). All pots contained a homogeneous mixture of finely sieved soil and Osmocote slow release fertilizer (14-14-14)). Mithen *et al.* (1984) stressed the importance of "available" area in competitive studies, so templates were designed to create equidistant spacing between plants and equal numbers of neighbours (Figure 1). These templates were used to to determine the placement of the seedlings in the lower density treatments. It was impossible to use templates for the higher density treatments due to crowding. When pricking out pots containing mixtures, the placement of individuals of each species was determined randomly. All seedlings were

FIGURE 1 : Templates used in pricking out seedlings into low density treatments



watered in with Green Valley Soluble Plant Starter Mix (10-52-17) to encourage root growth. Several days after pricking out was completed, the pots were checked and dead seedlings were replaced. Approximately 11 days after pricking out, when plants were established and new growth had occurred, the pots were moved to growth chambers for ozone treatment.

3.2 OZONE TREATMENTS

The exposure chambers used in these experiments were modified growth cabinets (CONVIRON, Controlled Environment Ltd. Model EF7). Charcoal-filtered air was supplied at a flow rate of 2.2 $\pm$ 0.3 m/sec at the entrance to the cabinets. A 14-hour photoperiod (6 AM - 8 PM) was used in all chambers. Day and night temperatures were 24^{o}C and 16^{o}C, respectively. Photosynthetically active radiation at plant level was 90 uEm^{-2}s^{-1}. Relative humidity was not controlled and varied between 55% and 80%. Plants were watered to capacity each day at the end of the exposure period.

Three treatments were applied. One chamber received only charcoal-filtered air, and acted as a no-ozone control. The other two ozone treatments were 75 ppb for 7 hr/daily and 150 ppb for 3.5 hr/daily, which represent the same ambient dose. The 75 ppb/7 hr treatment and the 150 ppb/3.5 hr treatments began 3 and 6.5 hours after the beginning of the photoperiod, respectively. The shorter exposure treatment was applied in the afternoon in order to mimic anthropogenically derived diel peaks of ozone (Fowler and Cape, 1982). Ozone was generated by passing a stream of charcoal-filtered air over a bank of germicidal lamps (Sylvania Germicidal Lamp, Type B) contained in an air-tight plexiglass chamber. Previous use of this system indicated that no NO_x was generated.

Ozone was monitored continuously (Dasibi Environmental Corp. Model 1003-AH). Monitors were calibrated regularly at the Environmental Laboratory, B.C Ministry of the Environment. Inputs to the chambers receiving ozone were sampled every 40 minutes, during which time a feed-back control system maintained the 150 ppb treatment. The 75 ppb treatment was kept constant by manually manipulating the voltage to the germicidal bulbs.

During the 3-week exposure period the treatments were rotated through the chambers at least once to eliminate chamber effects. The chamber positions of the pots were also randomly changed at that time to avoid position effects.

3.3 COMPETITION TREATMENTS

Seven experiments were carried out over a two year period following the completion of two preliminary experiments which are not reported here (Table 1). Each consisted of a binary combination of the three species, BYG, GFT and RPW. The replication of each binary mixture was treated as a block.

Within each binary experiment there were both monocultures and mixtures at different total densities. The experiments were designed to incorporate both additive and replacement series for each series (Table 2). Experiment 3 did not include the 20 plants/pot monocultures due to lack of space. Neither experiment 3 nor 4 included replacement series at total density 25 due to lack of space in the chambers and poor germination, respectively.

The number of plants per pot used represent actual densities similar to those found in infested fields at the Agricultural Research Station, Agassiz, B.C. and those used in previous competition experiments with these same species (Minjas,1982).

3.4 HARVESTS

At the end of the 3-week exposure period, all plants were harvested. The root mass was cleaned and the plants cut just above the uppermost root in RPW and within 5 mm of the root for BYG and GFT. The inflorescences were separated from each plant and the number of tillers (for BYG and GFT) and leaves were counted. Each individual plant, its reproductive parts and the root mass/pot was dried in paper bags in a forced air drier at

TABLE 1: LISTING OF INDIVIDUAL EXPERIMENTS

EXPT. #	SPECIES MIXTURE	DATE OF FIRST SOWING	DATE OF HARVEST
3	BYG/GFT	05/11/84	10/12/84
4	BYG/RPW	16/04/85	28/05/85
5	GFT/RPW	16/05/85	27/06/85
6	BYG/GFT	09/06/85	18/07/85
7	BYG/GFT BYG/RPW GFT/RPW	15/07/85	26/08/85
8	BYG/RPW	13/08/85	24/09/85
9	GFT/RPW	20/02/86	08/04/86

TABLE 2: DENSITY COMBINATIONS USED IN EXPERIMENTS

density (# plants/4" square pot) of components.

SPECIES A B SPECIES	0	5	10	15	20
0		5	10	15	20
5	5	5 5	10 5	15 5	20 5
10	10	5 10	10 10	15 10	
15	15	5 15	10 15		
20	20	5 20			

Additive series run horizontally and vertically.

Replacement series run diagonally from left to right.

80^0 C for a minimum of 6 days. The plant materials were cooled and weighed using a Mettler AE100 balance.

3.5 DATA ANALYSIS

3.5.1 Analysis of Variance

Two sets of ANOVAs were run on the data set. One set was carried out on the individual per plant variables for each species to examine the treatment effects on a per plant basis. Another set of ANOVAs was run on the variables on a total per pot basis for each species, to enable an examination of the population dynamics under each treatment regime. The experiments were treated as blocks, and the ANOVAs were carried out on each species in three different analyses. The monocultures, the total densities less than or equal to 20 plants/pot, and the total densities equal to 25 plants/pot were analyzed separately because of the design of the experiments.

3.5.2 Regression Analyses

Based on the results of the ANOVAs, comparisons of the experimental means and standard deviations and the fact that in experiment 3, plants were grown in a different size pot, the data from that experiment were not included in the regression analysis.

The total aboveground yields (vegetative + reproductive) of BYG, RPW and GFT in monoculture and in mixture were analyzed by the multiple linear regression analysis (MLR) using Equation 3 (page 20). Using the partial regression coefficients generated from the equations, competitive indices for each species and a measure of niche differentiation for each species mixture were calculated.

The analyses were repeated using a regression in which an interaction term was incorporated:

$$1/w_1 = b_{1,0} + b_{1,1}N_1 + b_{1,2}N_2 + b_{12}N_1N_2 \quad \ldots(6)$$

Sequential simple regression (SSR) analyses were also performed. Computation of optimal values of Θ consistently produced numbers less than -1, so the straight reciprocal relationship, where $\Theta = 1$ was used in all regression analyses. The reciprocal of the total aboveground yield of BYG, GFT and RPW in monoculture was regressed against the density of the species according to Equation 4 (page 21). The reciprocal of the deviation of the mixture yields from the monoculture yields was then regressed against the density of the second species in the mixture and forced through the origin (Equation 5, page 21), to yield a coefficient of inter-specific competition, $B_{1,2}$. Competition indices and a measure of niche differentiation were calculated from the regression coefficients, as for the multiple linear regression approach.

The yield of the indicator species at different constant densities was analyzed by the square root regression method (Equation 1, page 15) of Dew (1972). The monoculture data were included in the analysis in association with a negligibly small dummy value (1×10^{-2}) of the associated species density. The dummy value is needed because the regression involves the square root of the density of the associated species. Predicted values were used to obtain curves depicting the results of the effects of increasing densities of one species on the yields of the second species at constant density.

Replacement series and additive series curves were generated using predicted values from the sequential simple regressions.

3.5.3 Replacement Series

The analysis of Thomas (1975) was used to fit parameters to the two-species competition model proposed by de Wit (1960) (Equation 2, page 16), and to determine whether different binary mixtures were competing for the same space. The 4 parameter model tests whether the standard deviations of the two populations are equal. If this hypothesis is rejected, then the 3 parameter model can be tested. If the 3-parameter model proved to be significant, the species were interpreted to be competing for different space.

3.5.4 Size Frequency Distributions

Size frequency distributions were calculated by pooling the data from each pot of the same density treatment and ozone treatment and calculating the mean number of individuals in each size class. The data from experiment 3 were not included for the reasons given previously. The size classes chosen were multiples of 5% of the total plant weight per pot in order to allow a more discriminating analysis of the size frequencies.

4. RESULTS

4.1 VISUAL OBSERVATIONS

Over all the experiments, BYG grew the tallest, tillered very rarely, and produced the sturdiest aboveground and belowground tissue. RPW monopolized the canopy when grown in mixture with GFT. When grown in combination with BYG, RPW grew taller and lost many of its lower leaves. The elongated RPW plants produced in mixture with BYG were very unsturdy, lacking the supportive structure necessary to remain upright. RPW plants had very fine, fragile root systems.

GFT tillered readily, producing many more leaves than BYG, but was, in all experiments, a relatively short plant that failed to maintain its share of the canopy. GFT plants flowered in all experiments.

The mean yields for each species over experiments 3 - 9 under each density and ozone treatment are in Appendix A.

4.2 ANALYSES OF VARIANCE

Each experiment was treated as a block in the analysis of variance. This precluded some of the density treatments from being analyzed together. The density treatments equal to or less than 20 plants per pot were analyzed separately from the treatments of total density equal to 25 plants per pot. These density treatments will be referred to as low and high density, respectively, for convenience.

4.2.1 BYG individual

Analysis of variance done on the individual per plant data showed a significant effect of ozone on vegetative aboveground dry weight of BYG in monocultures (Table 3). This effect had a significant deviation from linearity, which represents the fact that the plants in the 75 ppb/7 hr treatment had a higher mean weight than either the 0 or 150 ppb/3.5 hr

TABLE 3: Significant treatment effects (ANOVA) for barnyardgrass yield variables (per plant) in monoculture and mixtures.

		BYG MONO	BYG/GFT $\leq$ 20	BYG/GFT = 25	BYG/RPW $\leq$ 20	BYG/RPW = 25
VEGETATIVE DRY WEIGHT	BLOCK	****	****	-	****	-
	OZONE	**	-	-	- (.1139)	-
	LIN	-	-	-	*	-
	DEV	**	-	-	-	-
	ERR(A)	-	-	-	-	-
	COMP	**	-	*	-	-
	OZONE*COMP	-	-	-	-	-
	ERR(B)	****	**	****	****	***
REPRODUCTIVE DRY WEIGHT	BLOCK	****	N/A	-	****	***
	OZONE	-		-	-	**
	LIN	-		-	-	-
	DEV	-		-	-	**
	ERR(A)	***		**	***	-
	COMP	-		-	-	-
	OZONE*COMP	-		-	-	-
	ERR(B)	****		**	****	***
NUMBER OF LEAVES	BLOCK	****	N/A	****	****	****
	OZONE	-		-	-	-
	LIN	-		-	-	-
	DEV	-		-	-	-
	ERR(A)	****		-	****	****
	COMP	****		***	*	-
	OZONE*COMP	-		-	-	-
	ERR(B)	****		-	****	****
NUMBER OF TILLERS	BLOCK	****	N/A	-	****	-
	OZONE	-		-	-	-
	LIN	-		-	-	-
	DEV	-		-	-	-
	ERR(A)	****		-	****	-
	COMP	**		-	-	-
	OZONE*COMP	-		-	-	-
	ERR(B)	****		**	****	-
	TOTAL DF	1351	903	838	900	840

- = ns
* p = .1
** p = .05
*** p = .01
**** p = .001

treatments. The only other significant effect of ozone on individual plant variables was on reproductive dry weight/individual of BYG in combination with RPW at higher densities. This also had a significant deviation from linearity.

There was a significant difference between density treatments in individual vegetative dry weight of BYG in monoculture and in combination with GFT at total density=25. There were no differences in reproductive dry weight of BYG in any species combination or in monoculture, suggesting that under the conditions used the reproduction of individuals was not governed by density or the presence of other species. There was, however, a significant difference in the number of leaves produced by individuals in the different densities of the monoculture, and when BYG was in combination with GFT at high density and with RPW at the lower densities. The only significant difference in the number of tillers per individual between density treatments was in the monoculture.

4.2.2 BYG totals/pot

The significant non-linear ozone effect on BYG individual plant vegetative dry weight in monoculture also showed up as a population effect when the total vegetative dry weight/pot was analyzed (Table 4). However, in mixture with RPW at low density, there was a significant linear ozone effect on vegetative dry weight, which did not show up in the analysis of individuals. As in the per plant analysis, there was a significant ozone effect on BYG reproductive dry weight per pot in mixture with RPW at high densities. This ozone effect at the total/pot level also significantly deviated from linearity, with 75 ppb producing more reproductive tissue than the 0 or 150 ppb treatments.

Significant differences between density treatments in total/pot vegetative weight, number of leaves and number of tillers showed up in all monocultures and species mixtures. No significant effect of density treatment on BYG reproductive dry weight was seen.

TABLE 4: Significant treatment effects (ANOVA) for barnyardgrass yield variables (total per pot) in monoculture and mixture

		BYG MONO	BYG/RPW ≤ = 20	BYG/RPW = 25	BYG/GFT ≤ 20	BYG/GFT = 25
VEGETATIVE DRY WEIGHT	BLOCK	****	****	-	****	-
	OZONE	**	*	-	-	-
	LIN	*	**	-	-	-
	DEV	**	-	-	-	-
	ERR(A)	-	-	-	-	-
	COMP	****	***	****	***	**
	OZONE*COMP	-	-	-	-	-
	ERR(B)	***	****	**	**	**
REPRODUCTIVE DRY WEIGHT	BLOCK	****	**	****	N/A	-
	OZONE	-	-	**		-
	LIN	-	-	-		-
	DEV	-	-	**		-
	ERR(A)	****	**	-		-
	COMP	-	-	- (.11)		-
	OZONE*COMP	-	-	-		-
	ERR(B)	****	**	***		
NUMBER OF LEAVES	BLOCK	****	****	****	N/A	***
	OZONE	-(.17)	-	-		-
	LIN	*	-	-		-
	DEV	-	-	-		-
	ERR(A)	-	****	**		-
	COMP	****	****	****		****
	OZONE*COMP	-	-	-		-
	ERR(B)	-	**	****		-
NUMBER OF TILLERS	BLOCK	****	****	-	N/A	-
	OZONE	-	-	-		-
	LIN	-	-	-		-
	DEV	-	-	-		-
	ERR(A)	**	****	-		-
	COMP	****	****	****		****
	OZONE*COMP	-	-	-		-
	ERR(B)	-	**	-		*

-		= ns
*	p	= .1
**	p	= .05
***	p	= .01
****	p	= .001

4.2.3 GFT individual

There were no significant ozone effects on any of the individual per plant variables which were measured (Table 5). There were significant differences in vegetative dry weight between the density treatments of GFT in mixture with RPW at both high and low densities. There were no significant effects of density on reproductive dry weight/plant. GFT density treatments in monoculture and in mixture with RPW at low density differed significantly in the number of leaves/plant and the number of tillers/plant.

4.2.4 GFT pot totals

In contrast to the individual plant analysis, the totals/pot revealed one significant ozone effect: GFT in mixture with RPW at low densities showed a significant linear ozone effect on vegetative dry weight (Table 6). There were significant density effects on vegetative dry weight, number of leaves and number of tillers in the monoculture and in all the species combinations analyzed. No density effects on reproductive dry weight were evident.

4.2.5 RPW individual

Analysis of variance on RPW in monoculture showed a significant inversely linear effect of ozone on vegetative dry weight per plant (Table 7). A similar non-significant trend existed in combination with BYG at high density, attributable to the significant linear effect of ozone on the number of leaves per plant. RPW did not flower in combination with BYG or GFT at high density nor with GFT at low density. There was also a significant linear effect of ozone on the number of leaves per plant when RPW was in mixture with BYG at high density. There were significant differences between density treatments for vegetative dry weight/plant in monoculture and in mixture with BYG and GFT at low densities. As well, RPW in monoculture and in mixture with GFT at low and

TABLE 5: Significant treatment effects (ANOVA) for green foxtail yield variables (per plant) in monoculture and mixtures.

		GFT MONO	GFT/BYG ≤ 20	GFT/BYG = 25	GFT/RPW ≤ 20	GFT/RPW = 25
VEGETATIVE DRY WEIGHT	BLOCK	****	****	****	****	****
	OZONE	-	-	-	-	-
	LIN	-	-	-	-	-
	DEV	-	-	-	-	-
	ERR(A)	**	****	****	-	**
	COMP	-	-	-	****	**
	OZONE*COMP	-	-	-	-	-
	ERR(B)	****	****	****	-	****
REPRODUCTIVE DRY WEIGHT	BLOCK	****	****	-	****	****
	OZONE	-	-	-	-	-
	LIN	-	-	-	-	-
	DEV	-	-	-	-	-
	ERR(A)	**	****	-	*	***
	COMP	-	-	-	-	-
	OZONE*COMP	-	-	-	-	-
	ERR(B)	****	-	-	-	****
NUMBER OF LEAVES	BLOCK	****	N/A	****	****	****
	OZONE	-		-	-	-
	LIN	-		-	-	-
	DEV	-		-	-	-
	ERR(A)	****		**	****	****
	COMP	***		-	****	-
	OZONE*COMP	-		-	-	-
	ERR(B)	****		****	***	****
NUMBER OF TILLERS	BLOCK	****	N/A	****	****	****
	OZONE	-		-	-	-
	LIN	-		-	-	-
	DEV	-		-	-	-
	ERR(A)	****		-	****	****
	COMP	***		-	***	-
	OZONE*COMP	-		-	-	-
	ERR(B)	****		****	-	****
	TOTAL DF	1348	886	877	893	1347

-		= ns
*	p	= .1
**	p	= .05
***	p	= .01
****	p	= .001

TABLE 6: Significant treatment effects (ANOVA) for green foxtail yield variables (total per pot) in monoculture and mixtures.

		GFT MONO	GFT/RPW $\leq$ 20	GFT/RPW = 25	GFT/BYG $\leq$ 20	GFT/BYG = 25
VEGETATIVE DRY WEIGHT	BLOCK	**	****	****	****	****
	OZONE	-	*	-	-	-
	LIN	-	*	-	-	-
	DEV	-	-	-	-	-
	ERR(A)	-	-	*	**	-
	COMP	****	****	****	****	***
	OZONE*COMP	-	-	-	-	-
	ERR(B)	**	-	****	****	**
REPRODUCTIVE DRY WEIGHT	BLOCK	****	****	****	****	-
	OZONE	-	-	-	-	-
	LIN	-	-	-	-	-
	DEV	-	-	-	-	-
	ERR(A)	-	-	-	****	-
	COMP	-	-	-	-	-
	OZONE*COMP	-	N/A	-	-	-
	ERR(B)	-	-	****	**	-
NUMBER OF LEAVES	BLOCK	****	****	****	N/A	
	OZONE	-	-	-		-
	LIN	-	-	-		-
	DEV	-	-	-		-
	ERR(A)	****	***	***		-
	COMP	****	****	****		****
	OZONE*COMP	-	-	-		-
	ERR(B)	***	***	***		-
NUMBER OF TILLERS	BLOCK	****	****	****	N/A	****
	OZONE	-	-	-		-
	LIN	-	-	-		-
	DEV	-	-	-		-
	ERRA(A)	****	***	****		-
	COMP	****	****	****		****
	OZONE*COMP	-	-	-		-
	ERR(B)	****	**	****		-

-	= ns
*	p = .1
**	p = .05
***	p = .01
****	p = .001

TABLE 7: Significant treatment effects (ANOVA) for redroot pigweed yield variables (per plant) in monoculture and mixtures.

		RPW MONO	RPW/BYG ≤ 20	RPW/BYG = 25	RPW/GFT ≤ 20	RPW/GFT = 25
VEGETATIVE DRY WEIGHT	BLOCK	****	****	***	****	****
	OZONE	*	-	-(.1211)	-	-
	LIN	**	-	*	-	-
	DEV	-	-	-	-	-
	ERR(A)	-	-	-	-	****
	COMP	**	**	-	*	-
	OZONE*COMP	-	-	-	-	-
	ERR(B)	****	-	****	***	****
REPRODUCTIVE DRY WEIGHT	BLOCK	****	****	N/A	N/A	N/A
	OZONE	-	-			
	LIN	-	-			
	DEV	-	-			
	ERR(A)	-	-			
	COMP	-	-			
	OZONE*COMP	-	-			
	ERR(B)	-	**			
NUMBER OF LEAVES	BLOCK	****	****	-	****	****
	OZONE	-	-	*	-	-
	LIN	-	-	**	-	-
	DEV	-	-	-	-	-
	ERR(A)	****	****	-	-	-
	COMP	****	-	-	**	**
	OZONE*COMP	-	-	-	-	-
	ERR(B)	***	***	****	****	**
	TOTAL DF:	1777	868	825	897	1291

-	= ns
*	p = .1
**	p = .05
***	p = .01
****	p = .001

high density showed significant differences in the number of leaves/plant between density treatments.

4.2.6 RPW totals/pot

As in the ANOVAs on individual plant variables, total vegetative dry weight/pot showed a significant ozone effect on RPW in monoculture (Table 8). A significant ozone effect on vegetative dry weight was also seen when RPW was in mixture with BYG at high density. Both of these effects were linear. There were significant differences between density treatments for total vegetative dry weight and number of leaves in monoculture and all mixture combinations. A significant difference between density treatments for reproductive dry weight was seen for RPW in mixture with BYG at low density.

4.2.7 Root totals/pot

There was a strongly significant inverse linear ozone effect on root weight/pot in the RPW monocultures as determined by Analysis of Variance (Table 9). Mixtures of both GFT and BYG with RPW at low densities also showed weakly significant adverse ozone effects on root dry weight/pot.

The ANOVA also revealed a significant ozone*competition interaction effect on root dry weight in mixtures of GFT and RPW at high density.

In all cases, the ANOVA revealed significant effects of density treatment on the root weight/pot. The results of the BYG/GFT treatment combination at low densities could not be analyzed because there was only one experimental block; root weight was not measured in Experiment 3.

TABLE 8: Significant treatment effects (ANOVA) for redroot pigweed yield variables (total per pot) in monoculture and mixtures.

		RPW MONO	RPW/BYG ≤ 20	RPW/BYG = 25	RPW/GFT ≤ 20	RPW/GFT = 25
VEGETATIVE DRY WEIGHT	BLOCK	****	****	-	****	****
	OZONE	*	-	*	(.11)	-
	LIN	**	-	*	*	-
	DEV	-	-	-	-	-
	ERR(A)	-	-	-	-	***
	COMP	**	****	- (.10*)	***	***
	OZONE*COMP	-	-	-	-	-
	ERR(B)	****	-	*	****	-
REPRODUCTIVE DRY WEIGHT	BLOCK	****	****	N/A	N/A	N/A
	OZONE	-	-			
	LIN	-	-			
	DEV	-	-			
	ERR(A)	-	-			
	COMP	-(.13)	*			
	OZONE*COMP	-	-			
	ERR(B)	****	**			
NUMBER OF LEAVES	BLOCK	****	****	-	****	****
	OZONE	-	-	-	-	-
	LIN	-	-	-	-	-
	DEV	-	-	-	-	-
	ERR(A)	***	**	-	-	***
	COMP	****	****	****	****	****
	OZONE*COMP	-	-	-	-	-
	ERR(B)	****	****	-	*	***

- = ns
* p = .1
** p = .05
*** p = .01
**** p = .001

TABLE 9: Significant treatment effects (ANOVA) on total root weight per pot for monocultures and mixtures.

MONOCULTURES

	BYG	RPW	GFT
BLOCK	****	****	****
OZONE	-	***	-
LIN	-	***	-
DEV	-	-	-
ERR(A)	-	-	-
COMP	****	***	****
OZONE*COMP	-	-	-
ERR(B)	**	-	-

DENSITY $\leq$ 20

	BYG/GFT	BYG/RPW	GFT/RPW
BLOCK	N/A	****	****
OZONE		-(.11)	*
LIN		*	**
DEV		-	-
ERR(A)		-	-
COMP		**	**
OZONE*COMP		-	-
ERR(B)		****	***

DENSITY = 25

	BYG/GFT	BYG/RPW	GFT/RPW
BLOCK	-	-	***
OZONE	-	-	-
LIN	-	-	-
DEV	-	-	-
ERR(A)	-	-	-
COMP	*	*	****
OZONE*COMP	-	-	*
ERR(B)	-	**	-

-	= ns
*	p = .1
**	p = .05
***	p = .01
****	p = .001

4.3 REGRESSION ANALYSES

4.3.1 Multiple Linear Regressions

The multiple regression analysis of Spitters(1983) uses the partial regression coefficients to describe the degree of intra-specific competition, inter-specific competition and niche differentiation of a single species in mixture with another species and in monoculture (Equation 3, page 20). The coefficients $\mathbf{b}_{1,0}$, $\mathbf{b}_{1,1}$, and $\mathbf{b}_{1,2}$ are presented in Table 10.

GFT and RPW in combination with each other and BYG show a decreasing virtual biomass of an isolated plant as the ozone concentration is increased as indicated by an increasing value of the intercept ($\mathbf{b}_{1,0}$). However, BYG in mixture with RPW shows a slight increase of the virtual biomass of an isolated plant in both the 75 and 150 ppb ozone treatments over the control. In contrast, BYG in mixture with GFT shows a larger increase in the virtual biomass of an isolated plant only in the 75 ppb treatment relative to the control treatment.

In all but three cases (BYG with RPW in filtered-air and BYG with both RPW and GFT at 150 ppb), the model is significant; however throughout the coefficients of determination (R^2) are low, ranging from 0.04 to 0.19 indicating that the models do not explain a large proportion of the variation.

If the partial regression coefficients were significantly different from 0, they were interpreted as representing an effect of either intra- or inter-specific competition on the yield of that species. BYG shows a significant effect of intra-specific competition only in the model with GFT at 75 ppb, which could be explained by a combination of its own enhanced growth in that ozone treatment and GFT's poor competitive ability, as illustrated by the lack of a significant GFT inter-specific effect on BYG in any of the ozone treatments. The negative interspecific coefficients in the BYG in mixture with GFT models in the 0 and 150 ppb ozone treatments indicate that the presence of GFT has a

TABLE 10: Results of multiple linear regression model.

Species Combination	$b_{1,0}$	$b_{1,1}$	$b_{1,2}$	R^2	Model
0					
BYG+RPW	6.77	.011	.173*	.04	ns
+GFT	5.92	.115	- .094	.07	*
GFT+BYG	16.18	.444**	.564***	.12	***
+RPW	19.77	.166	.771****	.13	***
RPW+BYG	9.61	.394*	.485***	.08	**
+GFT	8.26	.414**	.221	.05	*
75 ppb/7 hrs					
BYG+RPW	4.64	.142	.188**	.06	*
+GFT	3.44	.206***	.065	.10	**
GFT+BYG	16.95	.519**	.842****	.19	****
+RPW	20.95	.275	.747***	.10	***
RPW+BYG	13.16	.244	.385**	.05	*
+GFT	9.86	.463**	.333**	.05	**
150 ppb/3.5 hrs					
BYG+RPW	5.86	.103	.219**	.05	ns
+GFT	6.34	.098	- .074	.06	ns
GFT+BYG	20.61	.184	.685***	.15	***
+RPW	21.64	.096	1.04****	.18	****
RPW+BYG	13.11	.317	.592***	.09	***
+GFT	13.47	.229	.356**	.04	*

* p = .1
** p = .05
*** p = .01
**** p = .001

significant positive inter-specific effect on the yield of BYG in the control, but this trend fails to reach significance in the 150 ppb treatment.

RPW has a significant inter-specific effect on BYG in all ozone treatments and *vice versa*. RPW is not significantly affected by GFT inter-specific competition in the control but is in both the 75 and 150 ppb treatments. Intra-specific competition appears to be more important to the yield of RPW than the inter-specific effect of GFT in the control.

The yield of GFT is very significantly affected by inter-specific competition from the other two species in all ozone treatments and only shows a significant effect of intra-specific competition in the models including BYG at the 0 and 75 ppb ozone levels.

Expansion of the multiple regression model to include an interaction term (Equation 6, page 32) yields the coefficients presented in Table 11. An examination of the intercepts shows that the same pattern exists over the ozone treatments for all species mixtures as shown in Table 10. The coefficients of determination, R^2, are improved slightly by the addition of the extra term, but fewer of the models are significant.

Two partial regression coefficients for the interaction term are significant. The interaction between the density of RPW and GFT has a significant effect on the yield of GFT in the control ozone treatment, and the interaction between the density of BYG and GFT has a significant effect on the yield of GFT at the 150 ppb ozone level. The presence of the interaction term in the GFT-RPW model in the control treatment causes the intra-specific coefficient to be significant, whereas it was not in the simpler model. The interaction effect is a negative one, meaning that the interaction of the two densities increases the yield of GFT.

In the GFT-BYG model at the 150 ppb ozone level, the presence of the significant positive interaction, which indicates a negative effect of the interaction of the two densities on GFT yield, causes both the intra- and inter-specific coefficients to be negative, and the significance of the inter-specific competition, seen in the simpler model, is lost.

TABLE 11: Results of multiple linear regression model with interaction.

Species Combination	$b_{1,0}$	$b_{1,1}$	$b_{1,2}$	b_{12}	R^2	Model
<u>0 ppb</u>						
BYG+RPW	5.97	.089	.349*	-.021	.05	ns
+GFT	6.68	.044	-.238	.017	.08	*
GFT+BYG	14.97	.557**	.809**	-.028	.13	**
+RPW	15.24	.620**	1.588****	-.099**	.17	****
RPW+BYG	9.11	.446*	.611*	-.016	.08	**
+GFT	7.02	.543**	.475	-.032	.05	*
<u>75 ppb/7 hrs</u>						
BYG+RPW	4.76	.130	.162	.003	.06	ns
+GFT	2.72	.278***	.225*	-.020	.13	**
GFT+BYG	17.83	.432	.647	.023	.19	***
+RPW	21.82	.187	.586	.020	.10	***
RPW+BYG	12.24	.337	.615*	-.029	.05	ns
+GFT	8.85	.569**	.556*	-.028	.06	*
<u>150 ppb/3.5 hrs</u>						
BYG+RPW	4.89	.200	.432**	-.026	.06	ns
+GFT	5.63	.170*	.091	-.021	.08	*
GFT+BYG	23.50	-.109	-.007	.086**	.19	***
+RPW	20.79	.184	1.201**	-.019	.19	****
RPW+BYG	13.69	.258	.432	.020	.09	**
+GFT	12.62	.3174	.539	-.023	.04	ns

* p = .1
** p = .05
*** p = .01
**** p = .001

Because the interaction term does not appear to shed much light on the data in terms of explaining the variation, the simpler models were used to calculate the competitive indices as described by Spitters (1983a).

Competition indices (the ratios of the partial regression coefficients obtained in the multiple linear regression models) are shown in Table 12. For GFT with BYG, and RPW with BYG or GFT, competitive ability decreases as the ozone concentration is increased. This agrees with the interpretation of the intercepts of the simple multiple regression models for these species. However, GFT in mixture with RPW at 75 ppb appears to have more competitive ability than in the other two ozone treatments. This is also true of BYG in mixture with RPW. BYG has a much stronger competitive ability than GFT in the 75 ppb treatment. The negative signs of the coefficients in the filtered-air or in 150 ppb ozone represent the significant positive effect of GFT inter-specific competition on the yield of BYG in these treatments.

The indices indicate that BYG is a much stronger competitor than GFT, as is RPW. BYG is a 3.17 times stronger competitor than GFT in the 75 ppb treatment; RPW is a 1.87 times stronger competitor than GFT in the control treatment. RPW and BYG are shown to be similar in their competitive abilities. GFT has very poor competitive ability in mixture with RPW but slightly better in mixture with BYG.

The overall order of decreasing competitive abilities over the three ozone treatments appears to be:

0 ppb	75 ppb	150 ppb
RPW-GFT	BYG-GFT	BYG-GFT
BYG-GFT	RPW-GFT	RPW-GFT
RPW-BYG	BYG-RPW	RPW-BYG
GFT-BYG	RPW-BYG	BYG-RPW
GFT-RPW	GFT-BYG	GFT-BYG
BYG-RPW	GFT-RPW	GFT-RPW

TABLE 12: Competition indices† from multiple linear regression model.

SPECIES COMBINATION	OZONE TREATMENT 0	75 ppb/7 hr	150 ppb/3.5 hr
BYG +RPW	.064 (1)*	.775 (1)	.470 (1)
BYG +GFT	-1.223 (0)	3.169 (1)	-1.324 (0)
GFT +BYG	.787 (2)	.616 (2)	.269 (1)
GFT +RPW	.215 (1)	.368 (1)	.092 (1)
RPW +BYG	.812 (2)	.634 (1)	.535 (1)
RPW +GFT	1.873 (1)	1.390 (2)	.643 (1)

† $b_{1,1}/b_{1,2}$

* ( ) = NUMBER OF SIGNIFICANT PARTIAL REGRESSION COEFFICIENTS MAXIMUM IS (2)

Indices of niche differentiation calculated for the species mixtures from their competitive ability indices are presented in Table 13. Only with BYG-GFT in 75 ppb does this double quotient exceed unity, indicating that there is niche differentiation, i.e. the species are competing for different resources. In all other combinations and ozone treatments, the species appear to be competing for the same resources. However, it should be noted that in no case were all the contributing coefficients significantly different from zero.

Table 13. The niche differentiation indices from the multiple linear regression analyses.

	0 ppb	75 ppb	150 ppb
BYG-GFT	-.9625(2)*	1.9521(3)	-.3562(1)
BYG-RPW	.0520(2)	.4914(3)	.2514(2)
GFT-RPW	.4027(2)	.5115(3)	.0592(2)

* number of significant partial regression coefficients - maximum is 4

4.3.2 Sequential Simple Regressions

The results of these analyses are shown in Table 14 and depicted in an additive series form in Figures 2 through 7. As in the multiple linear regression analysis, the virtual yield of an isolated plant of GFT and RPW decreases with increasing ozone concentration, while that of an isolated plant of BYG is higher in the 75 ppb ozone treatment than in the control or 150 ppb treatment.

TABLE 14: Results of sequential simple regression model.

0		$B_{1,0}$	$B_{1,1}$ or $B_{1,2}$†	R^2	Model
BYG	MONO	6.97	.0189	.00	ns
	+RPW		.1497**	.08	**
	+GFT		-.104**	.09	*
GFT	MONO	14.77	.538**	.13	**
	+BYG		.603****	.28	****
	+RPW		.900****	.36	****
RPW	MONO	6.58	.563**	.12	**
	+BYG		.615****	.29	****
	+GFT		.249**	.08	**
<u>75 ppb/ 7 hrs</u>					
BYG	MONO	3.24	.241**	.18	**
	+RPW		.233****	.20	****
	+GFT		.056	.04	ns
GFT	MONO	17.56	.415	.07	ns
	+BYG		.870****	.40	****
	+RPW		.922****	.35	****
RPW	MONO	8.69	.547**	.11	**
	+BYG		.537****	.23	****
	+GFT		.368***	.12	***
<u>150 ppb/ 3.5 hrs</u>					
BYG	MONO	5.28	.199*	.09	*
	+RPW		.196**	.10	**
	+GFT		-.063	.04	ns
GFT	MONO	19.87	.153	.02	ns
	+BYG		.763****	.33	****
	+RPW		1.142****	.40	****
RPW	MONO	11.38	.377*	.06	*
	+BYG		.692****	.29	****
	+GFT		.417***	.14	****

* p = .1
** p = .05
*** p = .01
**** p = .001

† $B_{1,1}$ monoculture
$B_{1,2}$ mixture

FIGURE 2: Relationships of estimated total yields (g) of BYG in monoculture and in the presence of three densities of GFT, and of GFT at these densities, in three ozone treatments. The additive series curves were derived from Equations 4 and 5. The curves for the indicator species were obatained using Equation 1 (Dew, 1972).

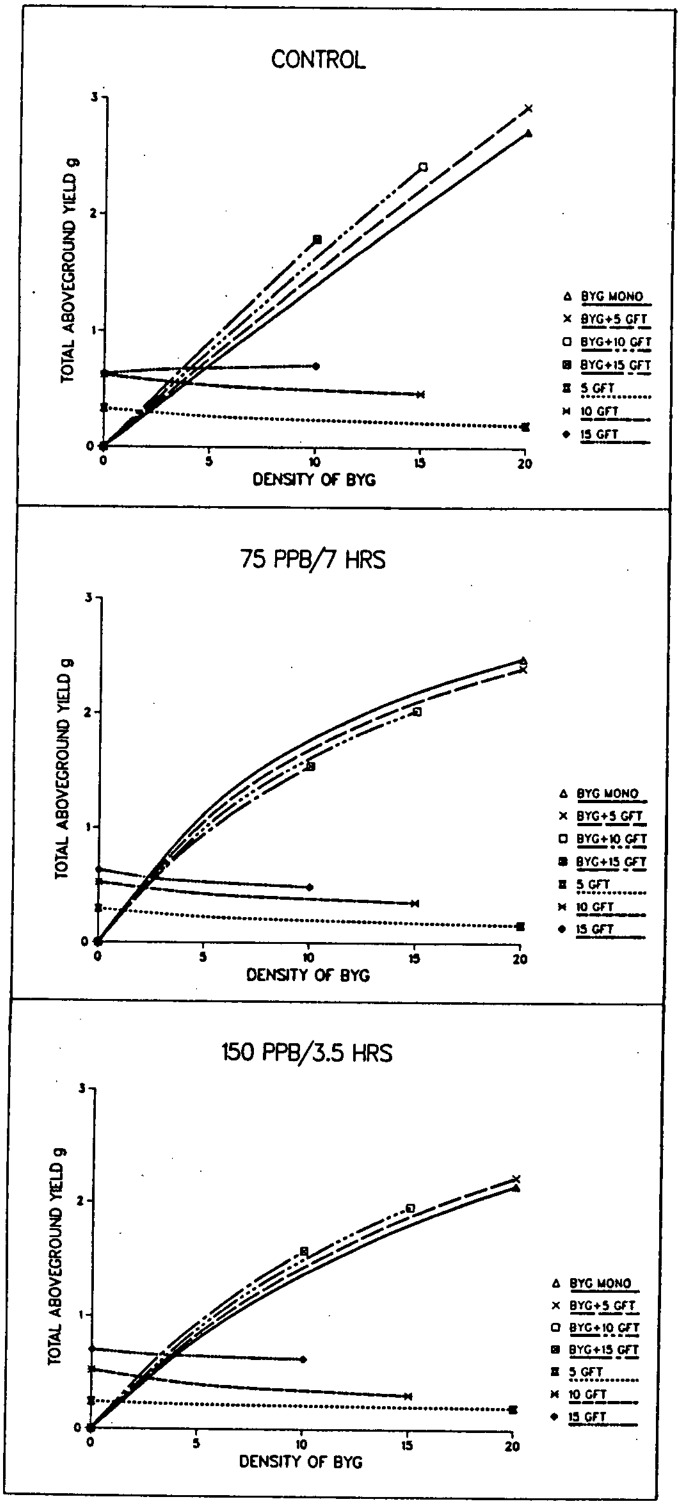

CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
DENSITY OF BYG
BYG MONO
BYG+5 GFT
BYG+10 GFT
BYG+15 GFT
5 GFT
10 GFT
15 GFT

FIGURE 3 : Relationships of estimated total yields (g) of BYG in monoculture and in the presence of three densities of RPW, and of RPW at these densities in three ozone treatments. The curves were derived as for Figure 2.

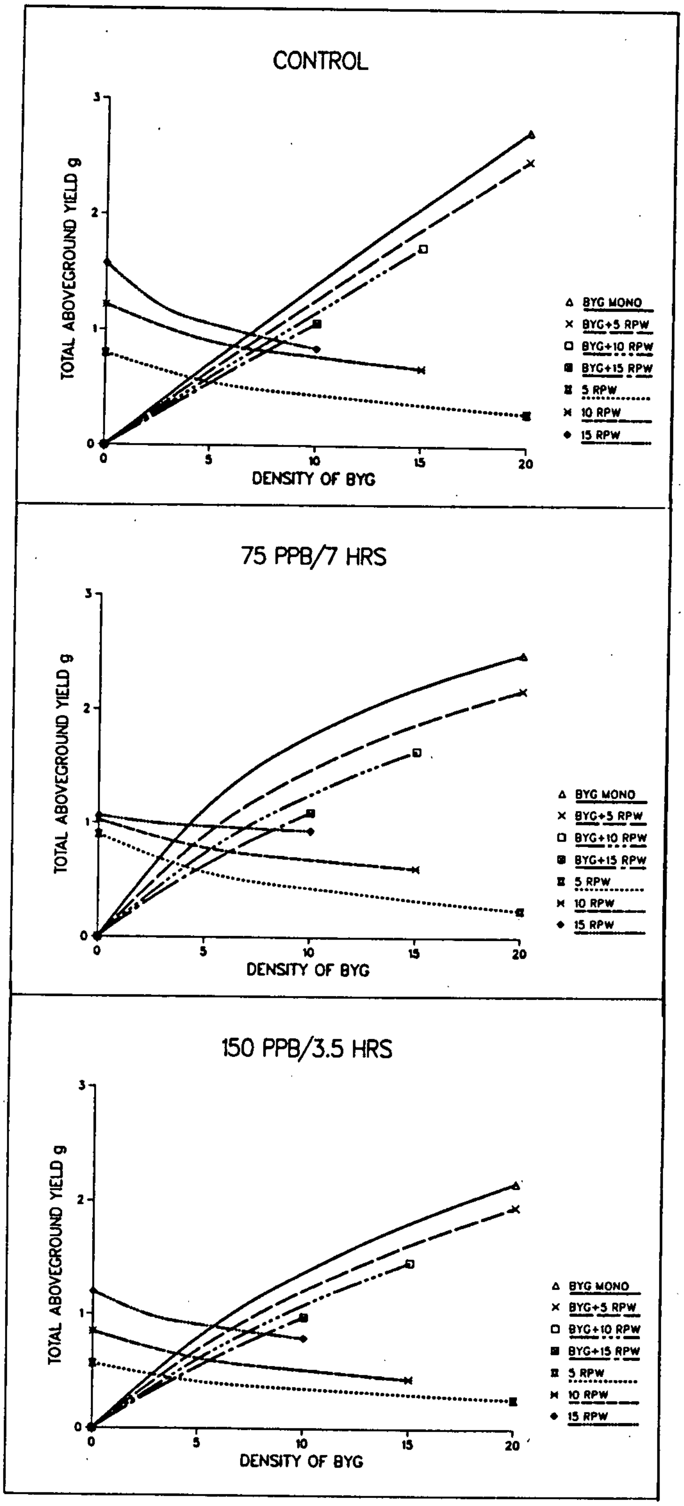
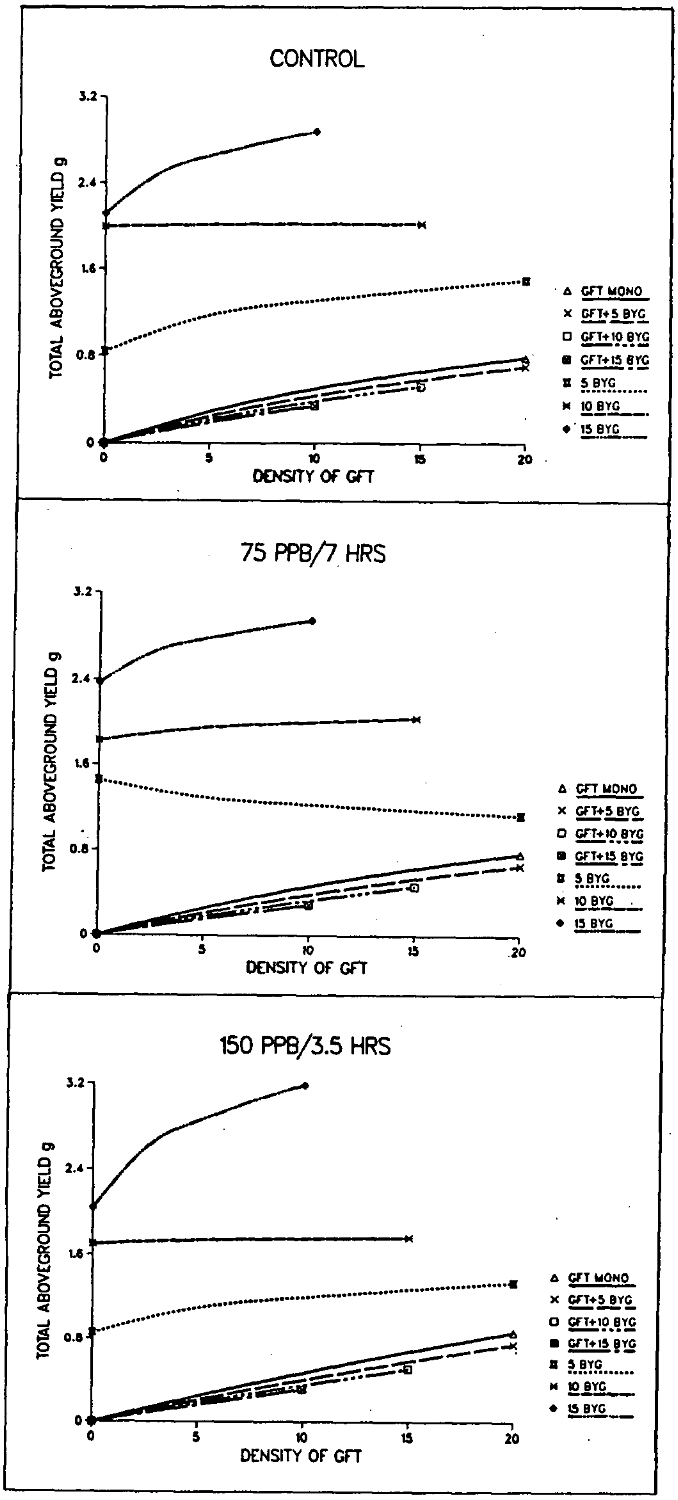

CONTROL
TOTAL ABOVEGROUND YIELD g
DENSITY OF BYG
BYG MONO
BYG+5 RPW
BYG+10 RPW
BYG+15 RPW
5 RPW
10 RPW
15 RPW
75 PPB/7 HRS
150 PPB/3.5 HRS

FIGURE 4: Relationships of estimated total yields (g) of GFT in monoculture and in the presence of three densities of BYG, and of BYG at these densities, in three ozone treatments. The curves were derived as for Figure 2.


CONTROL
TOTAL ABOVEGROUND YIELD g
DENSITY OF GFT
GFT MONO
GFT+5 BYG
GFT+10 BYG
GFT+15 BYG
5 BYG
10 BYG
15 BYG
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
DENSITY OF GFT
GFT MONO
GFT+5 BYG
GFT+10 BYG
GFT+15 BYG
5 BYG
10 BYG
15 BYG
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
DENSITY OF GFT
GFT MONO
GFT+5 BYG
GFT+10 BYG
GFT+15 BYG
5 BYG
10 BYG
15 BYG

However, in comparison to the multiple linear regression analysis the coefficients of determination are for the most part appreciably higher (0-0.40), meaning that more of the variation is explained by the effect of density in this model.

In the case of BYG monoculture in the control treatment, none of the variation is explained by the density, agreeing with the multiple linear regression analysis (Table 10) in which BYG in the control treatment did not show any significant intra-specific competition in the presence of either RPW or GFT. This lack of a significant relationship shows up in Figures 2 and 3.

The non-significance of the models of BYG in mixture with GFT in the 75 and 150 ppb treatments indicates that GFT does not have any significant inter-specific effect on BYG yield in those treatments. This is apparent in Figure 2. There is a significant effect of intra-specific competition on yield of BYG in the 75 and 150 ppb ozone treatments. In Figures 2 and 3, this effect is demonstrated by the asymptotic nature of the monoculture curve in those ozone treatments, as compared to the control. In contrast, intra-specific competition only significantly effects GFT yield in the control, but not in the 75 or 150 ppb ozone treatments (Figures 4 and 5), which suggests the ozone is affecting yield to the point where density is no longer important in explaining the variation. RPW experiences significant intra-specific competition in all treatments (Figures 6 and 7).

GFT again shows a negative effect on yield of BYG in the control and 150 ppb ozone treatments, but only the former is statistically significant. In Figure 2 this negative effect shows up as an enhanced BYG yield with each addition of GFT. RPW, however, significantly effects BYG yield in all treatments. This significant inter-specific effect is depicted in Figure 3 as asymptotic curves at each density of RPW. Conversely, RPW and GFT experience very significant inter-specific competition from BYG in all treatments (Figures 6 and 4, respectively). RPW yield is significantly affected by GFT in all treatments (Figure 7), and GFT is highly significantly affected by RPW inter-specific competition in all treatments (Figure 5).

FIGURE 5: Relationships of estimated total yields (g) of GFT in monoculture and in the presence of three densities of RPW, and of RPW at these densities, in three ozone treatments. The curves were derived as for Figure 2.

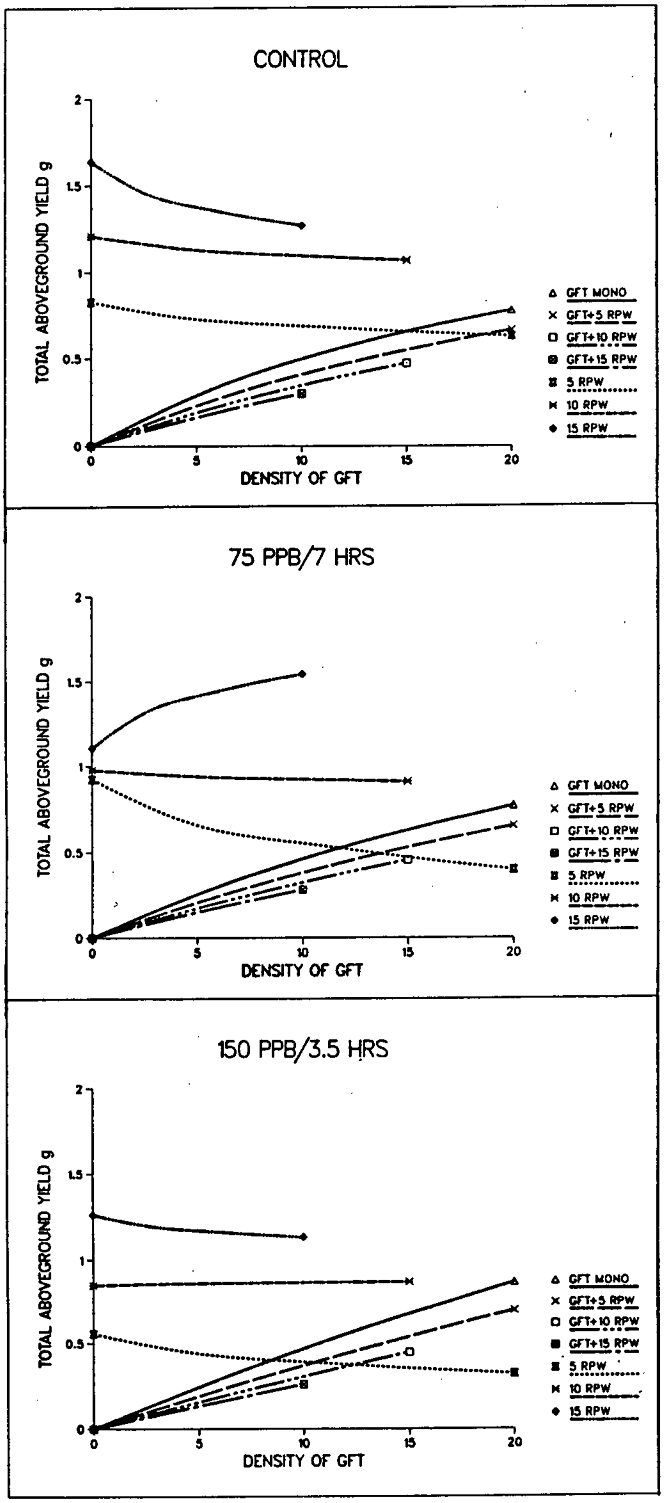

CONTROL
TOTAL ABOVEGROUND YIELD g
DENSITY OF GFT
GFT MONO
GFT+5 RPW
GFT+10 RPW
GFT+15 RPW
5 RPW
10 RPW
15 RPW
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
DENSITY OF GFT
GFT MONO
GFT+5 RPW
GFT+10 RPW
GFT+15 RPW
5 RPW
10 RPW
15 RPW
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
DENSITY OF GFT
GFT MONO
GFT+5 RPW
GFT+10 RPW
GFT+15 RPW
5 RPW
10 RPW
15 RPW

FIGURE 6: Relationships of estimated total yields (g) of RPW in monoculture and in the presence of three densities of BYG, and of BYG at these densities, in three ozone treatments. The curves were derived as for Figure 2.

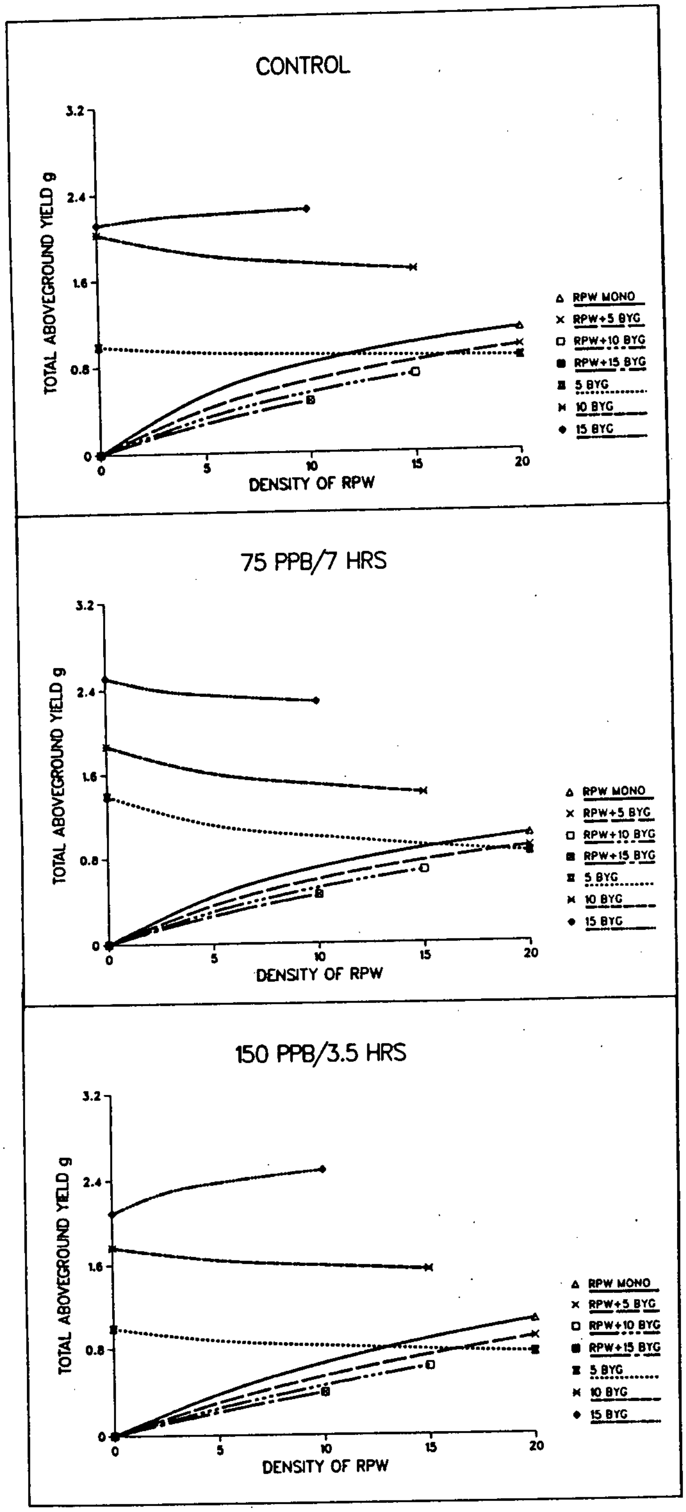
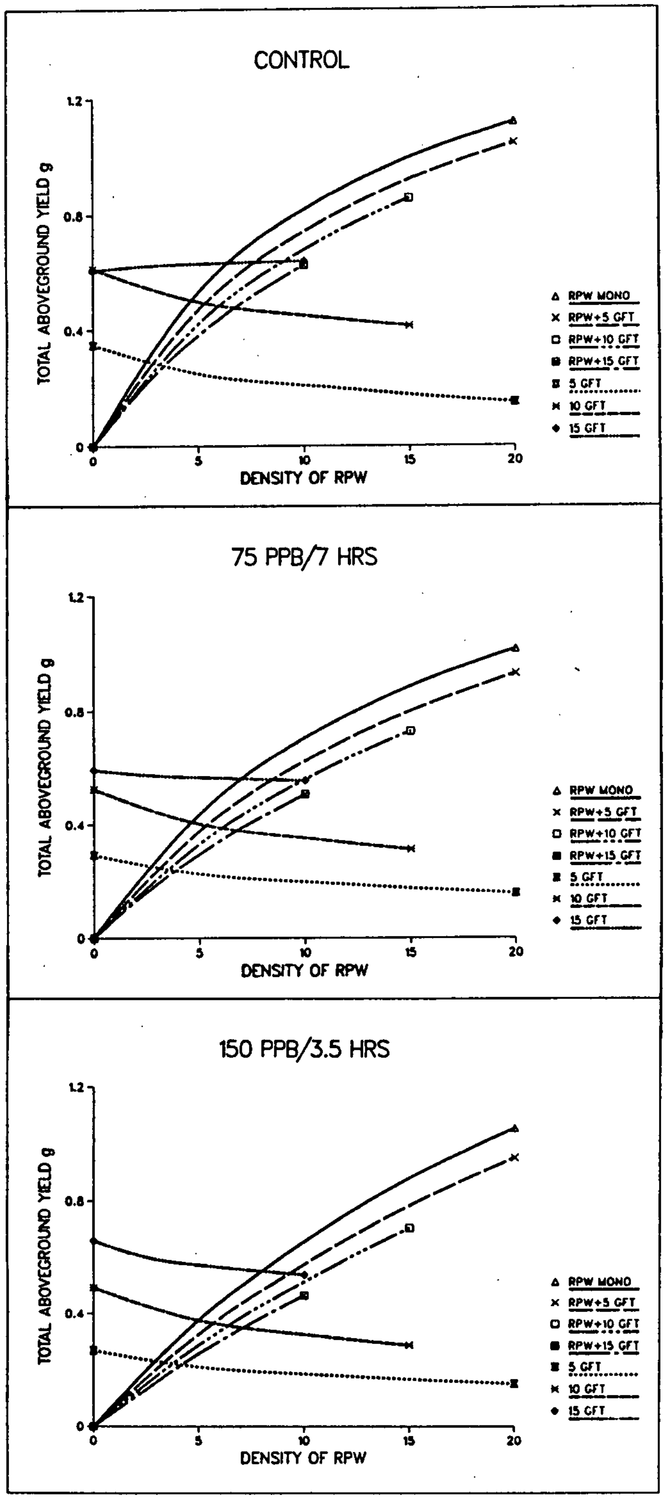

CONTROL
TOTAL ABOVEGROUND YIELD g
DENSITY OF RPW
RPW MONO
RPW+5 BYG
RPW+10 BYG
RPW+15 BYG
5 BYG
10 BYG
15 BYG
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
DENSITY OF RPW
RPW MONO
RPW+5 BYG
RPW+10 BYG
RPW+15 BYG
5 BYG
10 BYG
15 BYG
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
DENSITY OF RPW
RPW MONO
RPW+5 BYG
RPW+10 BYG
RPW+15 BYG
5 BYG
10 BYG
15 BYG

FIGURE 7: Relationships of estimated total yields (g) of RPW in monoculture and in the presence of three densities of GFT, and of GFT at these densities, in three ozone treatments. The curves were derived as for Figure 2.


CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
DENSITY OF RPW
RPW MONO
RPW+5 GFT
RPW+10 GFT
RPW+15 GFT
5 GFT
10 GFT
15 GFT

The competition indices derived from these regressions are presented in Table 15. The indices show similar trends as for those derived from the multiple linear regression analysis (Table 12). The competition abilities of RPW with GFT, GFT with RPW and GFT with BYG again decrease with increasing ozone concentration. In addition, the index for BYG over GFT is larger in the 75 ppb treatment than in the other two. However, there are a few discrepancies between the competition indices from the two forms of analysis. BYG in mixture with GFT in the control shows a much lower competitive ability than in the previous analysis (Table 12), although the index is still negative. RPW in mixture with BYG shows somewhat more competitive ability in the 75 ppb treatment than in the other two treatments in the sequential simple regression (Table 15), rather than showing a trend of decreasing ability as the ozone concentration increased in the previous analysis (Table 12). The converse is true of GFT in mixture with RPW, which now suggests a trend of decreasing competitive ability as the ozone concentration is increased, rather than more competitive ability in the 75 ppb treatment (Table 12).

From this analysis, the ranking of the competitive abilities of the species for each ozone treatment is:

0 ppb	75 ppb	150 ppb
RPW-GFT	BYG-GFT	BYG-GFT
RPW-BYG	RPW-GFT	BYG-RPW
GFT-BYG	BYG-RPW	RPW-GFT
GFT-RPW	RPW-BYG	RPW-BYG
BYG-GFT	GFT-BYG	GFT-BYG
BYG-RPW	GFT-RPW	GFT-RPW

The indices for niche differentiation, are shown in Table 16. Unlike the indices derived from the multiple linear regression model, which indicated that all species were competing for the same resources in all treatments except BYG and GFT at 75 ppb, this analysis

TABLE 15: Competition indices† from sequential simple regression model.

Species Combination	OZONE TREATMENT 0	75 ppb/7 hrs	150 ppb/3.5 hrs
BYG +RPW	.126 (1)*	1.034 (2)	1.015 (2)
BYG +GFT	-.182 (1)	4.304 (1)	-3.159 (1)
GFT +BYG	.892 (2)	.477 (1)	.200 (1)
GFT +RPW	.598 (2)	.450 (1)	.134 (1)
RPW +BYG	.915 (2)	1.019 (2)	.545 (2)
RPW +GFT	2.261 (2)	1.486 (2)	.904 (2)

† $b_{1,1}/b_{1,2}$

* ( ) = NUMBER OF SIGNIFICANT PARTIAL REGRESSION COEFFICIENTS MAXIMUM IS (2)

suggests that BYG and RPW at 75 ppb and GFT and RPW at 0 ppb also show niche differentiation. Furthermore, in these latter situations the double quotient is based on coefficients each of which was significant.

Table 16. Niche differentiation indices from the sequential simple regressions.

	0 ppb	75 ppb	150 ppb
BYG-GFT	-.1621(3)*	2.0528(2)	-.6333(2)
BYG-RPW	.1155(3)	1.0535(4)	.5531(4)
GFT-RPW	1.3516(4)	.6690(3)	.1211(3)

* number of significant partial regression coefficients - maximum is 4

4.3.3 Square-root Regressions

The method of analysis of Dew (1972) uses a simple square root linear regression to describe the crop loss due to the addition of known densities of a weed (Equation 1, page 15). The coefficients of determination and significance levels are in Table 17; the curves based on values predicted by the regressions are shown in Figures 2 through 7.

The regression of GFT density on BYG yield is only significant at density 5 in the control treatment and at density 15 in the 150 ppb treatment. The positive nature of the coefficients reflects the enhancing effect of GFT on BYG yield which was evident, but not significant, in the SSR model. Figure 4 demonstrates this beneficial relationship. The

TABLE 17: Coefficients of determination from square-root regression.

Species Combination	DENSITY	OZONE TREATMENT 0	75 ppb/ 7 hrs	150 ppb/ 3.5 hrs
RPW +BYG	5	.14**†	.18**	.13**
	10	.10*	.08	.15**
	15	.18**	.01	.07
	20	.12	.01 (+)	.15
BYG +RPW	5	.01	.13**	.04
	10	.04	.07	.01
	15	.00 (+)	.01	.05 (+)
	20	.55***	.04	.02
BYG +GFT	5	.15* (+)	.06	.10 (+)
	10	.00 (+)	.02 (+)	.00 (+)
	15	.08 (+)	.05 (+)	.29** (+)
	20	.13	.02	.02 (+)
GFT +BYG	5	.20**	.35***	.06
	10	.07	.19**	.35***
	15	.02 (+)	.13	.02
	20	.18	.18	.12
RPW +GFT	5	.02	.13**	.09*
	10	.01	.01	.00 (+)
	15	.04	.06 (+)	.01
	20	.00	.14	.01
GFT +RPW	5	.33****	.28***	.33****
	10	.15**	.20**	.30***
	15	.01 (+)	.01	.06
	20	.05	.04	.20*

* p = .10
** p = .05
*** p = .01
**** p = .001
† significance level of model

regression of BYG density on GFT yield is only significant in the 0 and 75 ppb treatments at density 5 and the 75 and 150 ppb treatments at density 10. Figure 2 reflects this.

The regression of BYG density on RPW yield is significant in all ozone treatments at density 5, in the control and 150 ppb treatment at density 10 and only in the control at density 15. This would suggest that as the density of RPW increases, the presence of ozone in some way prevents BYG from significantly affecting RPW yield. These trends are seen in Figure 3. The regression for RPW on BYG is only significant in the 75 ppb ozone treatment at density 5 and in the control treatment at density 20 (Figure 6).

The regression of GFT density on RPW yield is only significant at the lowest density of RPW under the two ozone-added treatments (Figure 5). However, the model regressing RPW density against GFT yield is very significant in all ozone treatments at densities 5 and 10, and slightly significant at density 20 in the 150 ppb treatment. These effects are seen in Figure 7.

4.4 REPLACEMENT SERIES

The method of Thomas (1970) detected no significant heterogeneity between species in the three mixtures using the 4-parameter model. As this satisfied one of the assumptions underlying the three-parameter model, it could be tested. The results of testing the 4-parameter and 3-parameter models are presented in Table 18.

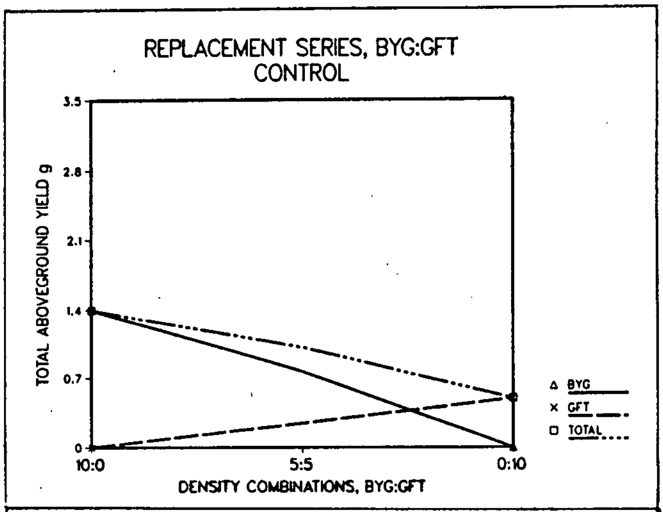
The 3-parameter model of BYG-GFT replacement series mixtures at total density 10 and 15 indicates that in all ozone treatments the species are competing for the same space, except at the highest density (20) in both the filtered air control and 150 ppb treatments. The replacement series diagrams for BYG-GFT in mixture at total density 10, 15, 20 and 25 plants per pot are shown in Figures 8, 9, 10 and 11 respectively. In all total densities and ozone treatments, the yield total shows a beneficial effect of the two species growing together. At total density 10 and 15 (Figures 8 and 9) BYG does better in the 75 ppb

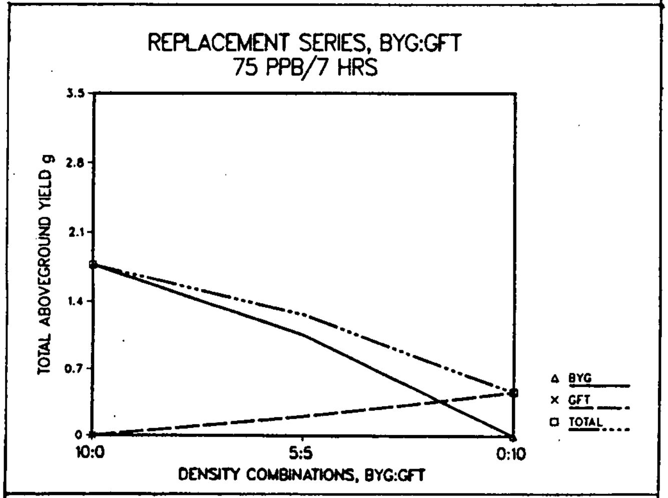
TABLE 18: Results of replacement series model analysis

Total Density	Species Mixture	K_{12}	K_{21}	between models	$K_{12} \times K_{21}$
0	BYG : GFT				
	10	0.840	0.739	ns	0.62
	15	1.776	0.590	ns	1.05
	20	3.249	1.758	***	5.71
	BYG : RPW				
	10	3.321	0.210	ns	0.70
	15	2.905	0.354	ns	1.03
	20	1.730	0.957	ns	1.66
	GFT : RPW				
	10	0.921	0.561	ns	0.52
	15	0.699	0.903	ns	0.63
	20	1.181	9.355	***	11.05
75 ppb/ 7 hrs	BYG : GFT				
	10	2.920	0.512	ns	1.50
	15	2.744	0.718	ns	1.97
	20	2.106	0.835	ns	1.76
	BYG : RPW				
	10	1.459	0.197	ns	0.29
	15	2.522	2.246	***	5.66
	20	1.570	0.680	ns	1.07
	GFT : RPW				
	10	0.689	0.708	ns	0.50
	15	0.903	0.361	**	0.32
	20	0.679	3.427	ns	2.33
150 ppb/ 3.5 hrs	BYG : GFT				
	10	0.943	0.349	ns	0.33
	15	2.015	0.703	ns	1.42
	20	4.528	0.950	***	4.30
	BYG : RPW				
	10	1.990	0.269	ns	0.54
	15	1.714	0.611	ns	1.05
	20	1.725	0.533	ns	0.92
	GFT : RPW				
	10	1.209	0.547	ns	0.66
	15	0.614	0.447	***	0.27
	20	0.511	2.827	ns	1.44

** p = .05
*** p = .01

FIGURE 8: Replacement series diagrams for BYG and GFT at total density of 10 plants/pot for three ozone treatments. The diagrams were constructed by connecting points which were obtained from Equations 4 and 5.


REPLACEMENT SERIES, BYG:GFT
CONTROL
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
10:0
5:5
0:10
DENSITY COMBINATIONS, BYG:GFT
BYG
GFT
TOTAL


REPLACEMENT SERIES, BYG:GFT
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
10:0
5:5
0:10
DENSITY COMBINATIONS, BYG:GFT
BYG
GFT
TOTAL

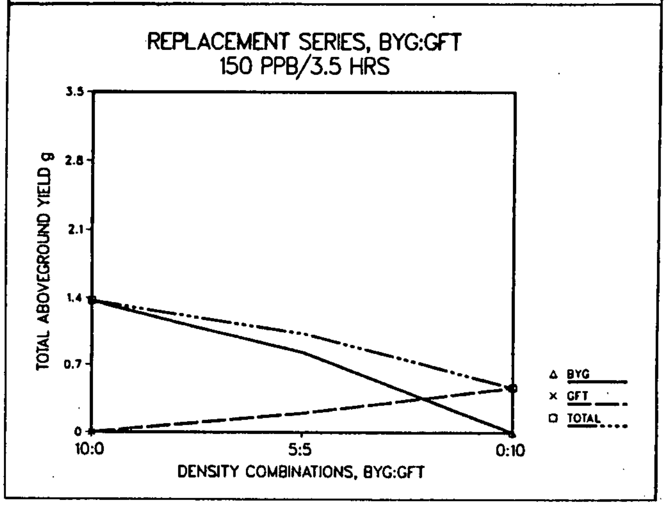
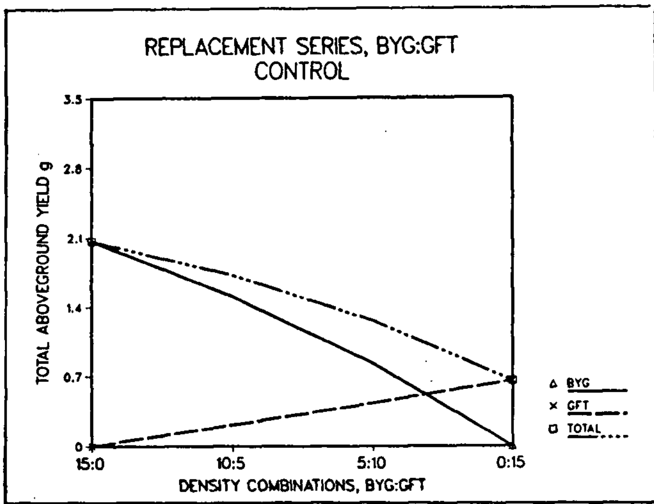
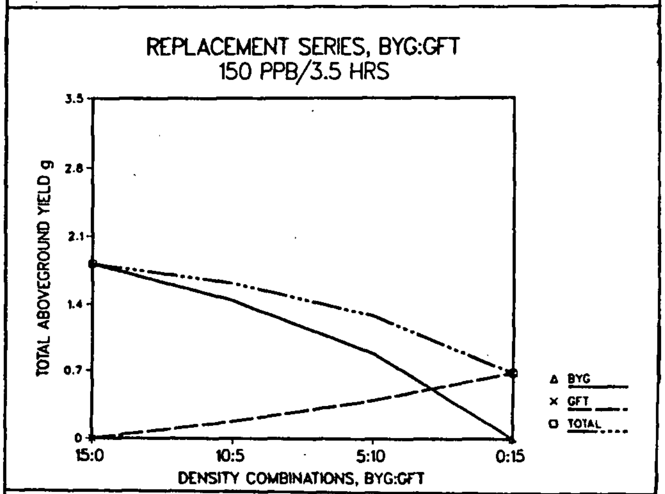

REPLACEMENT SERIES, BYG:GFT
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
10:0
5:5
0:10
DENSITY COMBINATIONS, BYG:GFT
BYG
GFT
TOTAL

FIGURE 9: Replacement series diagrams for BYG and GFT at total density of 15 plants/pot for three ozone treatments. The diagrams were constructed as for Figure 8.


REPLACEMENT SERIES, BYG:GFT
CONTROL
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
15:0
10:5
5:10
0:15
DENSITY COMBINATIONS, BYG:GFT
BYG
GFT
TOTAL


REPLACEMENT SERIES, BYG:GFT
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
15:0
10:5
5:10
0:15
DENSITY COMBINATIONS, BYG:GFT
BYG
GFT
TOTAL

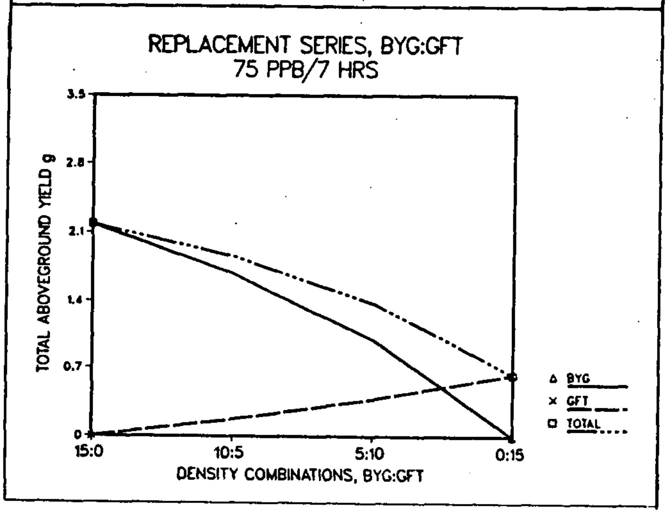

REPLACEMENT SERIES, BYG:GFT
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
15:0
10:5
5:10
0:15
DENSITY COMBINATIONS, BYG:GFT
BYG
GFT
TOTAL

FIGURE 10: Replacement series diagrams for BYG and GFT at total density of 20 plants/pot for three ozone treatments. The curves were derived from Equations 4 and 5.

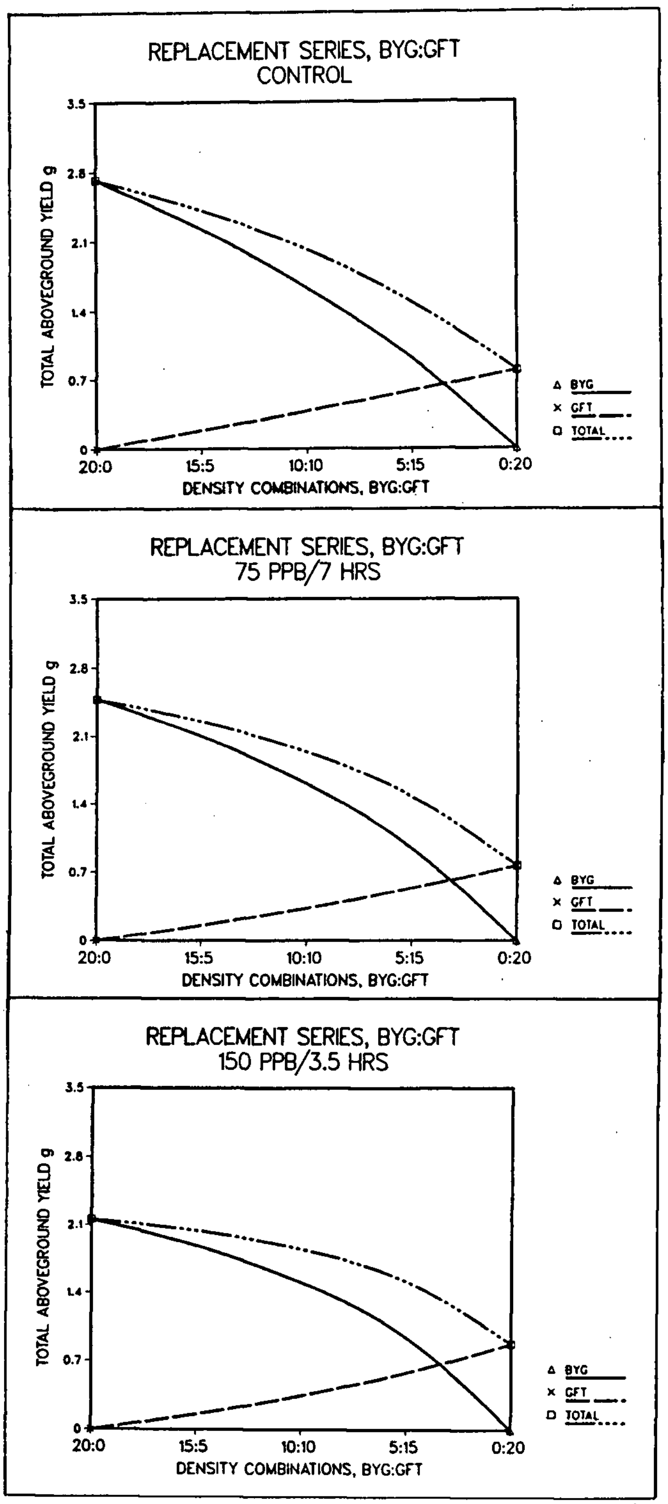
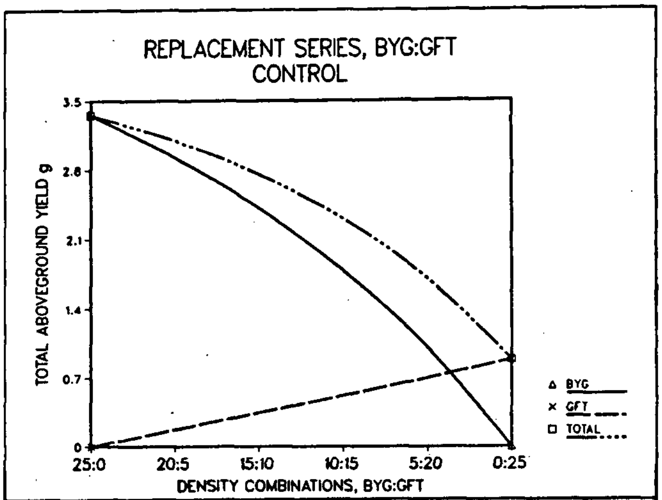
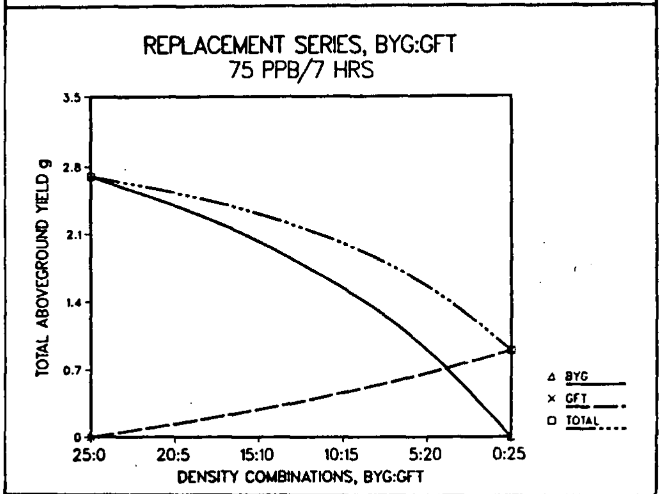

REPLACEMENT SERIES, BYG:GFT
CONTROL
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
20:0
15:5
10:10
5:15
0:20
DENSITY COMBINATIONS, BYG:GFT
BYG
GFT
TOTAL
REPLACEMENT SERIES, BYG:GFT
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
20:0
15:5
10:10
5:15
0:20
DENSITY COMBINATIONS, BYG:GFT
BYG
GFT
TOTAL
REPLACEMENT SERIES, BYG:GFT
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
20:0
15:5
10:10
5:15
0:20
DENSITY COMBINATIONS, BYG:GFT
BYG
GFT
TOTAL

FIGURE 11: Replacement series diagrams for BYG and GFT at total density of 25 plants/pot for three ozone treatments. The curves were derived as for Figure 10.


REPLACEMENT SERIES, BYG:GFT
CONTROL
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
25:0
20:5
15:10
10:15
5:20
0:25
DENSITY COMBINATIONS, BYG:GFT
BYG
GFT
TOTAL


REPLACEMENT SERIES, BYG:GFT
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
25:0
20:5
15:10
10:15
5:20
0:25
DENSITY COMBINATIONS, BYG:GFT
BYG
GFT
TOTAL

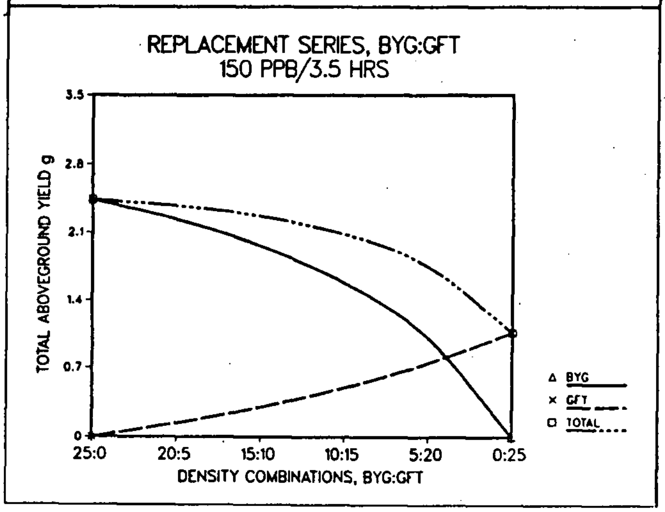

REPLACEMENT SERIES, BYG:GFT
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
25:0
20:5
15:10
10:15
5:20
0:25
DENSITY COMBINATIONS, BYG:GFT
BYG
GFT
TOTAL

FIGURE 12: Replacement series diagrams for BYG and RPW at total density of 10 plants/pot for three ozone treatments. The diagrams were constructed as for Figure 8.

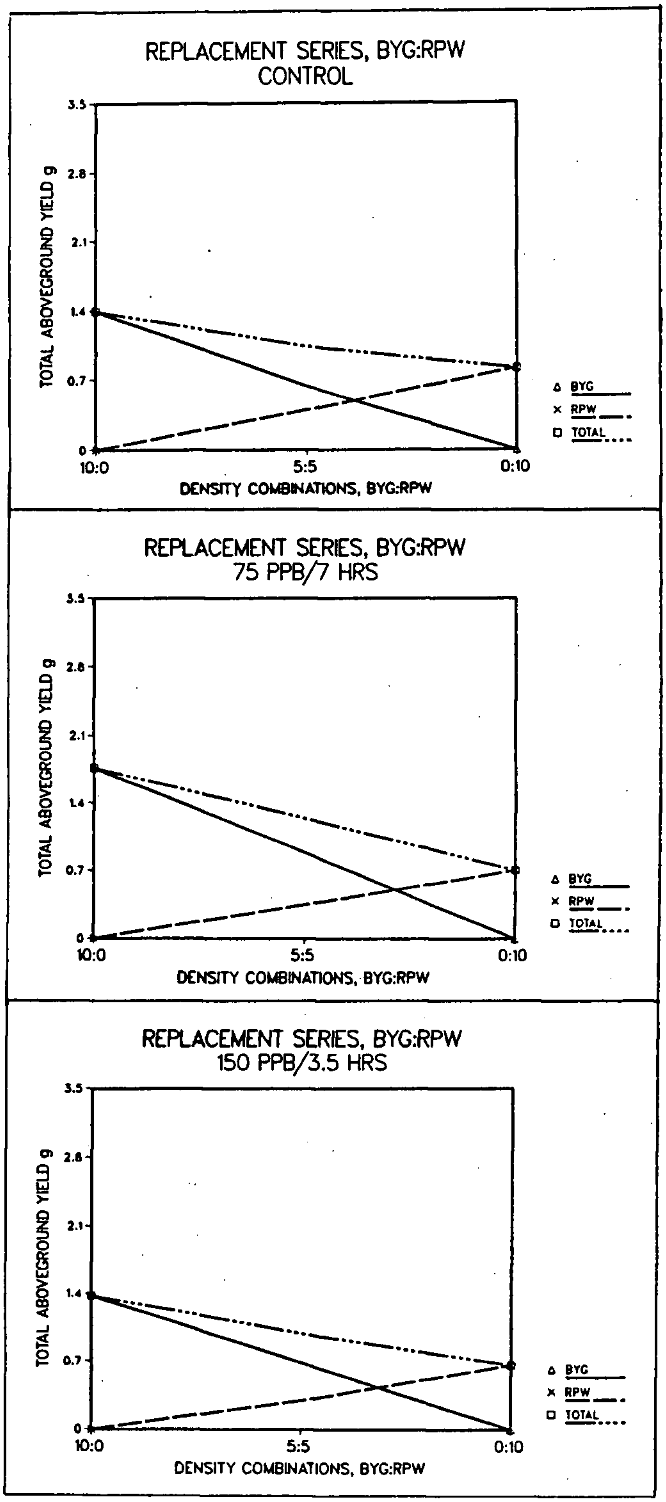
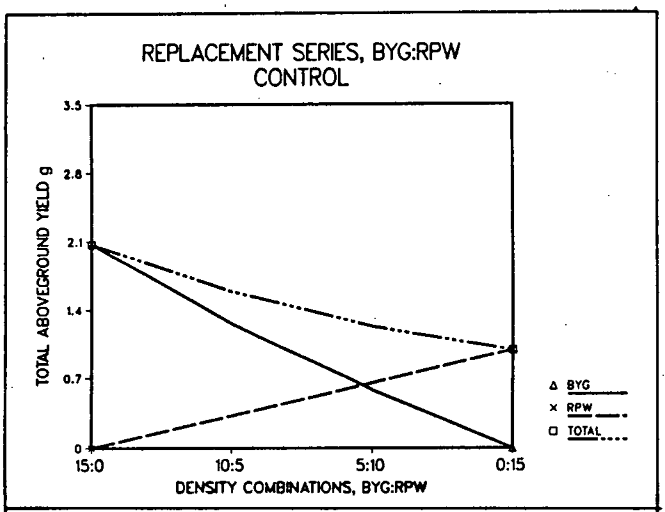
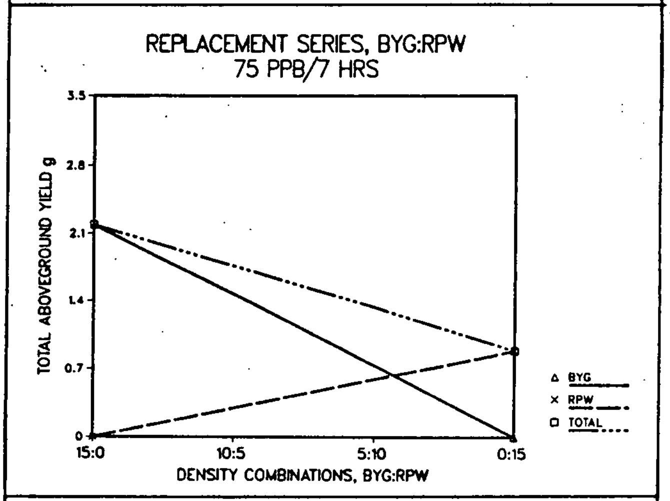
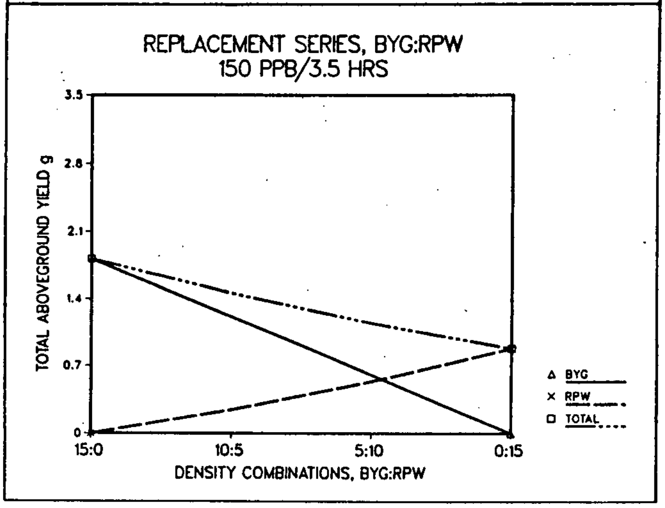

REPLACEMENT SERIES, BYG:RPW
CONTROL
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
10:0
5:5
0:10
DENSITY COMBINATIONS, BYG:RPW
BYG
RPW
TOTAL
REPLACEMENT SERIES, BYG:RPW
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
10:0
5:5
0:10
DENSITY COMBINATIONS, BYG:RPW
BYG
RPW
TOTAL
REPLACEMENT SERIES, BYG:RPW
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
10:0
5:5
0:10
DENSITY COMBINATIONS, BYG:RPW
BYG
RPW
TOTAL

FIGURE 13: Replacement series diagrams for BYG and RPW at total density of 15 plants/pot for three ozone treatments. The diagrams were constructed as for Figure 8.


REPLACEMENT SERIES, BYG:RPW
CONTROL
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
15:0
10:5
5:10
0:15
DENSITY COMBINATIONS, BYG:RPW
BYG
RPW
TOTAL


REPLACEMENT SERIES, BYG:RPW
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
15:0
10:5
5:10
0:15
DENSITY COMBINATIONS, BYG:RPW
BYG
RPW
TOTAL


REPLACEMENT SERIES, BYG:RPW
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
15:0
10:5
5:10
0:15
DENSITY COMBINATIONS, BYG:RPW
BYG
RPW
TOTAL

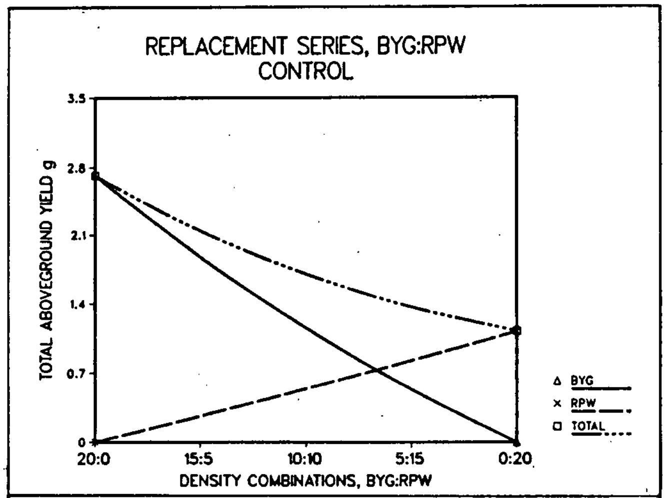
treatment than in the control or 150 ppb treatment. In the higher total densities (Figures 10 and 11) the yield of BYG decreases as the ozone concentration increases. GFT appears to be behaving in a linear fashion in all cases, whereas the yield of BYG is enhanced by the presence of GFT. The convex nature of the total yield curves is due to this enhanced yield of BYG, which is an indication of BYG's more vigorous and aggressive nature.

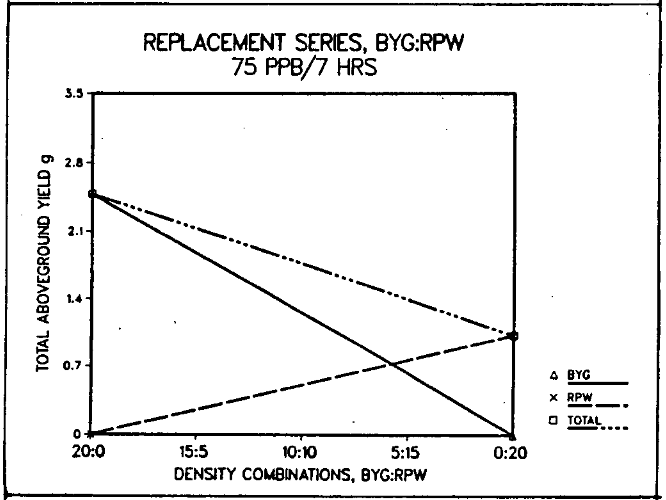
A test of the 3-parameter model on the replacement series mixtures of BYG and RPW indicates the species are crowding for the same space in all cases except at total density of 15 under the 75 ppb ozone treatment. The replacement series diagrams for BYG-RPW mixtures at total densities 10, 15, 20 and 25 are shown in Figures 12, 13, 14 and 15, respectively. At the lower total densities (Figures 12 and 13), the yield total curves are linear in all ozone treatments, representing an even replacement of biomass as each species is replaced by the other. At the higher densities (Figures 14 and 15), the 75 and 150 ppb treatments show a linear replacement of BYG with RPW, however the control ozone treatment shows concave total yield curves. This means that in the control treatment at high density, the mixture yields less than would be expected if the species simply replaced each other. This disadvantageous effect of inter-specific competition is relieved by the addition of ozone. The curves for RPW are linear in both cases, with the BYG yield appearing to show the most decrease in yield.

Results of the 3-parameter model for the mixture of GFT and RPW indicate that the two species are competing for the same space in all ozone treatments at density =10. Both the 75 and 150 ppb treatments at density=15 are crowding for different space, in contrast to the control treatment where they crowd for similar space. Exactly the opposite situation exists at total density of 20, where under the control treatment the species are crowding for different space, and under both the 75 and 150 ppb treatments the species are crowding for the same space.

The replacement series diagrams for RPW and GFT in mixture at total densities of 10, 15, 20 and 25 are shown in Figures 16, 17, 18 and 19, respectively. In all total densities,

FIGURE 14: Replacement series diagrams for BYG and RPW at total density of 20 plants/pot for three ozone treatments. The curves were derived as for Figure 10.


REPLACEMENT SERIES, BYG:RPW
CONTROL
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
20:0
15:5
10:10
5:15
0:20
DENSITY COMBINATIONS, BYG:RPW
BYG
RPW
TOTAL


REPLACEMENT SERIES, BYG:RPW
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
20:0
15:5
10:10
5:15
0:20
DENSITY COMBINATIONS, BYG:RPW
BYG
RPW
TOTAL

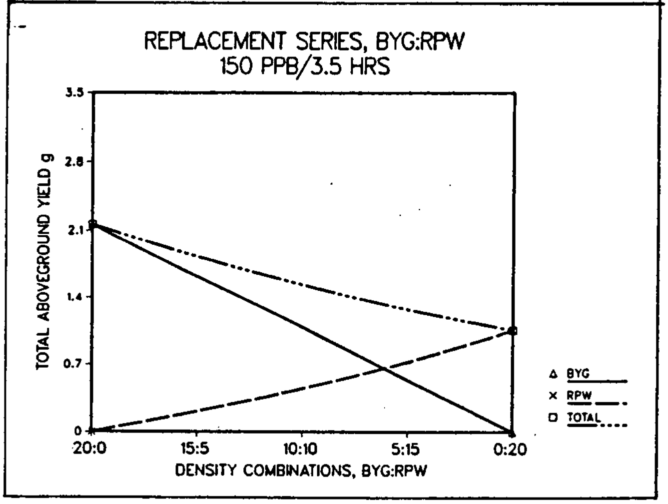

REPLACEMENT SERIES, BYG:RPW
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
20:0
15:5
10:10
5:15
0:20
DENSITY COMBINATIONS, BYG:RPW
BYG
RPW
TOTAL

FIGURE 15: Replacement series diagrams for BYG and RPW at total density of 25 plants/pot for three ozone treatments. The curves were derived as for Figure 10.

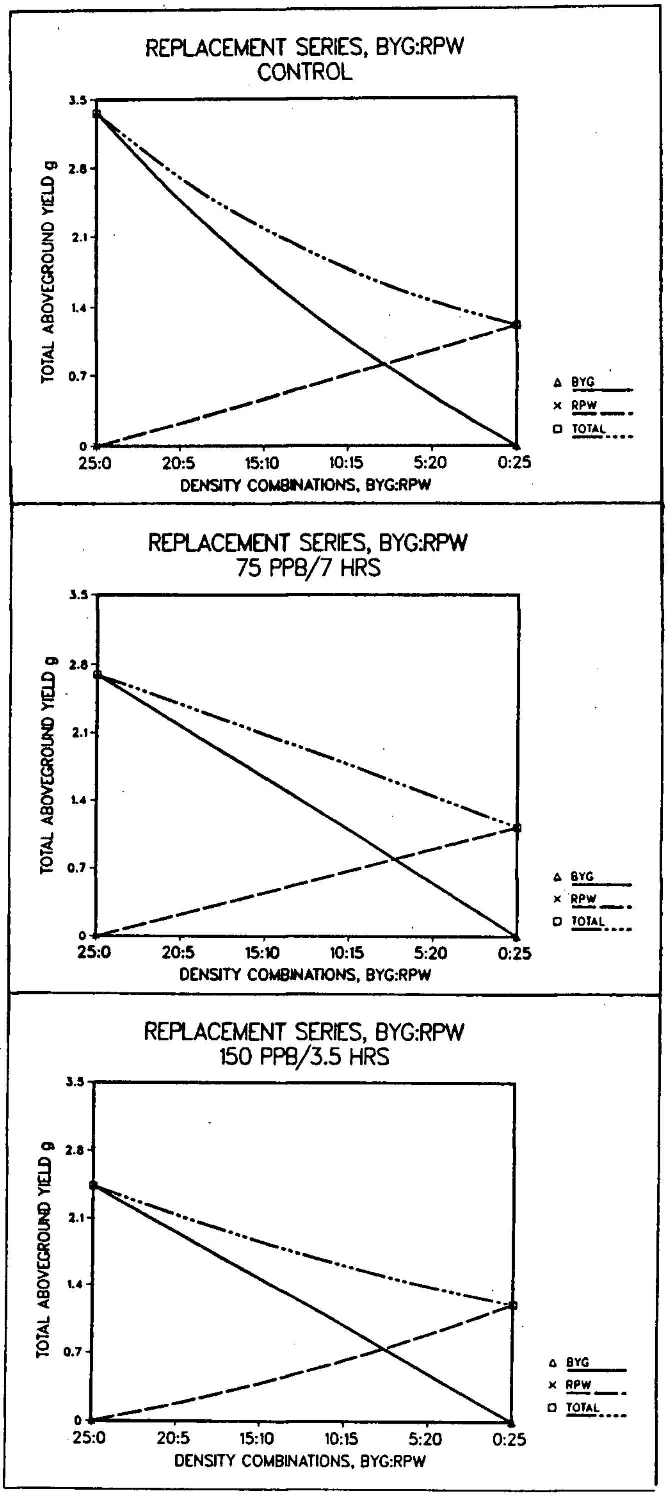

REPLACEMENT SERIES, BYG:RPW
CONTROL
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
25:0
20:5
15:10
10:15
5:20
0:25
DENSITY COMBINATIONS, BYG:RPW
BYG
RPW
TOTAL
REPLACEMENT SERIES, BYG:RPW
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
25:0
20:5
15:10
10:15
5:20
0:25
DENSITY COMBINATIONS, BYG:RPW
BYG
RPW
TOTAL
REPLACEMENT SERIES, BYG:RPW
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
3.5
2.8
2.1
1.4
0.7
0
25:0
20:5
15:10
10:15
5:20
0:25
DENSITY COMBINATIONS, BYG:RPW
BYG
RPW
TOTAL

FIGURE 16: Replacement series diagrams for GFT and RPW at total density of 10 plants/pot for three ozone treatments. The diagrams were constructed as for Figure 8.

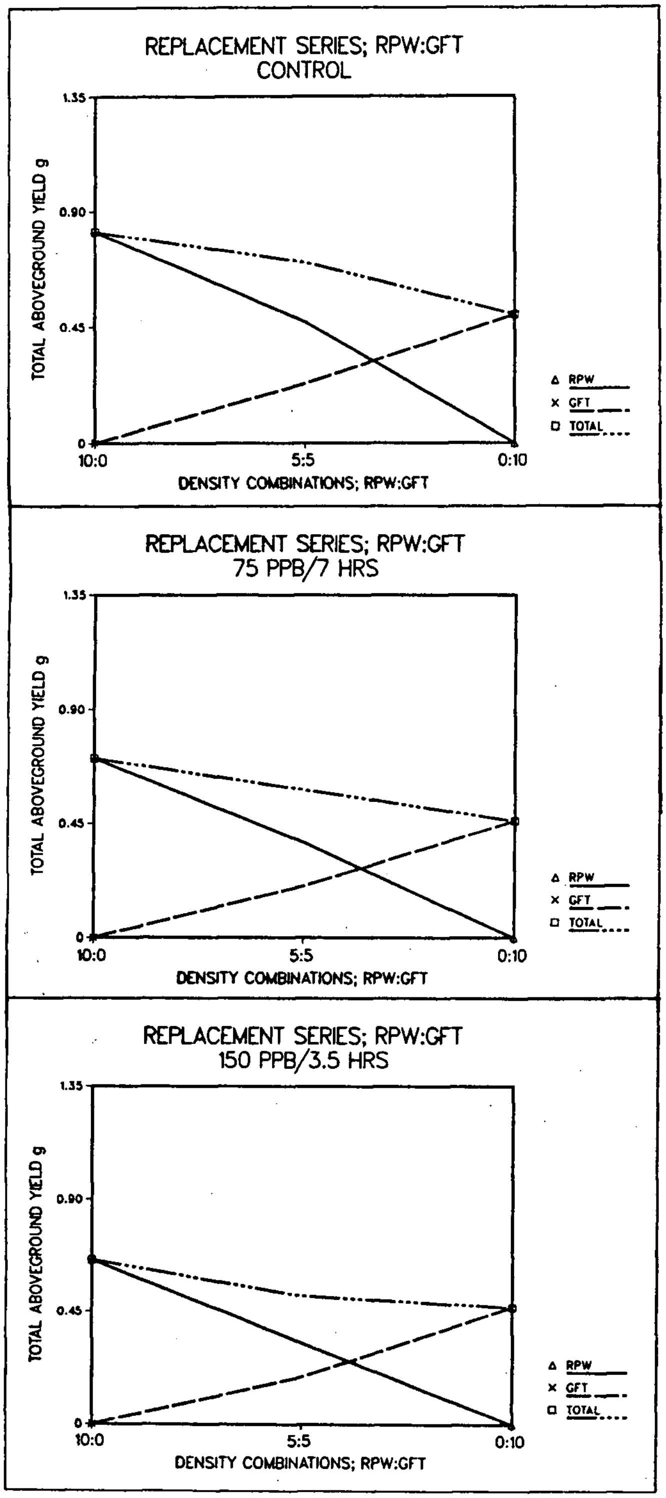

REPLACEMENT SERIES; RPW:GFT
CONTROL
TOTAL ABOVEGROUND YIELD g
1.35
0.90
0.45
0
10:0
5:5
0:10
DENSITY COMBINATIONS; RPW:GFT
RPW
GFT
TOTAL
REPLACEMENT SERIES; RPW:GFT
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
1.35
0.90
0.45
0
10:0
5:5
0:10
DENSITY COMBINATIONS; RPW:GFT
RPW
GFT
TOTAL
REPLACEMENT SERIES; RPW:GFT
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
1.35
0.90
0.45
0
10:0
5:5
0:10
DENSITY COMBINATIONS; RPW:GFT
RPW
GFT
TOTAL

FIGURE 17: Replacement series diagrams for GFT and RPW at total density of 15 plants/pot for three ozone treatments. The diagrams were constructed as for Figure 8.

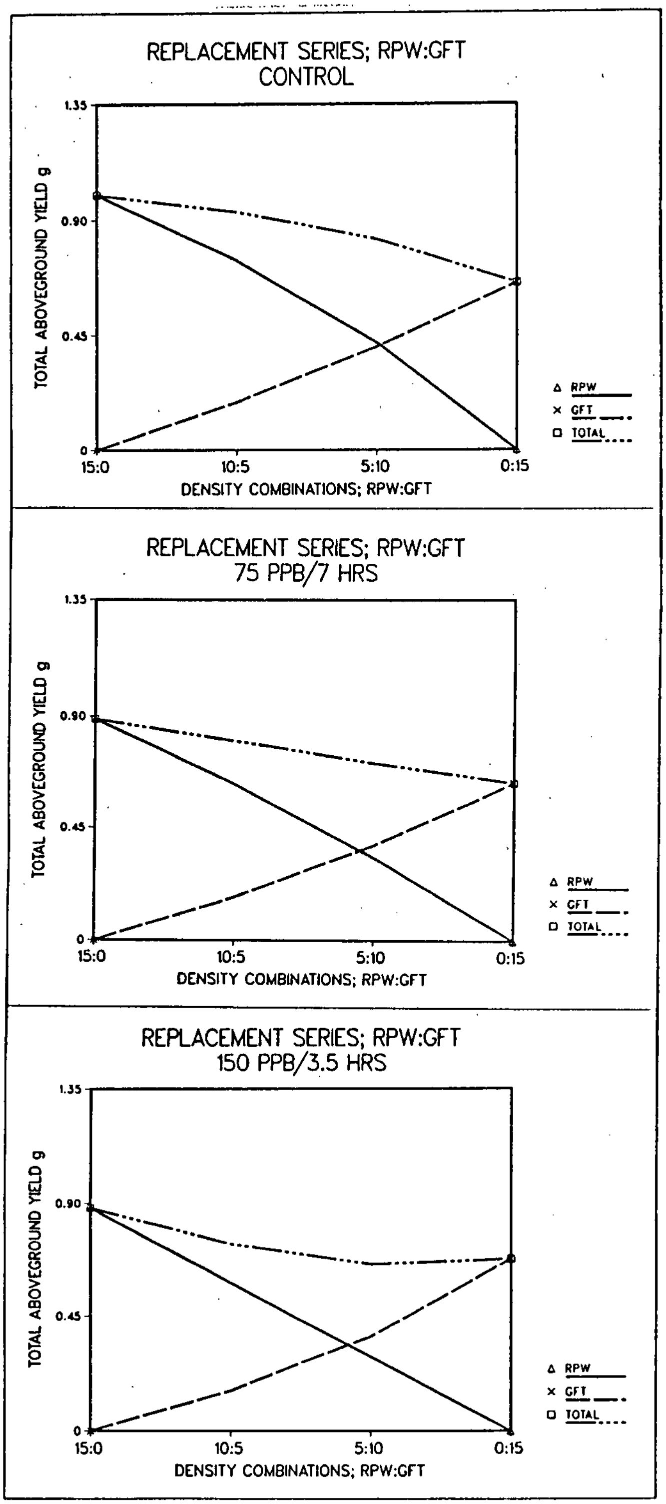

REPLACEMENT SERIES; RPW:GFT
CONTROL
1.35
0.90
0.45
0
TOTAL ABOVEGROUND YIELD g
15:0
10:5
5:10
0:15
DENSITY COMBINATIONS; RPW:GFT
RPW
GFT
TOTAL
REPLACEMENT SERIES; RPW:GFT
75 PPB/7 HRS
1.35
0.90
0.45
0
TOTAL ABOVEGROUND YIELD g
15:0
10:5
5:10
0:15
DENSITY COMBINATIONS; RPW:GFT
RPW
GFT
TOTAL
REPLACEMENT SERIES; RPW:GFT
150 PPB/3.5 HRS
1.35
0.90
0.45
0
TOTAL ABOVEGROUND YIELD g
15:0
10:5
5:10
0:15
DENSITY COMBINATIONS; RPW:GFT
RPW
GFT
TOTAL

FIGURE 18: Replacement series diagrams for GFT and RPW at total density of 20 plants/pot for three ozone treatments. The curves were derived as for Figure 10.

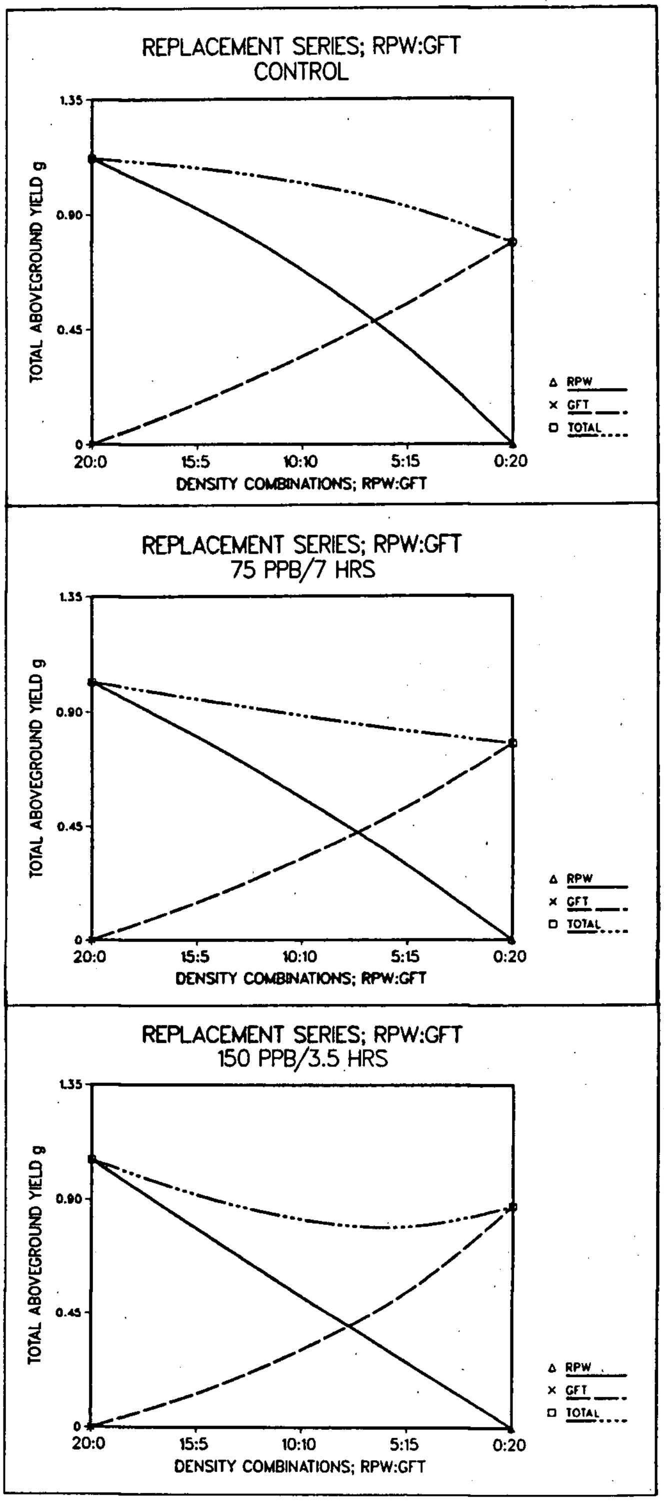
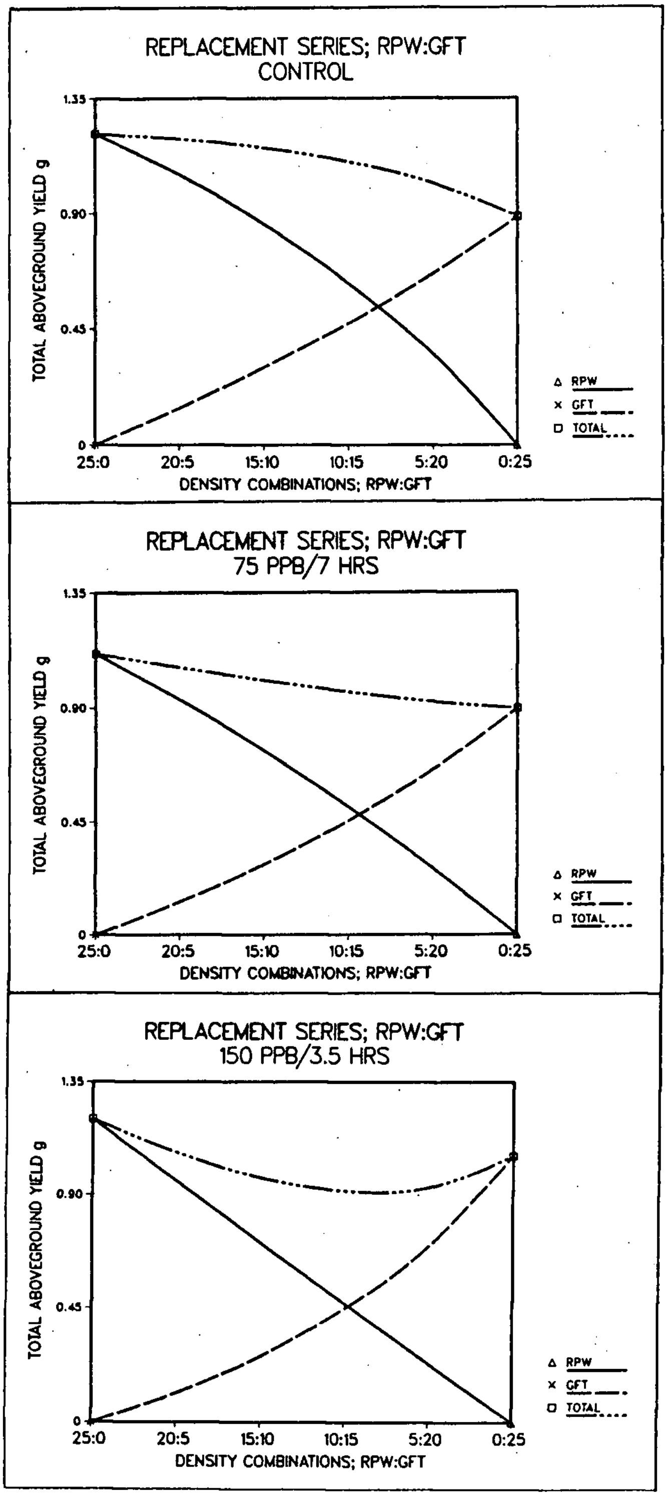

REPLACEMENT SERIES; RPW:GFT
CONTROL
TOTAL ABOVEGROUND YIELD g
1.35
0.90
0.45
0
20:0
15:5
10:10
5:15
0:20
DENSITY COMBINATIONS; RPW:GFT
RPW
GFT
TOTAL
REPLACEMENT SERIES; RPW:GFT
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
1.35
0.90
0.45
0
20:0
15:5
10:10
5:15
0:20
DENSITY COMBINATIONS; RPW:GFT
RPW
GFT
TOTAL
REPLACEMENT SERIES; RPW:GFT
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
1.35
0.90
0.45
0
20:0
15:5
10:10
5:15
0:20
DENSITY COMBINATIONS; RPW:GFT
RPW
GFT
TOTAL

FIGURE 19: Replacement series diagrams for GFT and RPW at total density of 25 plants/pot for three ozone treatments. The curves were derived as for Figure 10.


REPLACEMENT SERIES; RPW:GFT
CONTROL
TOTAL ABOVEGROUND YIELD g
1.35
0.90
0.45
0
25:0
20:5
15:10
10:15
5:20
0:25
DENSITY COMBINATIONS; RPW:GFT
RPW
GFT
TOTAL
REPLACEMENT SERIES; RPW:GFT
75 PPB/7 HRS
TOTAL ABOVEGROUND YIELD g
1.35
0.90
0.45
0
25:0
20:5
15:10
10:15
5:20
0:25
DENSITY COMBINATIONS; RPW:GFT
RPW
GFT
TOTAL
REPLACEMENT SERIES; RPW:GFT
150 PPB/3.5 HRS
TOTAL ABOVEGROUND YIELD g
1.35
0.90
0.45
0
25:0
20:5
15:10
10:15
5:20
0:25
DENSITY COMBINATIONS; RPW:GFT
RPW
GFT
TOTAL

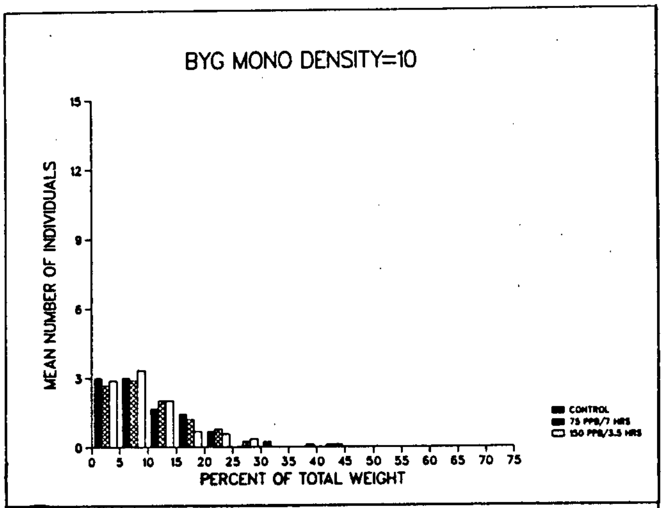
the control ozone treatment displays an over-yielding effect of the mixture on the total yield, the 75 ppb ozone treatment shows an apparently even replacement of the species with the total yield behaving in a linear fashion and the 150 ppb ozone treatment displays an under-yielding situation where the total yield is less than would be expected if the species replaced each other without negative inter-specific competition effects. This implies that with the addition of an increasing concentration of ozone, the inter-specific relation of GFT-RPW changes from one of mutual benefit to one of mutual inhibition. From the data, it is clear that GFT is contributing the most to the under-yielding situation; its yield curves are concave in all total densitites in the 150 ppb treatment.

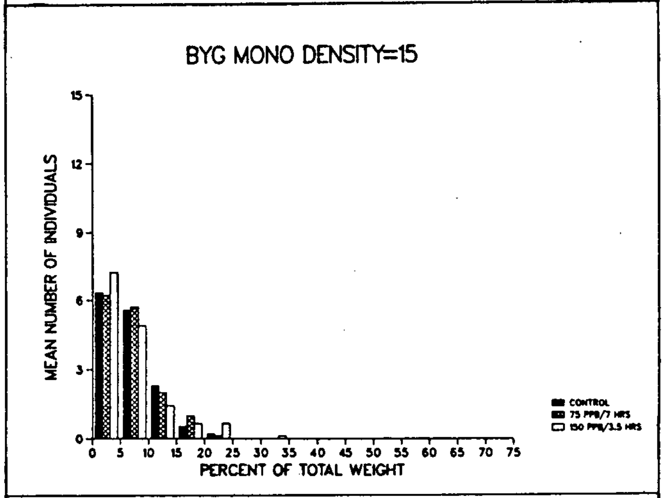
4.5 SIZE FREQUENCY DISTRIBUTIONS

4.5.1 BYG

The frequency diagrams for BYG in monoculture, in mixture with GFT and in mixture with RPW are in Figures 20, 21 and 22 respectively. As the total density per pot increases, the frequency diagrams become more skewed, displaying a hierarchy of plant sizes consisting of many small plants and a few large plants. At any of the three densities of BYG (clearly in the case of the higher densities), the addition of either RPW or GFT causes a more skewed distribution (for example, Figures 20b, 22d and 22e for 15 BYG with 0,5 or 10 RPW). However, comparing the distributions at constant total density, the competitive dominance of BYG is shown by the decreased skewness as the density of the second species increases (for example, compare 20c, for 20 BYG, with Figures 22d (15 BYG + 5 RPW) and Figure 22b (10 BYG + 10 RPW)). No clear effect of ozone is observed in these figures.

FIGURE 20: Size frequency diagrams for BYG in monoculture.


BYG MONO DENSITY=10
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


BYG MONO DENSITY=15
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

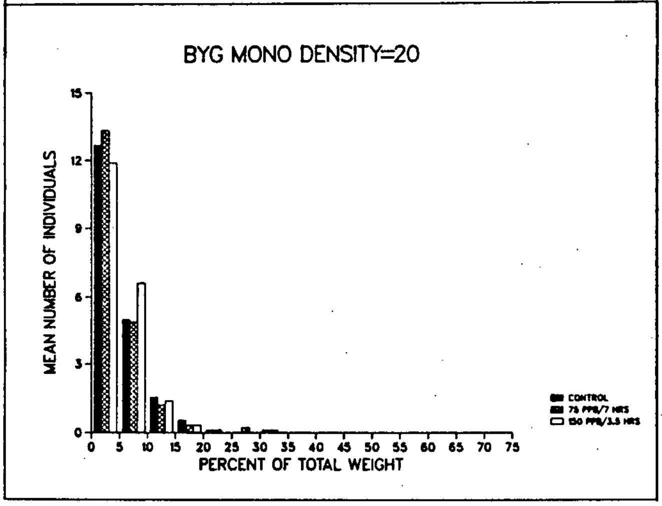
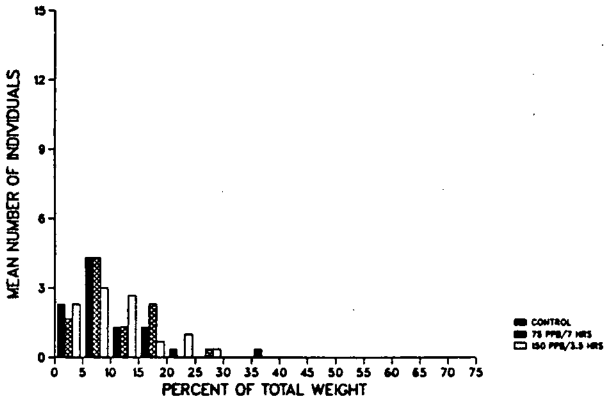
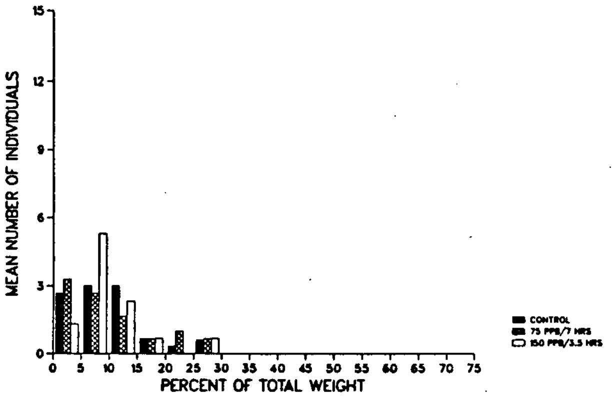

BYG MONO DENSITY=20
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

FIGURE 21: Size frequency diagrams for BYG in mixture with GFT.

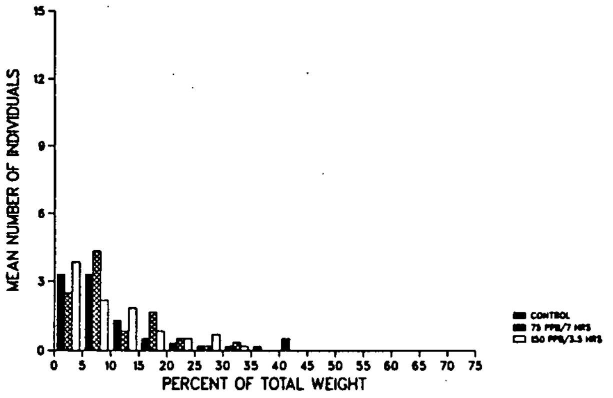
10 BYG IN MIXTURE WITH 5 GFT

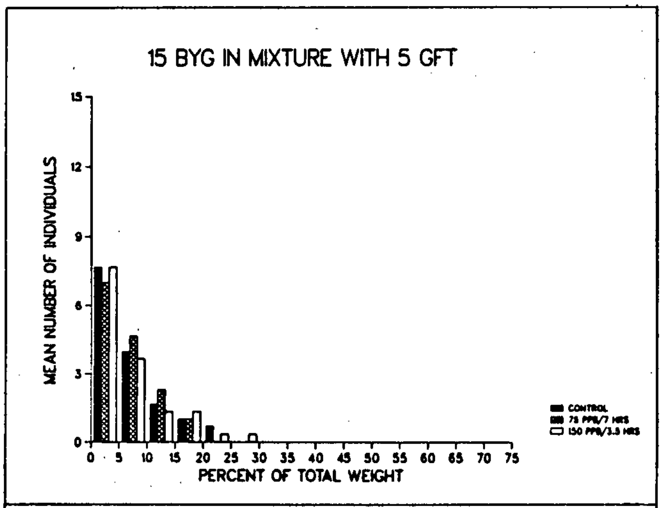


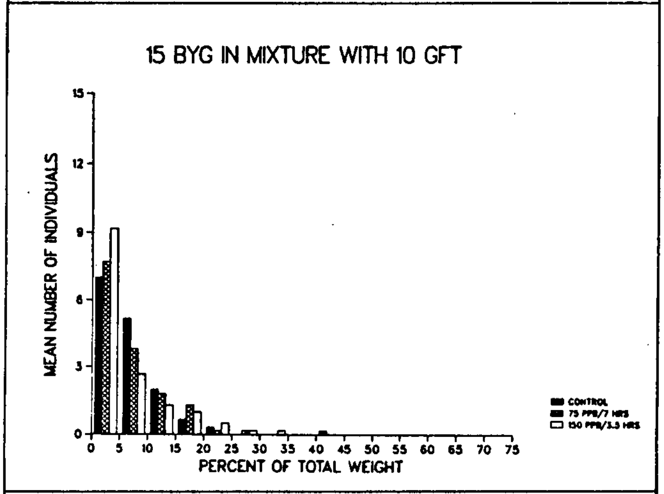
10 BYG IN MIXTURE WITH 10 GFT



10 BYG IN MIXTURE WITH 15 GFT




15 BYG IN MIXTURE WITH 5 GFT
MEAN NUMBER OF INDIVIDUALS
0
3
6
9
12
15
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


15 BYG IN MIXTURE WITH 10 GFT
MEAN NUMBER OF INDIVIDUALS
0
3
6
9
12
15
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

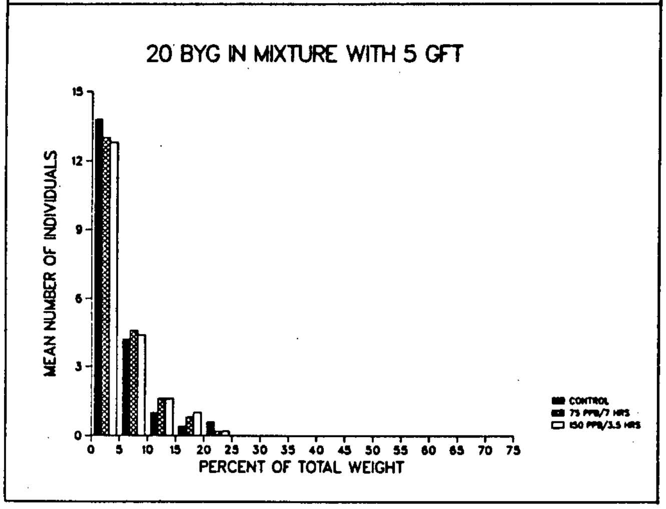
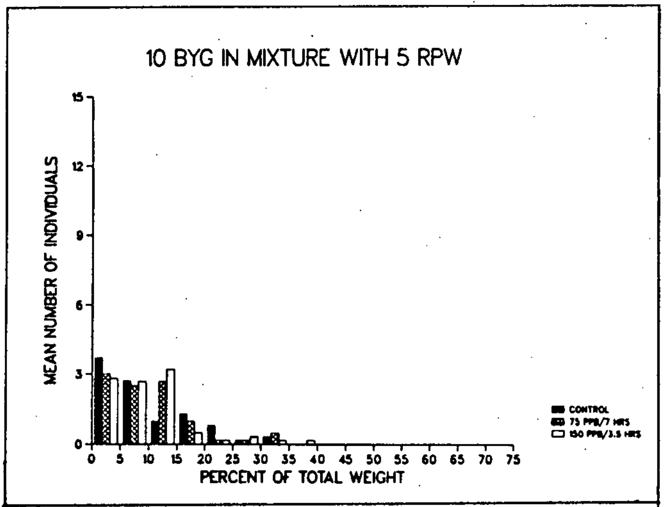
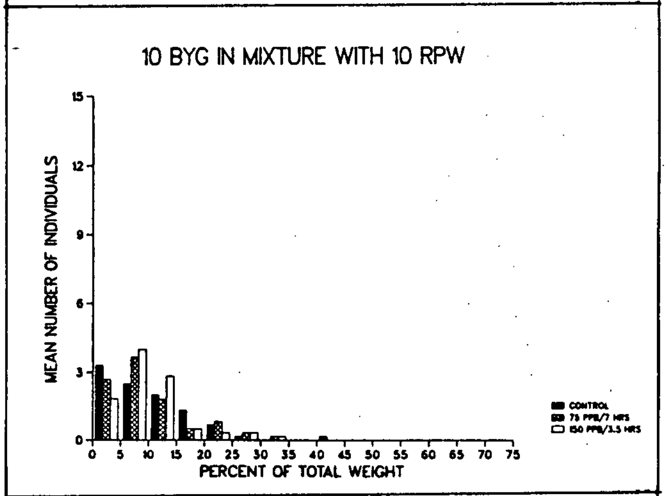
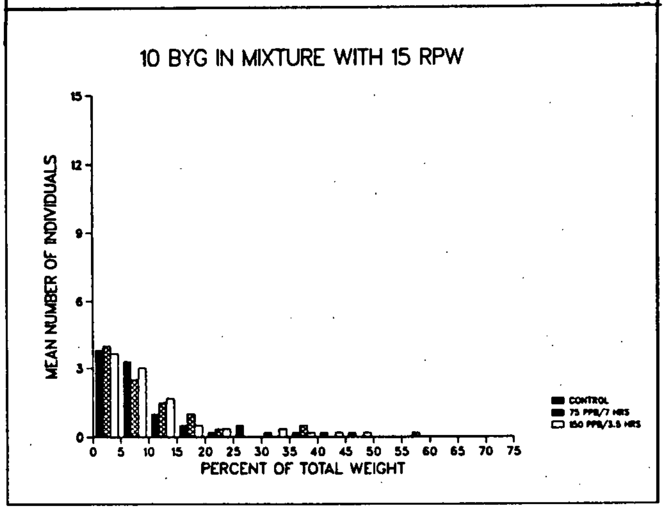
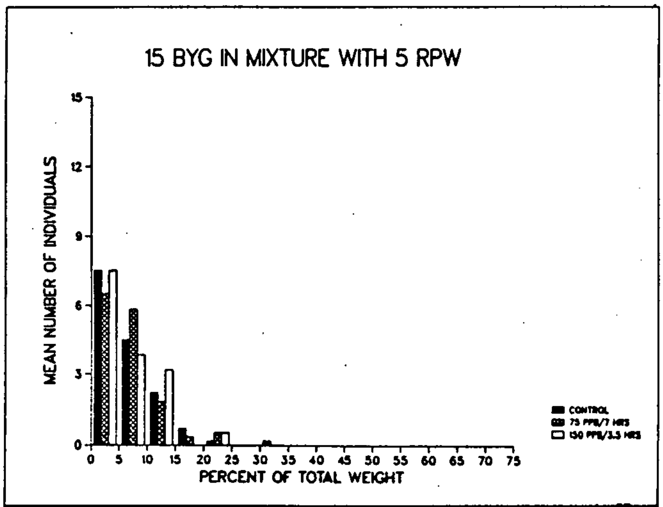

20 BYG IN MIXTURE WITH 5 GFT
MEAN NUMBER OF INDIVIDUALS
0
3
6
9
12
15
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

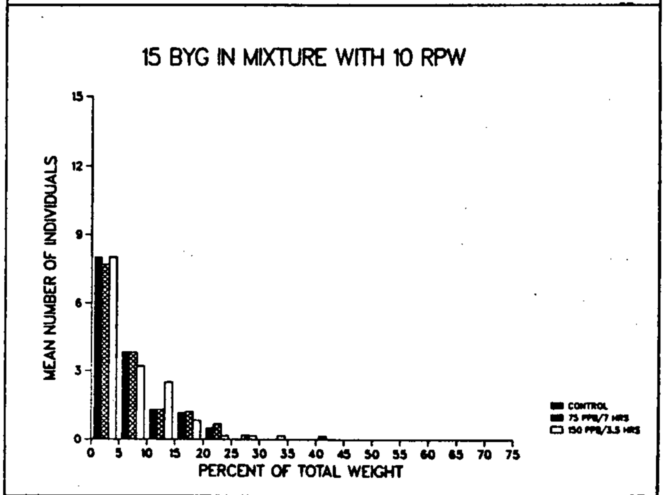
FIGURE 22: Size frequency diagrams for BYG in mixture with RPW.

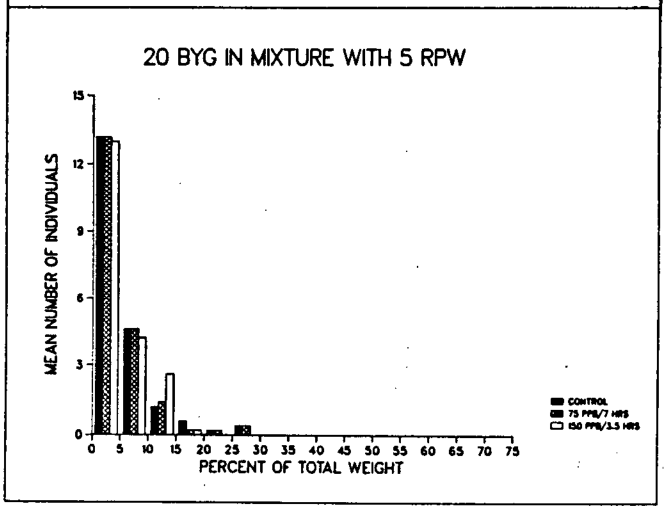

10 BYG IN MIXTURE WITH 5 RPW
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


10 BYG IN MIXTURE WITH 10 RPW
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


10 BYG IN MIXTURE WITH 15 RPW
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


15 BYG IN MIXTURE WITH 5 RPW
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
0 3 6 9 12 15
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


15 BYG IN MIXTURE WITH 10 RPW
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
0 3 6 9 12 15
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


20 BYG IN MIXTURE WITH 5 RPW
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
0 3 6 9 12 15
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

4.5.2 GFT

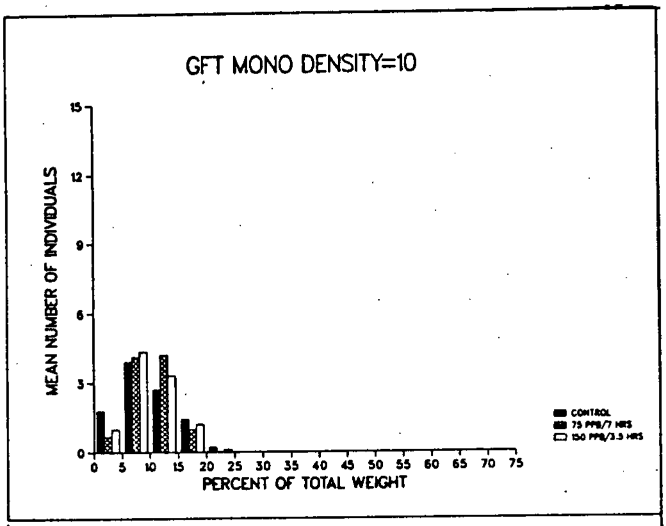
The frequency diagrams for GFT monocultures, in mixture with BYG and in mixture with RPW are shown in Figures 23, 24 and 25, respectively. Unlike BYG, GFT appears much less hierarchical in its size distributions in all densities. There are very few individuals in the higher percentage weight classes in any density treatments. Contrary to Wiener's (1986) suggestion that a suppressed species would display more size inequality in mixture than in monoculture, GFT does not appear to display any size inequality in mixture or in monoculture with the exception of monoculture density 20 under the control treatment. This treatment has quite a large number of small individuals and a few large ones. The same total density mixtures with BYG and RPW have a much more even size distribution. The 75 ppb and 150 ppb ozone treatments do not have this size inequality in monoculture, which suggests that the ozone treatments are providing a similar stress as that of the interspecific competition of BYG and RPW. there are no apparent ozone effects on the size distribution of GFT.

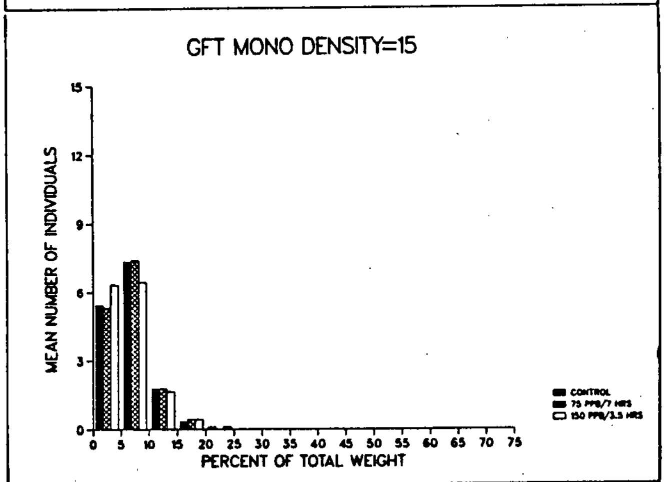
4.5.3 RPW

The frequency diagrams for RPW in monoculture, in mixture with BYG and in mixture with GFT are shown in Figures 26, 27 and 28, respectively. At all densities and in all ozone treatments, RPW displays more size inequality than either BYG or GFT. There are quite a number of individuals in the large percentage weight classes, even one plant in the 20:5 density treatment with GFT under the control ozone treatment which fell in the 70-75% weight class.

RPW has an equally skewed distribution both in monoculture and in the mixtures, which would suggest, by the interpretation of the dominance-suppression model of Weiner (1986) that it is neither suppressed nor competitively superior. However, size differences can also be due to inherent genetic variation, and it is possible that for a population of RPW, its genetic makeup would naturally produce a hierarchical distribution.

FIGURE 23: Size frequency diagrams for GFT in monoculture.


GFT MONO DENSITY=10
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


GFT MONO DENSITY=15
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

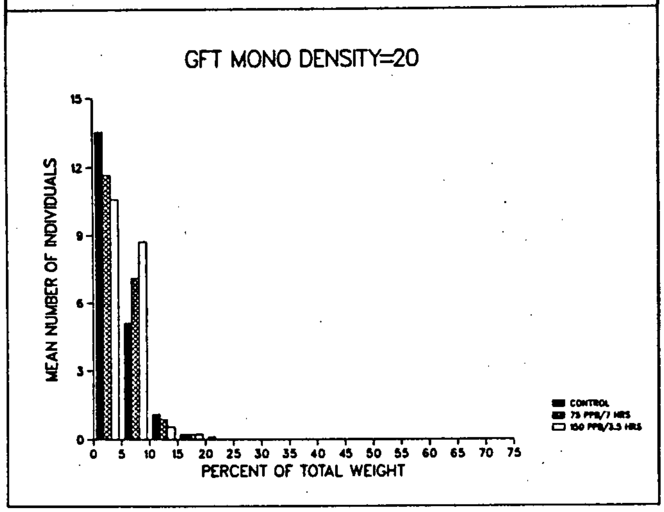
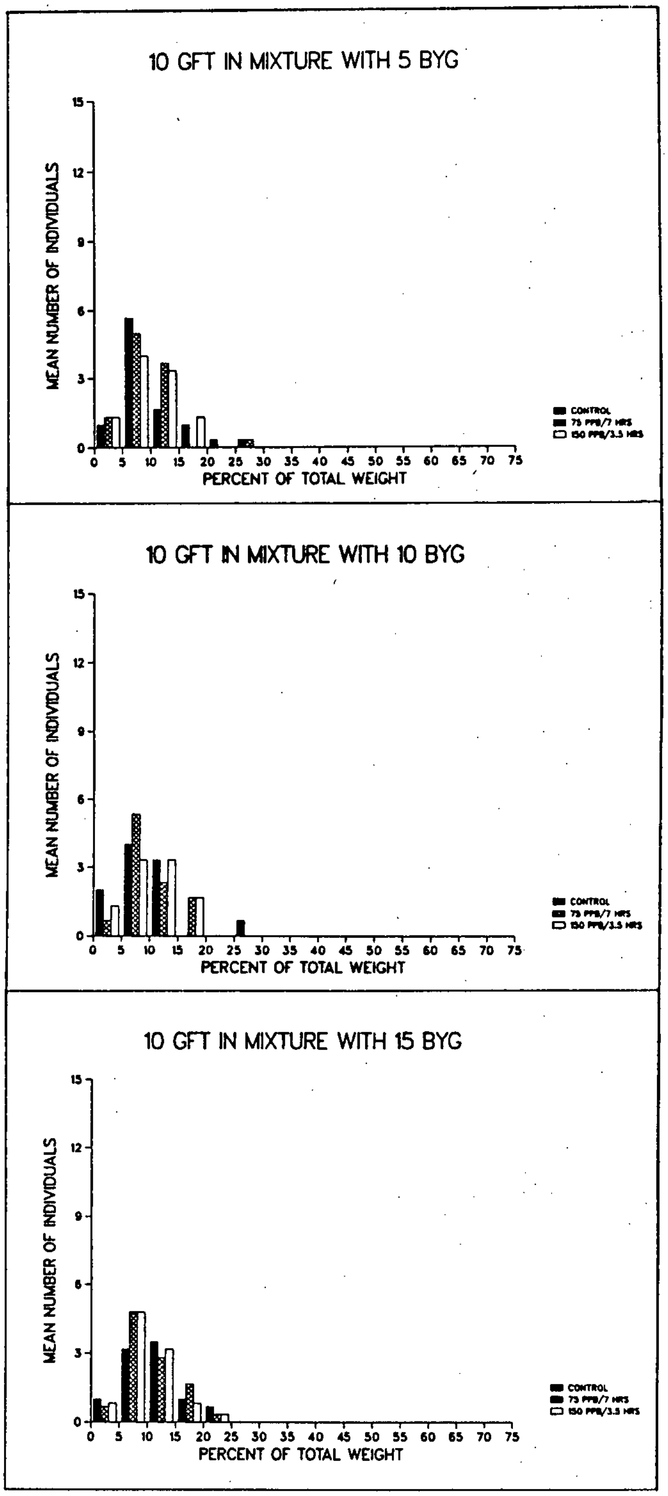

GFT MONO DENSITY=20
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

FIGURE 24: Size frequency diagrams for GFT in mixture with BYG.


10 GFT IN MIXTURE WITH 5 BYG
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
0 3 6 9 12 15
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS
10 GFT IN MIXTURE WITH 10 BYG
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS
10 GFT IN MIXTURE WITH 15 BYG
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

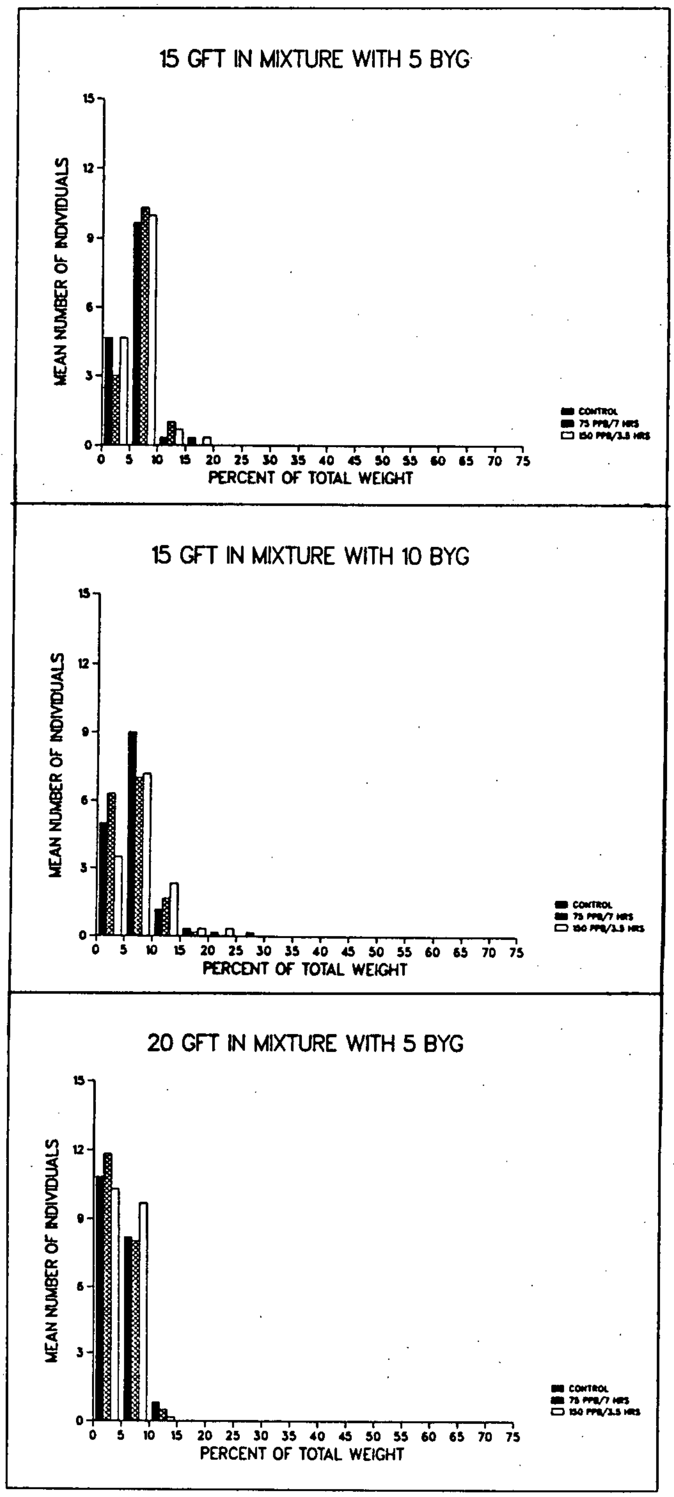
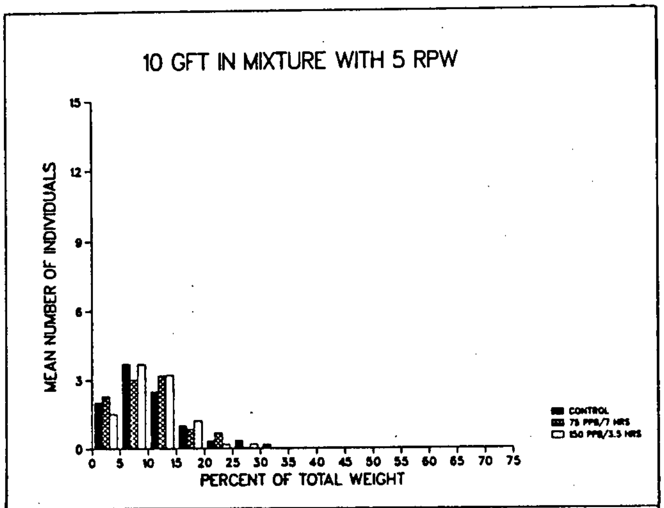
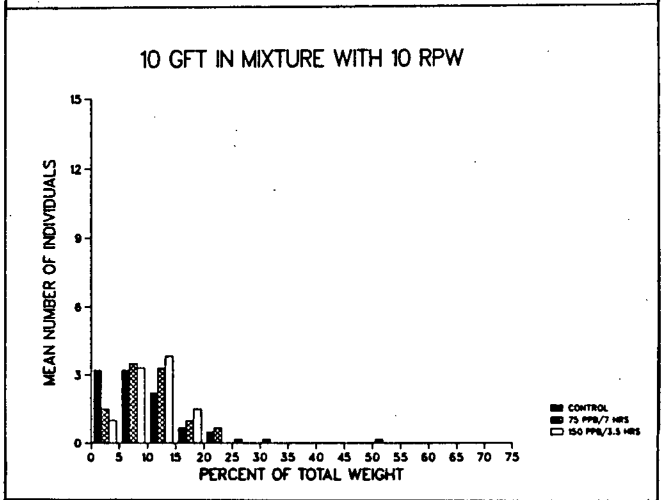
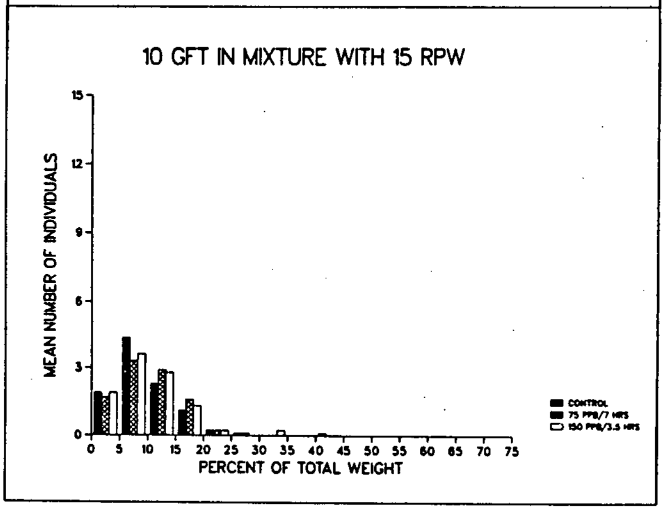
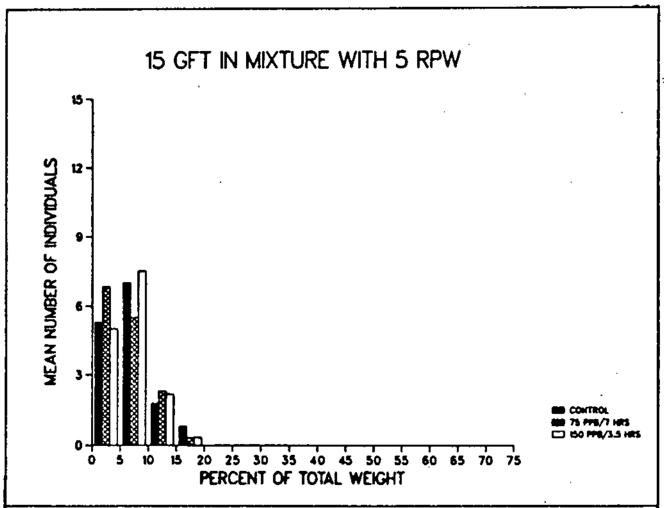

15 GFT IN MIXTURE WITH 5 BYG
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS
15 GFT IN MIXTURE WITH 10 BYG
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
20 GFT IN MIXTURE WITH 5 BYG
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT

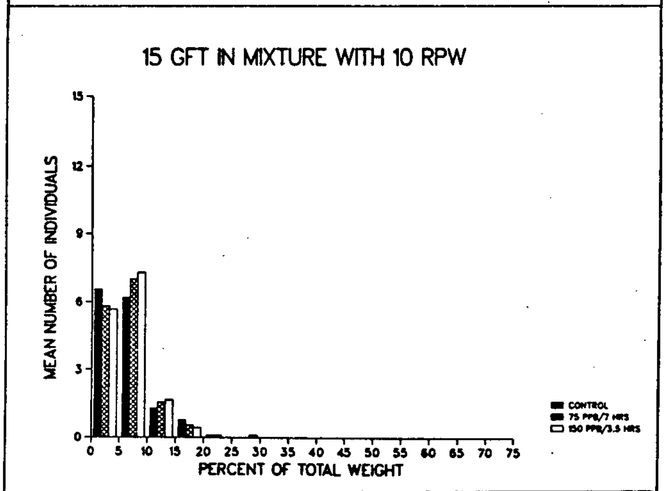
FIGURE 25: Size frequency diagrams for GFT in mixture with RPW.


10 GFT IN MIXTURE WITH 5 RPW
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
0
3
6
9
12
15
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


10 GFT IN MIXTURE WITH 10 RPW
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
0
3
6
9
12
15
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


10 GFT IN MIXTURE WITH 15 RPW
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
0
3
6
9
12
15
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


15 GFT IN MIXTURE WITH 5 RPW
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


15 GFT IN MIXTURE WITH 10 RPW
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

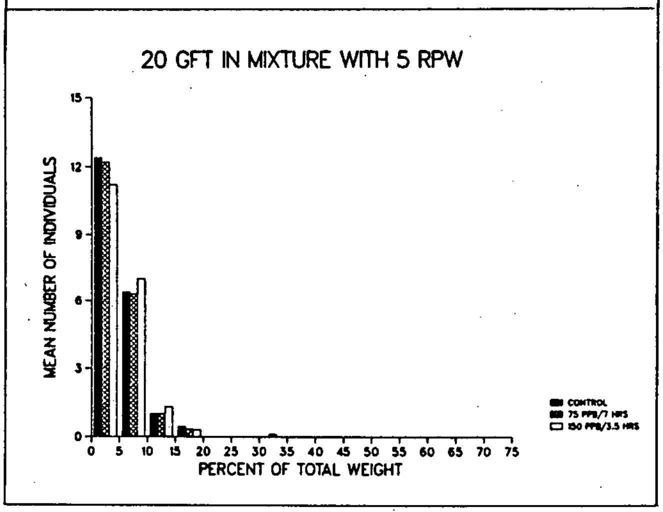
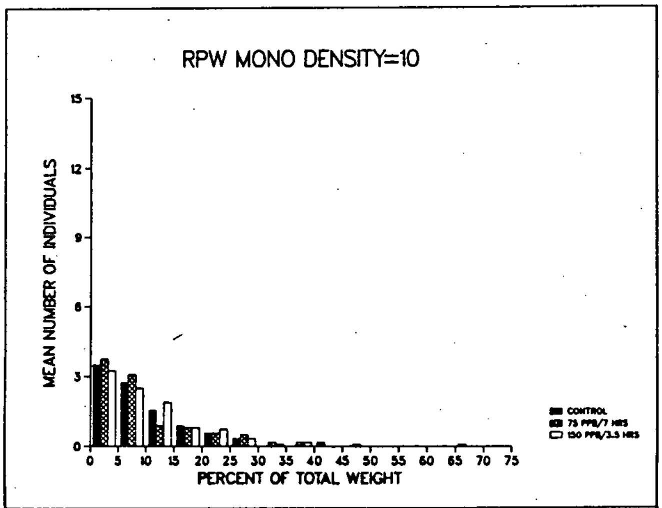
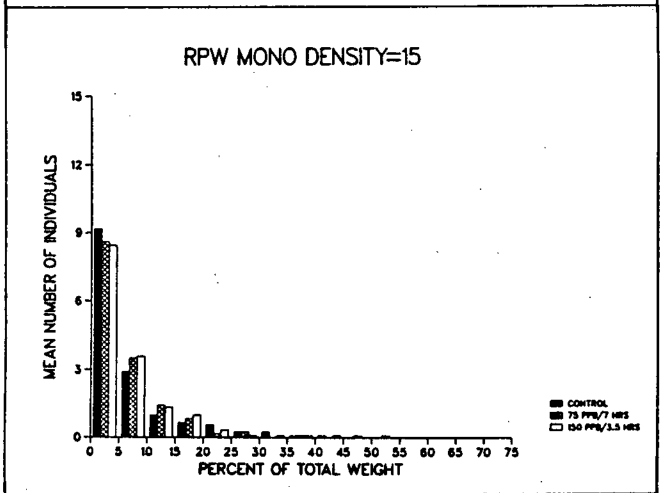

20 GFT IN MIXTURE WITH 5 RPW
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

FIGURE 26: Size frequency diagrams for RPW in monoculture.


RPW MONO DENSITY=10
MEAN NUMBER OF INDIVIDUALS
0
3
6
9
12
15
PERCENT OF TOTAL WEIGHT
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


RPW MONO DENSITY=15
MEAN NUMBER OF INDIVIDUALS
0
3
6
9
12
15
PERCENT OF TOTAL WEIGHT
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

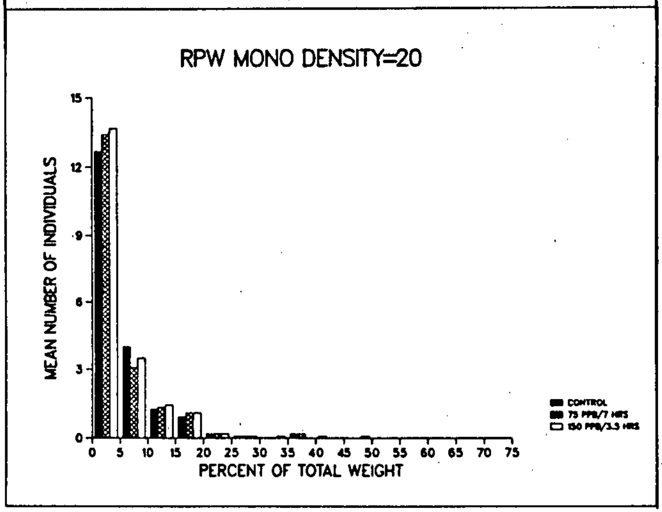
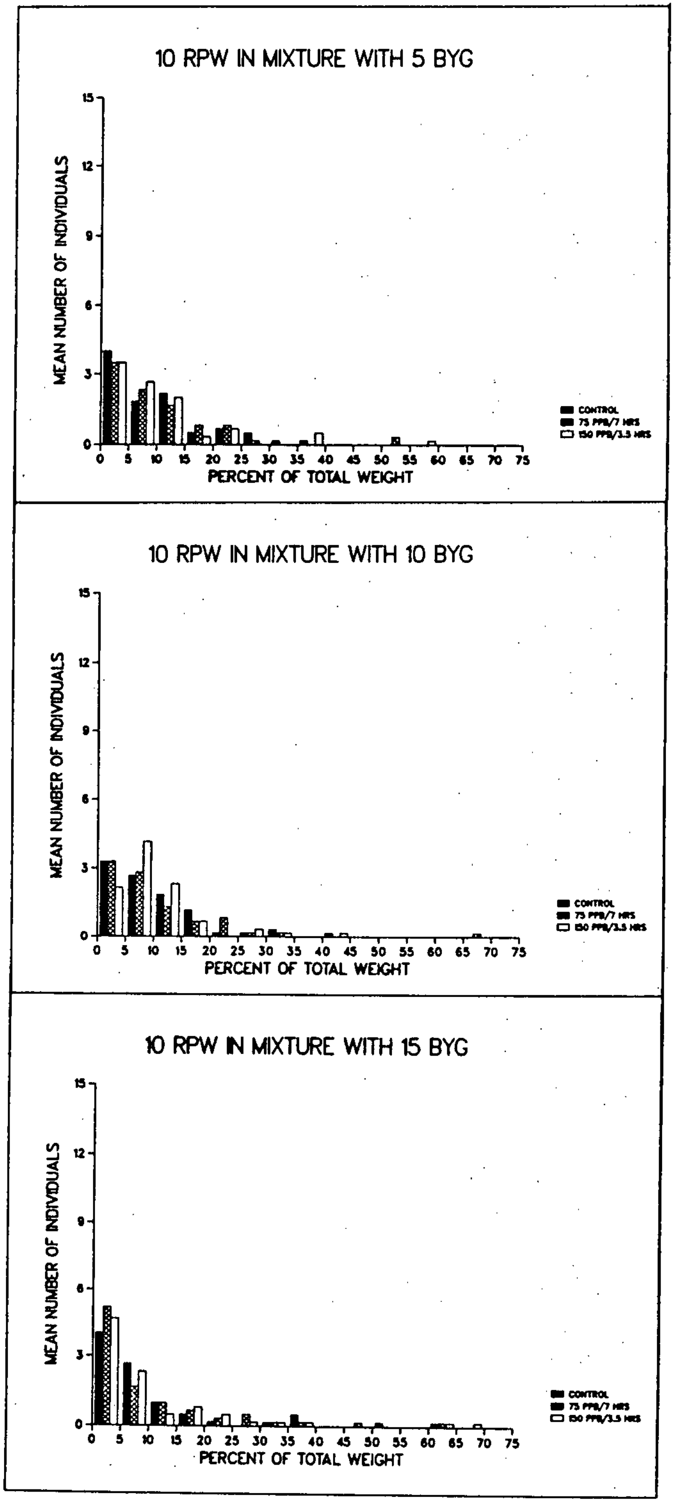

RPW MONO DENSITY=20
MEAN NUMBER OF INDIVIDUALS
0
3
6
9
12
15
PERCENT OF TOTAL WEIGHT
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

FIGURE 27: Size frequency diagrams for RPW in mixture with BYG.


10 RPW IN MIXTURE WITH 5 BYG
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS
10 RPW IN MIXTURE WITH 10 BYG
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS
10 RPW IN MIXTURE WITH 15 BYG
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

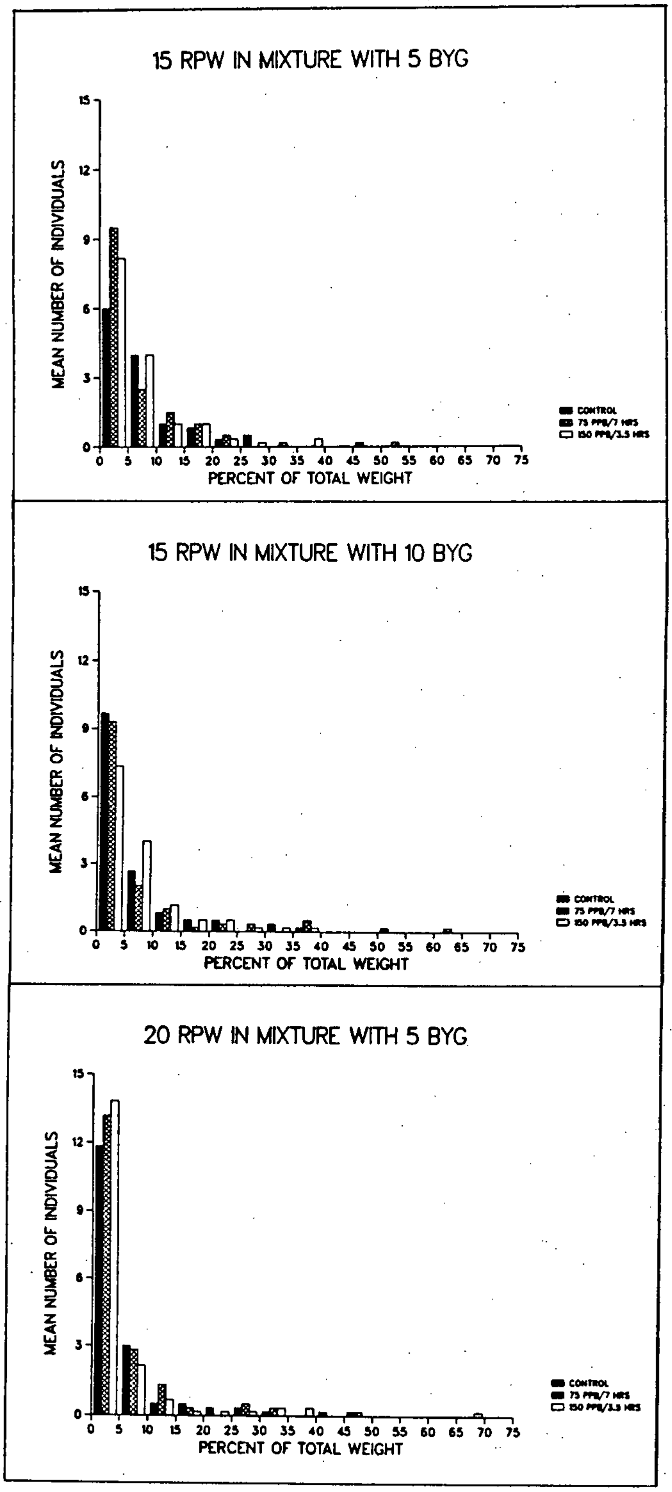
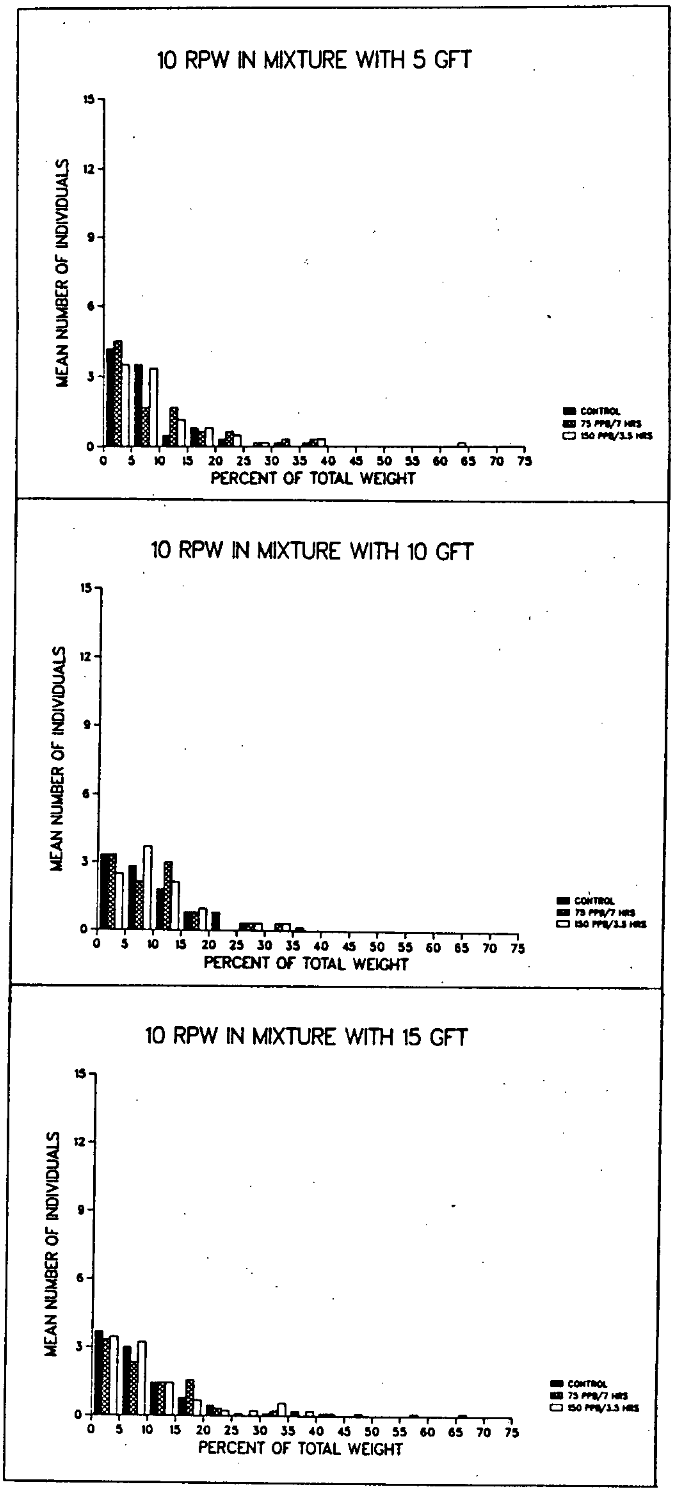
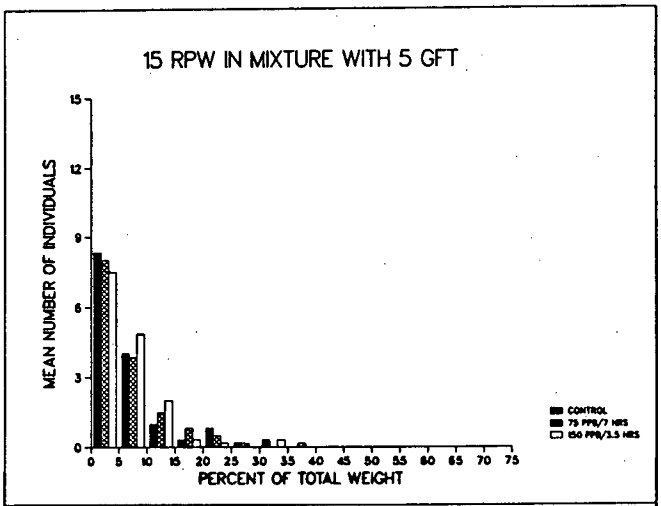
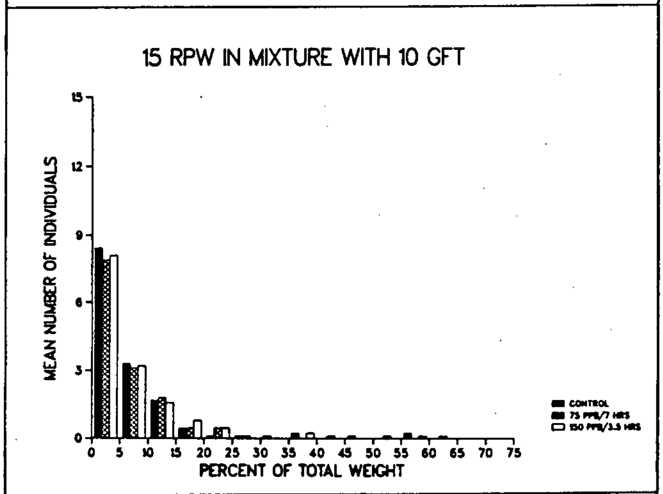
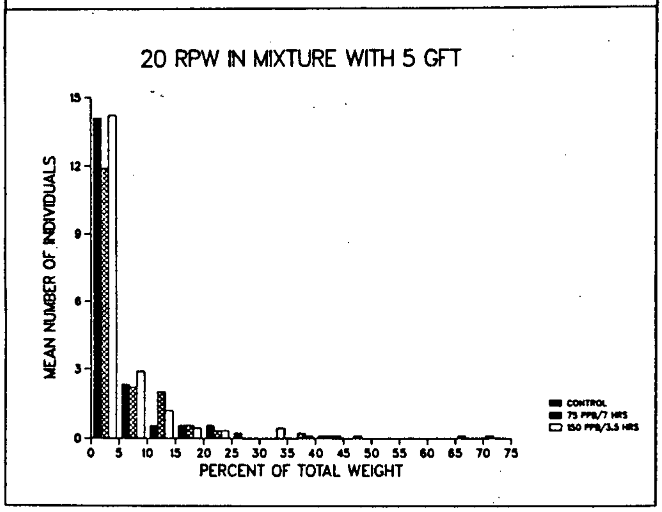

15 RPW IN MIXTURE WITH 5 BYG
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS
15 RPW IN MIXTURE WITH 10 BYG
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS
20 RPW IN MIXTURE WITH 5 BYG
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

FIGURE 28: Size frequency diagrams for RPW in mixture with GFT.


10 RPW IN MIXTURE WITH 5 GFT
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS
10 RPW IN MIXTURE WITH 10 GFT
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS
10 RPW IN MIXTURE WITH 15 GFT
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


15 RPW IN MIXTURE WITH 5 GFT
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
0 3 6 9 12 15
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


15 RPW IN MIXTURE WITH 10 GFT
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
0 3 6 9 12 15
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS


20 RPW IN MIXTURE WITH 5 GFT
MEAN NUMBER OF INDIVIDUALS
PERCENT OF TOTAL WEIGHT
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
0 3 6 9 12 15
CONTROL
75 PPB/7 HRS
150 PPB/3.5 HRS

5. DISCUSSION

One of the first points which is apparent in reviewing the results of the various experiments is the large amount of inherent variation. The analyses of variance consistently show significant block effects; i.e. the experiments differ significantly. The method of using experimental chambers as blocks was recommended by Hammer and Urquhart (1979) in order to remove the unwanted variation due to a lack of uniformity of plant responses to controlled environments. Many studies have shown that although controlled environment chambers supposedly offer a uniform environment to plants over treatments, there is a lack of uniformity among plants grown within a chamber, among plants in different chambers and among plants grown in the same chamber at different times (Hammer and Urquhart, 1979). It has been suggested that the between trials (runs over time) component of variance is more important than the between chamber variation. Differences in environmental conditions have been measured within and between chambers (Hammer and Langhans, 1972; Tibbitts *et al.*, 1976) and they may be responsible for much of the unwanted variability and lack of reproducibility in plant growth within and between chambers (Hammer and Urquhart,1979). Vibrations and handling of plants (Mitchell *et al.*, 1975) and contaminants (such as mercury, freon and volatile paint components) which are ubiquitous in chambers (Tibbetts *et al.*, 1977) may also contribute unwanted sources of variation.

Despite the large amount of variation in plant growth over the treatments and between experiments, the extremely conservative ANOVA test (Hammer and Urquhart, 1979) revealed many significant treatment effects after the variation due to blocks was removed.

In order to get a more general picture of the treatment (ozone and competition) effects over the range of experimental conditions experienced by the plants, the experiments were pooled for the regression analyses. There was no *a priori* reason to believe that the experiments would not be combinable. Specific analyses of each experiment for treatment effects would produce results which would be difficult to interpret because the causal differences between the experiments could not be quantified, since the environment was, as far as was possible, controlled. The differences between the experiments are abundantly clear in the regression analyses in that the coefficients of determination (R^2) are, for the most part, low. However, despite these low R^2s, many of the Multiple Linear Regression (MLR) and Sequential Simple Regression (SSR) models were significant. In essence, the trends discussed here are more conservatively significant and general in their application than they would be if the block effects were not significant.

Three differing types of competition analysis were used in this thesis; the multiple linear regression (MLR) analysis of Spitters (1983), the sequential simple regression (SSR) analyses of Jolliffe (personal communication) and the analysis of Thomas (1970) based on the replacement series approach to defining competitive interactions, which, when interpreted, describes which species are "crowding" for the same space at each replacement series density. The MLR and the SSR generated competitive indices and models which showed similar trends (Tables 10, 12, 14 and 15), with minor differences in magnitude. It is evident that the SSR model explains proportionally more of the variation than does the MLR (Tables 10 and 14). The interpretation of the regression coefficients in the SSR is much simpler and elegant; the monoculture data are entirely compartmentalized and do not contribute to the mixture coefficients, as is the case in the MLR analysis. This makes the differentiation between intra- and inter-specific competitive effects much clearer.

Three measures of niche differentiation were generated in this study; from the MLR, the SSR and from the replacement series analyses. A comparison of the results from the three analyses can be made (Table 19). There are discrepancies in the results. For example, the MLR suggests that GFT and RPW in the control treatment are competing for the same resources, whereas the SSR suggests there is niche differentiation. The replacement series model has GFT and RPW under the same control treatment competing for the same "space" at total density 10 and 15 but for different "space" at total density

TABLE 19: Summary of interpretations of niche differentiation from regression analyses (MLR and SSR) and replacement series. Same refers to species competing for the same space/resources; different refers to species not competing for the same space/resources.

	Species Mixture Total Density	MLR	SSR	Replacement Model
0	BYG:GFT	same(2)	same(3)	
	10			same
	15			same
	20			different
	BYG:RPW	same(2)	same(3)	
	10			same
	15			same
	20			same
	GFT:RPW	same(2)	different(4)	
	10			same
	15			same
	20			different
75 ppb/	BYG:GFT	different(3)	different(2)	
7 hrs	10			same
	15			same
	20			same
	BYG:RPW	same(3)	different(4)	
	10			same
	15			different
	20			same
	GFT:RPW	same(3)	same(3)	
	10			same
	15			different
	20			same
150 ppb/	BYG:GFT	same(1)	same(2)	
3.5 hrs	10			same
	15			same
	20			different
	BYG:RPW	same(2)	same(4)	
	10			same
	15			same
	20			same
	GFT:RPW	same(2)	same(3)	
	10			same
	15			different
	20			same

( ) NUMBER OF SIGNIFICANT REGRESSION COEFFICIENTS MAXIMUM IS (4)

20. The niche differentiation coefficients calculated from the MLR and SSR are based onpartial regression coefficients and regression coefficients, respectively. The statistical value of these indices rests solely on the significance of the coefficients which were used. Because the interpretation of the SSR coefficients is much more biologically meaningful, and because more of the coefficients were significant in the SSR analysis, the niche differentiation indices from those analyses are more representative of the actual data. In the case of GFT and RPW in the control treatment, the SSR index is supported by four significant coefficients, while the MLR has only two. As well, the three-parameter replacement series model uses a much smaller database than that of the SSR. Each replacement series for each species mixture is analyzed separately, consequently its interpretation depends on the total density, pure stand and mixture components chosen (Connolly, 1986). In contrast, the SSR looks first at all the monoculture data and then at all the mixture data for one species in the mixture. Given this, it may be suggested that the analyses represent different ways of looking at the data; if a more general picture is preferred, the SSR should be used. Hence, the interpretation of this example would suggest that GFT and RPW in the control treatment appear to be competing for different resources in the general sense; in a more specific interpretation, this niche differentiation effect is evident only in the total density of 20.

Taking into account the more general nature of the MLR and SSR analyses as compared to the more specific nature of the replacement series analyses, and the number of significant coefficients which go into each index of the MLR and SSR, every species combination can be subjected to an interpretation analogous to that used for the GFT/RPW control treatment, except for BYG/GFT at 75 ppb where both the MLR and the SSR suggest that BYG and GFT are competing for different resources. However, the replacement series model indicates that they are competing for the same space in all total densities. A possible explanation for this difference of interpretation may lie in the enhancing effect of the 75 ppb ozone treatment on BYG which complicates the straight interpretation of the indices.

Overall, the competitive abilities of the three species agree with those found in competition experiments carried out in the field (Minjas, 1982). BYG is the strongest competitor and GFT is the least competitive of the three species. The effects of inter-specific competition of both RPW and BYG on GFT yield is very significant under all three ozone treatments (Table 14). GFT appears to experience some intra-specific competition in the control, but not in either of the other two ozone treatments. As tested by the ANOVAs, GFT only experiences a weakly significant inversely linear effect of ozone on vegetative dry weight per pot when in combination with RPW at low density (Table 6).

One of the major objectives of this work was to determine if the presence of an air pollutant would change a plant's ability to compete. The data presented here indicate that although the nature and magnitude of the effect appears to be species-specific, there are differences between the ways the species studied competed in the presence of ozone as compared to the filtered-air control. The competitive abilities of RPW over GFT, GFT over RPW and GFT over BYG all decreased with increasing ozone concentration (Table 15). In contrast, BYG's competitive ability over both GFT and RPW was higher in the ozone-added treatments than in the control (Table 15).

There were also differences between ozone treatments in the way plants of the same species related to each other. BYG experienced no significant intra-specific competition in the filtered air control, in contrast to both ozone-added treatments (Table 14). On the other hand, there was a significant effect of intra-specific competition on GFT yield in the control, but no significant intra-specific effects in the 75 and 150 ppb treatments(Table 14).

The effect of ozone on BYG was extremely interesting, in that, in the prolonged low concentration of ozone, 75 ppb, BYG yield was greater than in the charcoal-filtered air control (Tables 3 and 4, and Appendix 1). The significant effect of intra-specific competition under the 75 ppb ozone treatment, but not under the control (Table 14), could be due to its enhanced yield under this treatment. However this would not account for the effect on intra-specific competition under 150 ppb ozone. Apparently the physiology of BYG is such that its growth is enhanced by a low level of ozone as compared to charcoal filtered-air under the experimental conditions employed in these studies. Growth enhancements caused by low levels of air pollutants have been reported in the literature, and Bennett *et al.* (1974) pointed out that this situation casts doubt on whether or not a filtered-air treatment is an appropriate control. A control treatment should provide an appropriate baseline to which one can compare elevated levels of the treatment. Considering the widespread nature of low-level ambient ozone concentrations (Fowler and Cape, 1982), Bennett *et al.* (1974) suggested that it would be more appropriate to use a concentration more representative of the real background situation as a control level. Hence, the BYG plants used in this study may have adapted to a low level of ozone. In that case, supplying those plants with filtered air would put them at a disadvantage.

BYG yield also appeared to be enhanced by the presence of GFT in mixtures (Table 14, Figure 2) under the 0 and 150 ppb ozone treatments. Competition studies on these two species carried out in the field did not show this type of enhancement (Minjas, 1982). The enhancing effect of GFT's presence on BYG yield may not have showed up in the 75 ppb ozone treatment because of the added enhancement of the BYG yield by the ozone treatment alone. The air velocity dynamics and light quality characteristics of a controlled-environment chamber are very different from the situation in the field. In most chambers, as in those used in the present studies, the air is circulated up through the canopy. This is in contrast to the field situation where wind direction and velocity may change very rapidly, but the transport of a pollutant is usually downward through the canopy. Because the enhancement was not evident in the BYG monocultures treated in the same chambers simultaneously with the BYG/GFT mixtures with 0 or 150 ppb ozone, the effect appears to be a localized one. One possible explanation of this enhancement by

GFT is allelopathic, i.e. the shorter GFT plants released some volatile compound beneficial to BYG which was circulated up towards the taller BYG plants by the air flow of the chamber system. Alternatively, the GFT plants may have released a soluble compound through their root systems which was disseminated through the soil.

RPW's competitive ability over GFT declined as the ozone concentration was increased (Table 15). RPW, of the three species studied, appears to be the most severely affected by ozone. There were inversely linear ozone effects on RPW vegetative yield both on a per plant and a per pot basis in monocultures and in mixture with BYG at high densities, and on a per pot basis in mixture with GFT at low densities (Tables 7 and 8). There was a significant inversely linear effect on the number of leaves per RPW plant in mixture with BYG at high densities. There was also a very significant inversely linear ozone effect on RPW root weight per pot in monocultures (Table 9). The weakly significant ozone effects on root weight per pot of the RPW/BYG and RPW/GFT mixtures at low densities is probably due to the effect on the RPW root component. However, there was no way to test this because the root masses could not be separated on a per species basis. The results of the replacement series of the RPW/GFT mixtures depicted in Figures 16-19 also could be explained by this extremely negative effect of ozone on RPW yield variables. The yield totals of RPW/GFT change from an over-yielding situation in the no-ozone control to an under-yielding situation under the highest ozone treatment. The significant interaction of the ozone and competition treatments on RPW/GFT total dry root weight/pot (Table 9) supports the replacement series trend.

RPW experiences significant intra-specific competition under all three ozone treatments (Table 14), but the effect is less significant in the 150 ppb treatment than in the other two. This could possibly be due to the significant effects of ozone on RPW vegetative dry weight, number of leaves and root mass, which would cause RPW to be less vigorous in the high ozone treatment.

In order to better explain the "unwanted" plant variation evident from the ANOVA and regression analyses, size frequency distributions were examined. Although the analysis of the size frequency distributions did not reveal any ozone effects, definite population features of the three species were seen. RPW had a very uneven size distribution over all density and ozone treatments (Figures 25-27). By the interpretation given by Weiner (1985) of the dominance and suppression theory of size distribution, this would suggest that RPW was neither suppressed nor competitively superior. From the regression analyses done in this study, we know this is not true; RPW is competitively superior to GFT and experiences significant inter-specific competition from BYG. As was suggested earlier, there are many reasons other than competition to explain an uneven size distribution, of which inherent genetic variation is one. Turner and Rabinowitz (1983) proposed that assymetry in size distributions reflected variance in exponential growth rates. The RPW populations examined in these studies show a great deal of inherent genetic variation for plant size, and it is possible that the stresses inflicted by being grown in controlled environment chambers (lower light intensity and air velocity, for example) may have exacerbated the variation in exponential growth rates, which was reflected in the very skewed nature of the size distributions.

In contrast, GFT, which the MLR and SSR analyses suggest was suppressed by the other two species in mixtures, did not show the expected increase in skewness with an increase in density. Turner and Rabinowitz (1983) in reviewing the literature on size frequency distributions, found that when skewness increased with density, the plants were dicots or conifers; in cases where skewness did not increase with density, the plants were grasses (*Festuca* and *Zea*). They suggest that light competition may be crucial in causing dominance and suppression, and that the erect "vertical" form of grass seedlings may render light competition less crucial than belowground resource depletion.

Another major objective of this study was to examine the differences, if any, between the effects of two ozone doses which differed in their concentration and exposure terms.

Although the two ozone treatments represent the same actual dose in terms of exposure, there were very obvious differences in the way each affected the plant yield variables and competitive interactions. It should be pointed out that although the analysis of variance ozone effects were broken down into linear and deviation from linearity contrasts, the ozone variable involved was concentration during the exposure period. Overall, the 150 ppb/3.5 hr exposure had a much more inhibitory effect on all measured yield variables than did the 75 ppb/7 hr treatment. This confirms the general observation that concentration is more important than duration of exposure in determining response, and that the simple product of concentration and duration of exposure (while defining the ambient dose) does not define the "effective" dose received by the plant (Runeckles,1974; Fowler and Cape, 1982). In the present studies, the low level concentration, given over a longer exposure period, may have allowed the plants to acclimate themselves to the ozone treatment, thereby reducing the amount of injury or growth impairment. A low level of ozone used as a pre-treatment has been shown to protect plants from acute injury (Rosen,1979).

The implications of these findings are far-reaching. If a plant's competitive ability is altered by the presence of low levels of ozone which are commonly experienced in many areas of North America, the dynamics of many plant communities may slowly be changing. As the more dramatic example of ponderosa pine in the San Bernadino valley makes very clear, many species may lose their dominant stature in ecosystems and will be slowly replaced by other, more resistant, species. The development of resistance to air pollutants has been shown to be quite rapid in some species (Taylor and Murdy, 1975; Taylor, 1978). However, if the genetic basis for that resistance is not inherent, the gradual weakening of long-lived plants would have serious effects. Effects on short-lived plants such as the annuals used in these studies, would have their most serious evolutionary implications if the reproductive capacity of the plant was decreased. A significant effect of ozone on the reproductive yield of BYG was described (Tables 3 and 4).

If that decrease in reproductive tissue translated into a decrease in its reproductive capacity, in terms of viable seed and number of offspring, even though BYG did prove to be the most competitive of the three species, and its growth was even enhanced by the low level dose of ozone, its success in an evolutionary sense would be limited by its inability to contribute as many progeny to later generations as the other, less successfully competitive species, GFT and RPW.

The extrapolation of the results discussed here to the field situation must be done with caution. As was pointed out by De Vos *et al.*(1983) and Lewis and Brennan (1977), there are differences in a plant's susceptibility to air pollutants in the field and in controlled-environment chambers. It is possible that the findings of this study would not translate directly to a field situation; however the doses used were low and are characteristic of those found in many areas, including the lower mainland of British Columbia. Even if the effects in the field were not as dramatic as in this study, subtle changes in a plant's competitive ability and reproductive success could translate into long term successional changes. It is evident that as Treshow (1968) and Smith (1974) postulated, the presence of an air pollutant changes the way plants interact with each other.

6. SUMMARY

1. The competition among binary mixtures of barnyardgrass (BYG), redroot pigweed (RPW) and greenfoxtail (GFT), subjected to different treatments with the air pollutant ozone during the early stages of growth was investigated using additive and replacement series designs.

2. Three approaches were used to investigate competitive behaviour; the multiple linear regression (MLR), sequential simple regression (SSR) and the replacement series analyses. The interpretation of the SSR method of analyzing competitive systems has more biological meaning than the MLR analyses, and the SSR explains much more of the biological variation than does the MLR. The replacement series model specifically analyzes at each total density, while the regression analyses utilize all appropriate monoculture and mixture data. Hence, the regression analyses give a more general interpretation of the data set.

3. The order of competitive ability of the three species was shown to be BYG > RPW > GFT, regardless of ozone treatment.

4. There were significant intra-specific effects on RPW in all ozone treatments. BYG only experienced significant intra-specific competition in the two ozone-added treatments. The intra-specific competitive relationships of GFT was significant only in the control treatment.

5. There were significant inter-specific competitive effects of BYG and RPW on each other and GFT in all ozone treatments. BYG yield was significantly enhanced by GFT inter-specific competition in the control treatment. GFT did not effect BYG yield in either the 75 ppb (for 7 hr) or 150 ppb (for 3.5 hr) treatments. There were weakly significant effects of GFT inter-specific competition on RPW yield under all treatments.

6. BYG yield was significantly enhanced by the low level of ozone, 75 ppb/7 hr, over the control and 150 ppb/3.5 hr treatment.

7. RPW was most severely affected by the presence of ozone. RPW plants showed significant declines in dry weight per plant and per pot, number of leaves per plant and on root dry weight per pot in monocultures.

8. The replacement series for RPW-GFT showed an over-yielding in the control, an equal replacement of biomass in the 75 ppb/7 hr treatment and an under-yielding in the 150 ppb/3.5 hr. This interaction between ozone treatment and density combination of RPW and GFT was significant for root dry weight.

9. The two ozone treatments, 75 ppb/7 hr and 150 ppb/3.5 hr, which represent the same ambient dose, had different effects on the species studied. Except for BYG yield which was enhanced in the 75 ppb/7 hr treatment, the other species in monoculture and in mixture were more severely affected by the acute 150 ppb/3.5 hr dose than the chronic 75 ppb/7 hr dose.

10. Size frequency diagrams confirmed that BYG is competitively superior to the other two species. The size of GFT plants did not appear to be sensitive to competitive suppression. RPW displayed a very skewed size frequency distribution under all density combinations, which suggests that the RPW population studied was genetically predisposed to this wide size distribution.

11. The results show that the presence of an air pollutant changes the way plants interact with each other. This could have far-reaching evolutionary and ecological consequences as the dynamics of plant communities, exposed to low levels of ozone air pollution, changed over time.

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APPENDIX 1

Mean yield variables per pot for all density-species combinations for experiments 3 - 9.

VEGETATIVE DRY WEIGHT (g), BYG:GFT

Mixture BYG:GFT Density		OZONE TREATMENT 0		75 ppb/7 hrs		150 ppb/3.5 hrs	
		Species					
		BYG	GFT	BYG	GFT	BYG	GFT
0	5		0.3355		0.3001		0.2443
0	10		0.5971		0.5136		0.4969
0	15		0.6304		0.6179		0.6707
0	20		0.9639		0.9091		1.000
5	0	0.9043		1.417		0.9252	
5	5	0.4804	0.2003	0.7265	0.1825	0.4529	0.1470
5	10	0.6126	0.3729	0.8076	0.3405	0.5395	0.3553
5	15	0.8841	0.5478	0.7853	0.5297	0.7920	0.5767
5	20	1.6158	0.6806	1.0166	0.6176	1.5031	0.7720
10	0	1.855		1.735		1.590	
10	5	1.468	0.1529	1.502	0.1458	1.484	0.1352
10	10	1.166	0.5559	1.104	0.3511	1.023	0.3005
10	15	1.9191	0.6868	1.9718	0.4734	1.4738	0.5108
15	0	2.178		2.439		2.045	
15	5	2.121	0.2133	1.274	0.1991	1.661	0.2063
15	10	2.4504	0.3038	3.2188	0.3364	3.2445	0.2942
20	0	3.285		3.137		2.615	
20	5	2.7864	0.1877	2.8802	0.1545	2.9324	0.1935

REPRODUCTIVE DRY WEIGHT (g), BYG:GFT

OZONE TREATMENT

Mixture BYG : GFT Density		0		75 ppb/7 hrs		150 ppb/3.5 hrs	
		Species					
		BYG	GFT	BYG	GFT	BYG	GFT
0	5		0.0081		0.0037		0.0090
0	10		0.0142		0.0099		0.0099
0	15		0.0098		0.0076		0.0117
0	20		0.0099		0.0069		0.0131
5	0	0.0116	0.0	0.0196	0.0	0.0125	0.0
5	5	0.0	0.0	0.0	0.0004	0.0	0.0003
5	10	0.0	0.0010	0.0	0.0024	0.0	0.0008
5	15	0.0	0.0017	0.0	0.0060	0.0	0.0004
5	20	0.0154	0.0	0.0	0.0	0.0	0.0008
10	0	0.0407	0.0	0.0026	0.0	0.0099	0.0
10	5	0.0	0.0005	0.0	0.0023	0.0	0.0003
10	10	0.0	0.0014	0.0	0.0024	0.0	0.0015
10	15	0.0	0.0	0.0	0.0	0.0	0.0
15	0	0.0009	0.0	0.0	0.0	0.0098	0.0
15	5	0.0	0.0011	0.0	0.0009	0.0	0.0004
15	10	0.0	0.0	0.0081	0.0005	0.0	0.0
20	0	0.0326	0.0	0.0094	0.0	0.0098	0.0
20	5	0.0	0.0	0.0	0.0	0.0	0.0

NUMBER OF LEAVES, BYG:GFT

		OZONE TREATMENT					
		0		75 ppb/7 hrs		150 ppb/3.5 hrs	
		Species					
Mixture BYG : GFT Density		BYG	GFT	BYG	GFT	BYG	GFT
0	5	46.9		50.3			
0	10	85.8		94.3			
0	15	108.1		114.1			
0	20	144.3		148.6			
5	0	34.8		35.8		37.6	
5	20	31.3	106.7	29.7	106.8	31.5	120.7
10	0	61.1		61.0		64.8	
10	15	55.8	92.8	61.2	84.8	54.5	73.2
15	0	88.5		87.6		90.1	
15	10	85.3	50.8	84.3	55.3	85.8	49.3
20	0	115.5		121.0		125.8	
20	5	104.4	29.4	113.4	28.0	111.4	27.4

NUMBER OF TILLERS, BYG:GFT

Mixture BYG : GFT Density		OZONE TREATMENT 0 BYG	0 GFT	75 ppb/7 hrs BYG	75 ppb/7 hrs GFT	150 ppb/3.5 hrs BYG	150 ppb/3.5 hrs GFT
0	5		11.4		12.0		11.9
0	10		21.7		23.2		24.3
0	15		23.7		24.8		29.4
0	20		31.9		34.0		40.4
5	0	6.9		6.4		7.9	
5	20	5.2	23.3	5.2	25.5	5.0	26.7
		11.0		11.6		12.8	
10	15	10.2	21.3	10.0	20.0	10.0	19.5
15	0	16.0		16.0		16.2	
15	10	15.5	12.0	15.0	12.3	15.0	10.3
20	0	20.9		21.6		21.7	
20	5	20.0	6.8	20.6	6.4	20.0	6.4

VEGETATIVE DRY WEIGHT (g), BYG:RPW

Mixture BYG:RPW Density		OZONE TREATMENT 0 BYG	0 RPW	75 ppb/7 hrs BYG	75 ppb/7 hrs RPW	150 ppb/3.5 hr BYG	150 ppb/3.5 hr RPW
0	5		0.8728		0.9854		0.5820
0	10		1.267		1.036		0.8771
0	15		1.636		1.121		1.218
0	20		1.303		1.213		1.323
5	0	0.9043		1.417		0.9252	
5	5	0.9813	0.3188	0.7600	0.2552	0.8160	0.2518
5	10	1.366	0.7686	1.347	0.7634	1.080	0.5559
5	15	0.8295	0.7939	0.9330	1.002	0.9393	0.8537
5	20	0.4853	0.9359	0.7519	1.1833	0.4786	0.7871
10	0	1.855		1.735		1.590	
10	5	2.091	0.2589	2.146	0.2673	2.230	0.3342
10	10	1.907	0.3751	1.424	0.4805	1.598	0.2924
10	15	1.3455	0.9745	1.494	0.9774	1.182	0.8882
15	0	2.178		2.439		2.045	
15	5	2.796	.3301	2.707	.2110	2.562	.2132
15	10	1.7603	.9610	1.9699	.7444	2.2843	.6463
20	0	3.285		3.137		2.615	
20	5	2.0368	.5993	2.6145	.5641	2.4432	.3841

REPRODUCTIVE DRY WEIGHT (g), BYG:RPW

Mixture BYG : RPW Density		OZONE TREATMENT 0 BYG	0 RPW	75 ppb/7 hrs BYG	75 ppb/7 hrs RPW	150 ppb/3.5 hrs BYG	150 ppb/3.5 hrs RPW
0	5		0.0036		0.0007		0.0020
0	10		0.0017		0.0022		0.0031
0	15		0.0032		0.0038		0.0026
0	20		0.0071		0.0048		0.0060
5	0	0.0116		0.0196		0.0125	
5	5	0.0	0.0037	0.0050	0.0032	0.0048	0.0020
5	10	0.0232	0.0064	0.0472	0.0080	0.0058	0.0054
5	15	0.0	0.0092	0.0	0.0074	0.0033	0.0079
5	20	0.0	0.0	0.0	0.0	0.0	0.0
10	0	0.0407		0.0026		0.0099	
10	5	0.0498	0.0020	0.0275	0.0036	0.0137	0.0037
10	10	0.0045	0.0019	0.0	0.0010	0.0120	0.0021
10	15	0.0088	0.0	0.0	0.0	0.0074	0.0
15	0	0.0009		0.0		0.0098	
15	5	0.0	0.0014	0.0	0.0044	0.0124	0.0020
15	10	0.0332	0.0	0.0524	0.0	0.0453	0.0
20	0	0.0326		0.0094		0.0098	
20	5	0.0249	0.0	0.0463	0.0	0.0	0.0

NUMBER OF LEAVES, BYG:RPW

OZONE TREATMENT

Mixture BYG : RPW Density		0		75 ppb/7 hrs		150 ppb/3.5 hrs	
		Species					
BYG	RPW	BYG	RPW	BYG	RPW	BYG	RPW
0	5		38.2		39.1		37.8
0	10		65.0		62.4		68.5
0	15		92.3		88.1		94.8
0	20		102.9		108.0		119.3
5	0	34.8		35.8		37.6	
5	5	30.17	29.7	31.50	28.8	36.3	29.2
5	10	33.3	60.5	31.7	60.2	35.7	59.7
5	15	28.3	71.0	30.2	84.2	31.8	84.3
5	20	25.8	55.6	27.5	75.5	25.2	57.8
10	0	61.1		61.0		64.8	
10	5	60.17	25.8	60.7	26.5	67.0	32.7
10	10	60.83	49.5	54.3	46.7	61.2	50.0
10	15	53.67	66.3	49.2	48.7	55.0	58.5
15	0	88.5		87.6		90.1	
15	5	87.0	27.8	85.0	28.8	94.5	29.8
15	10	79.5	46.0	79.2	40.2	84.3	38.2
20	0	115.5		121.0		125.8	
20	5	102.2	21.0	113.0	27.2	115.8	21.6

NUMBER OF TILLERS, BYG:RPW

OZONE TREATMENT

Mixture BYG : RPW Density		0 BYG	0 RPW	75 ppb/7 hrs BYG	75 ppb/7 hrs RPW	150 ppb/3.5 hrs BYG	150 ppb/3.5 hrs RPW
5	0	6.9		6.4		7.9	
5	5	6.2	N/A	6.3	N/A	9.0	N/A
5	10	5.3		5.7		7.7	
5	15	5.0		7.2		6.2	
5	20	5.2		5.0		5.0	
10	0	11.0		11.6		12.8	
10	5	10.8		11.3		11.5	
10	10	11.5		10.5		13.0	
10	15	10.0		10.2		10.0	
15	0	16.0		16.0		16.2	
15	5	16		14.8		21.2	
15	10	15.0		14.8		15.0	
20	0	20.9		21.6		21.7	
20	5	20.2		20.0		20.0	

VEGETATIVE DRY WEIGHT (g), GFT:RPW

Mixture GFT : RPW Density		OZONE TREATMENT 0		75 ppb/7 hrs		150 ppb/3.5 hrs	
		GFT	RPW	GFT	RPW	GFT	RPW
0	5		0.8728		0.9854		0.5820
0	10		1.267		1.036		0.8771
0	15		1.636		1.121		1.218
0	20		1.303		1.213		1.323
5	0	0.3355		0.3001		0.2443	
5	5	0.2781	0.6188	0.2260	0.5952	0.2623	0.3937
5	10	0.1573	0.6313	0.1748	0.5820	0.1579	0.6469
5	15	0.1833	1.664	0.1559	1.813	0.1392	1.448
5	20	0.1492	1.285	0.1744	0.8365	0.1478	1.281
10	0	0.5971		0.5136		0.4969	
10	5	0.4487	0.5101	0.3982	0.1854	0.3302	0.2088
10	10	0.5569	1.632	0.3977	1.485	0.3162	1.132
10	15	0.3440	1.138	0.2728	1.146	0.2979	0.9694
15	0	0.6304		0.6179		0.6707	
15	5	0.4557	0.8149	0.3820	0.6092	0.4583	0.5008
15	10	0.6967	0.9628	0.6205	0.8792	0.5795	0.8016
20	0	0.9639		0.9091		1.0005	
20	5	0.8205	0.6585	0.7785	0.5132	0.7228	0.3385

REPRODUCTIVE DRY WEIGHT (g), GFT:RPW

OZONE TREATMENT

Mixture GFT : RPW Density		0		75 ppb/7 hrs		150 ppb/3.5 hrs	
		Species					
		GFT	RPW	GFT	RPW	GFT	RPW
0	5		0.0036		0.0007		0.0020
0	10		0.0017		0.0022		0.0031
0	15		0.0032		0.0038		0.0026
0	20		0.0071		0.0048		0.0060
5	0	0.0081	0.0	0.0037	0.0	0.0090	0.0
5	5	0.0124	0.0	0.0017	0.0	0.0123	0.0
5	10	0.0056	0.0	0.0	0.0	0.0057	0.0
5	15	0.0090	0.0	0.0064	0.0	0.0024	0.0
5	20	0.0050	0.0	0.0021	0.0	0.0032	0.0
10	0	0.0142	0.0	0.0099	0.0	0.0099	0.0
10	5	0.010	0.0	0.0102	0.0	0.0092	0.0
10	10	0.0158	0.0	0.0094	0.0	0.0078	0.0
10	15	0.0184	0.0	0.0103	0.0	0.0103	0.0
15	0	0.0098	0.0	0.0076	0.0	0.0117	0.0
15	5	0.0144	0.0	0.0135	0.0	0.0183	0.0
15	10	0.0190	0.0	0.0187	0.0	0.0122	0.0
20	0	0.0099	0.0	0.0069	0.0	0.0131	0.0
20	5	0.0067	0.0	0.0147	0.0	0.0046	0.0

NUMBER OF LEAVES, GFT:RPW

OZONE TREATMENT

Mixture GFT : RPW Density		0		75 ppb/7 hrs		150 ppb/3.5 hrs	
		Species					
GFT	RPW	GFT	RPW	GFT	RPW	GFT	RPW
0	5		38.2		39.1		37.8
0	10		65.0		62.4		68.5
0	15		92.3		88.1		94.8
0	20		102.9		108.0		119.3
5	0	46.9		50.3		50.8	
5	5	38.3	34.2	38.5	36.4	48.8	33.0
5	10	31.3	53.2	32.7	56.0	37.5	60.2
5	15	29.2	90.7	32.7	90.2	32.0	92.7
5	20	28.7	89.9	29.6	81.8	31.1	99.3
10	0	85.8		94.3		93.0	
10	5	70	31.8	74.2	24.8	73.8	27.2
10	10	68.8	69.8	67.2	71.2	70.7	68.0
10	15	64.6	77.7	54.4	70.2	66.6	74.9
15	0	108.1		114.1		120.2	
15	5	91.0	36.2	87.5	34.8	105.7	33.0
15	10	97.1	59.0	102.8	51.2	101.0	51.9
20	0	144.3		148.6		166.9	
20	5	126.4	30.3	129.0	27.8	129.7	25.3

NUMBER OF TILLERS, GFT:RPW

OZONE TREATMENT

Mixture GFT : RPW Density		0 GFT	0 RPW	75 ppb/7 hrs GFT	75 ppb/7 hrs RPW	150 ppb/3.5 hrs GFT	150 ppb/3.5 hrs RPW
5	0	11.4		12.0		11.9	
5	5	8.2	N/A	8.3	N/A	12.0	N/A
5	10	5.8		5.8		9.0	
5	15	6.2		6.7		6.2	
5	20	5.4		6.4		6.6	
10	0	21.7		23.2		24.3	
10	5	13.3		15.3		15.5	
10	10	12.8		13.7		16.2	
10	15	14.1		12.4		14.8	
15	0	23.7		24.8		29.4	
15	5	18.2		18.8		24.2	
15	10	21.9		24.0		22.8	
20	0	31.9		34.0		40.4	
20	5	26.3		26.3		28.3	

MEAN TOTAL ROOT DRY WEIGHT (g), BYG:RPW

Mixture BYG	: RPW Density	OZONE TREATMENT 0	75 ppb/7 hrs	150 ppb/3.5 hrs
5	0	0.2115	0.2385	0.1646
5	5	0.2449	0.2088	0.1964
5	10	0.3684	0.3373	0.2326
5	15	0.3273	0.3401	0.3332
5	20	0.1967	0.2471	0.1501
10	0	0.3216	0.2946	0.2761
10	5	0.3498	0.3661	0.3765
10	10	0.4584	0.3514	0.4055
10	15	0.2989	0.2509	0.2793
15	0	0.4609	0.4592	0.4408
15	5	0.5296	0.5687	0.4718
15	10	0.3437	0.3267	0.4066
20	0	0.6270	0.6054	0.5207
20	5	0.3761	0.4273	0.3684

MEAN TOTAL ROOT DRY WEIGHT (g), GFT:RPW

Mixture GFT	: RPW Density	OZONE TREATMENT 0	75 ppb/7 hrs	150 ppb/3.5 hrs
5	0	0.0910	0.1034	0.911
5	5	0.1586	0.1276	0.1231
5	10	0.1567	0.1078	0.1400
5	15	0.1696	0.1173	0.0985
5	20	0.2611	0.1865	0.2745
10	0	0.1442	0.1514	0.1273
10	5	0.2765	0.3251	0.2508
10	10	0.3414	0.3360	0.2285
10	15	0.2539	0.3020	0.2362
15	0	0.1664	0.1862	0.2001
15	5	0.2486	0.2000	0.1835
15	10	0.3571	0.3405	0.3580
20	0	0.2441	0.2405	0.2602
20	5	0.3058	0.3070	0.2263

MEAN TOTAL ROOT YIELD PER POT (g), BYG:GFT

Mixture BYG:GFT Density		OZONE TREATMENT 0	75 ppb/ 7 hrs	150 ppb/3.5 hrs
0	5	0.0910	0.1034	0.0911
0	10	0.1442	0.1514	0.1273
0	15	0.1664	0.1862	0.2001
0	20	0.2441	0.2405	0.2602
5	0	0.2115	0.2385	0.1646
5	20	0.3925	0.2667	0.3834
10	0	0.3216	0.2946	0.2761
10	15	0.4414	0.4638	0.3895
15	0	0.4609	0.4592	0.4408
15	10	0.5776	0.7210	0.5212
20	0	0.6270	0.6054	0.5207
20	5	0.5438	0.5118	0.5635