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Resource Allocation by Plants under Air Pollution Stress: Implications for Plant-Pest-Pathogen Interactions[1]

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I. Abstract

Plant growth depends on the coordinated acquisition and allocation of carbon, water, and nutrient resources to the major plant organs (root, stem, leaf, flower, and fruit) and to the major classes of metabolic function (vegetative growth, maintenance, defense, and reproduction). Air pollutants like SO_2, NO_2, and O_3 can directly damage plant tissues and disrupt normal patterns of resource acquisition and allocation. These disruptions in turn potentially will influence the plant's ability to defend itself against pests and pathogens. This review summarizes the quantitative and qualitative changes that have been observed when plants are exposed to low levels of SO_2, NO_2, and O_3; the following generalizations emerge:

1. Root biomass is reduced more than shoot biomass in plants exposed to SO_2 or O_3, but NO_2 does not appear to induce the differential suppression of above- versus below-ground organs.
2. Quantitative allocation to leaves increases and to stem decreases under SO_2 pollution regimes; too few data are available to generalize about O_3 or NO_2 effects on leaf: stem ratio.
3. Root carbohydrate concentrations sometimes increase and sometimes decrease after SO_2 or O_3 fumigations. Leaf nitrogen concentrations tend to decrease after exposure to air pollutants, and leaf carbohydrate concentrations can increase or decrease. Too few data on leaf concentrations of lipids and secondary chemicals are available to justify any generalizations on pollutant responses.
4. Reproduction is suppressed by O_3, SO_2, and NO_2, with O_3 appearing to have the most marked effects. Seed lipid and protein composition can be altered by exposure to pollutants.

While both quantitative and qualitative changes in plant resource allocation after exposure to pollutants are common, the importance of these diverse changes for plant-pest and plant-pathogen interaction requires more comprehensive study. Ideally, the time course of plant growth and of metabolite pools critical to particular pests or pathogens should be followed in plants exposed to realistic pollutant regimes and related to pest or pathogen performance on the treated plants.

Résumé

La croissance des plantes dépend d'une acquisition et d'une allocation coordonnées du carbone, de l'eau et des éléments nutritifs, à leurs organes majeurs (racines, tiges, feuilles, fleurs et fruits), ainsi qu'aux grandes fonctions métaboliques (croissance végétative, maintien, défense contre les insectes, et reproduction). Les polluants de l'air, comme le dioxyde de soufre, le dioxyde d'azote et l'ozone, peuvent directement endommager les tissus de la plante, et altérer leurs patron normaux d'acquisition et d'allocation des ressources. Ces désordres organiques et métaboliques, à leur tour, peuvent influencer la capacité des plantes à se défendre entre les insectes et les agents pathogènes. Cet article de revue résume les principaux changements quantitatifs et qualitatifs, qui ont été observés suite à l'exposition de plantes à de faibles niveaux de SO_2, de NO_2 et d'ozone. De ces observations, on peut émettre les généralisations suivantes:

1. Lorsque des plantes sont exposées au SO_2 ou à l'ozone, la biomasse racinaire subit des réductions plus importantes que celle des tiges. Le NO_2, toutefois, ne semble pas avoir une telle action différentielle sur la biomasse des organes aériens ou souterrains.
2. L'exposition des plantes au SO_2 entraine une augmentation de l'allocation des ressources aux feuilles, et une diminution de celle aux tiges; trop peu de données sont disponibles, cependant, pour étendre cette généralisation aux effets de l'ozone ou du NO_2 sur les rapports feuilles : tiges.
3. Dans les racines, les concentrations d'hydrates de carbone peuvent augmenter ou diminuer après des fumigations au SO_2 ou à l'ozone. Dans les feuilles, les concentrations d'azote tendent à diminuer après une exposition à des polluants de l'air, et celles d'hydrates de carbone, peuvent augmenter ou diminuer selon les cas. A nouveau, on dispose de trop peu de données sur les concentrations de lipides et de composés secondaires dans les feuilles, san justifier toute généralisation sur leurs réponses aux agents polluants.
4. La reproduction de la plante est affectée par le SO_2, le NO_2 et l'ozone, ce dernier ayant les effets les plus marqués. Dans les graines, la composition en protéines et en lipides peut être en effet altérée par une exposition à des agents polluants.

Alors qu'on a fréquemment rapporté des changements, tant qualitatifs que quantitatifs, dans l'allocation des ressources des plantes, suite à une exposition à des agents polluants, l'importance de ces changements au niveau des interactions plantes-insectes et plantes-pathogènes suggère que de nouvelles études sont requises. En particuliers, de telles études devraient analyser la croissance des plantes, de même que l'évolution temporelle des réserves de métabolites, influençant les insectes et les pathogènes, chez des plantes exposées à des niveaux de pollution réalistes, et relier ces phénomènes au succès relatif des insectes ou des pathogènes sur les plantes ainsi traitées.

Резюме

Рост растения зависет от координированного приобретения и распределения углерода, воды и питательных веществ главным органам растения (корень, стебель, лист, цветок и плод) и главным классам

метаболической функции (вегетативный рост, поддержание, защита и размножене). Воздушные загрязняющие вещества так, как двуокись серы, двуокись азота и озон прямым путём повреждают ткани растения и разрушают обычные пути приобретения и распределения ресурсов. Эти разрушения по очереди потенциально будут оказывать влияние на способность растения защититься от вредителей и патох генов. Настоящее обозрение суммирует количественные и качественные изменения наблюдённые при подвержении растений низким уровням SO_2, NO_2 и O_3. Появляются следующие обобщения:

1. Уменьшается биомасса корней больше чем биомасса стеблей у растений подверженные воздействию SO_2 или O_3, а покажется, что NO_2 не вызывает дифференциальное подавление надземных органов по сравнению с подземными органов.

2. Количественное распределение листьям увеличивается и стеблю уменьшается при режимах загрязнения SO_2; не имеются достаточных данных для обобщения о влиянии O_3 и NO_2 на соотношение между листом и стеблём.

3. Концентрации углеводов в корнях иногда увеличивается и иногда понижается при окуривании загрязнителя SO_2 или O_3. Листовые концентрации азота имеют тенденцию уменьшиваться при воздейтвии на воздушные загрязняюшие вещества. Листовые концентрации углеводов или увеличиваются или понижаются. Не имеются достаточных данных о листовых концентрациях липидов и вторичных химикатов для обобщений о ответных реакциях к загрязнителям.

4. Размножение подавляют O_3, SO_2 и NO_3; покажется, что O_3 имеет самые заметные воздействия. При воздействию на загрязнители может измениться семенной состав липидов и белков.

Несмотря на то, что часто находятся и количественные и качественные изменения в распределение ресурсов растения при воздействию на загрязнители, значительность этих разных изменений в взаимоотношения растения и вредителя и растения и патогена требует более обстоятельного исследования. Идеально, необходимо изучать временной ход роста растения и метаболических фондов, критических особенным вредителям или патогенам, у растений подверженные реалистическим режимам загрязнителей и определить соотношение между этими факторами и успехам вредителя или патогена на обработанных растениях.

II. Introduction

Plant growth, from the seedling stage through reproductive maturity to senescence and death, proceeds by the accumulation and incremental allocation of resources to the major plant organs (root, stem, leaf, flower, and fruit) and to the major metabolic functions (growth, maintenance, defense, and reproduction). Carbon and energy are accumulated through photosynthetic processes, primarily localized in leaves, while water and mineral nutrients are acquired by uptake processes localized in the roots. Throughout growth, incoming resources are continually partitioned to the various plant organs and metabolic functions to achieve coordinated development at the whole plant level. Since we are only beginning to understand the physiological mechanisms controlling this partitioning and its environmental dependence (Bloom et al., 1985; Gifford & Evans, 1981), our ability to predict a priori how partitioning may change under pollution stress is limited.

Stress may elicit not only quantitative changes in the relative allocation of resources to different plant organs, but also qualitative changes in the composition of different tissues. The balance of structural and nonstructural carbohydrates, lipids, proteins, and secondary chemicals in tissues may be altered, with implications for the functioning of a particular organ. For example, an increase in leaf protein might enhance photosynthetic capacity but unless compensated by concomitant increases in secondary defensive chemicals might also make the leaves more vulnerable to attack by herbivores or pathogens. Such qualitative changes may follow directly from stress affecting the composition of existing tissues or indirectly from stress altering the rates of senescence and production of plant parts. At the whole plant level both direct and indirect changes in tissue quality presumably reflect the relative priority of allocation to growth, maintenance, defense, and reproduction under shortfalls in resource availability or accumulation. Because of the exponential and modular nature of plant growth (J. White, 1984), even under episodic stress regimes such quantitative and qualitative changes can have ramifications throughout the life of an individual plant.

The purpose of this review then is first, to gather together information on the quantitative and qualitative changes in resource allocation which have been observed in plants under moderate air pollution stress. Second, the available data will be summarized and interpreted from the point of view that quantitative and qualitative changes in resource allocation may affect plant susceptibility to attack by pests and pathogens (Heagle, 1982; Hughes & Laurence, 1984; Hughes et al., 1982; Huttunen, 1984; Laurence et al., 1983). Because of the extreme lack of standardization in concentration and duration of pollutant exposures used in different studies, it is impossible to give adequate attention to pollutant concentration and dose effects in this review. Emphasis has been placed on studies involving exposure to realistic levels of pollutants delivered either as repeated episodes of acute pollution or as chronic exposure. The generalizations that emerge definitely require more precise definition of concentration- and

1A) OZONE, SULFUR DIOXIDE, AND NITROGEN DIOXIDE: ALONE AND IN COMBINATION

1.8	5
1.7	7
1.6	
1.5	4
1.4	
1.3	1145
1.2	
1.1	02378
1.0	0112334556677788
0.9	001233333444556677889
0.8	0000112233444445555566777778888999
0.7	01111111222222223445566777777788888899999
0.6	0222334456677778899
0.5	011334445666667799999
0.4	1246778889999
0.3	113445678999
0.2	1258
0.1	34667

1B)

OZONE ALONE

1.1	3
1.0	03456
0.9	0489
0.8	058
0.7	125688
0.6	6
0.5	34679
0.4	
0.3	3499
0.2	1
0.1	6

NITROGEN DIOXIDE ALONE

1.8	5
1.7	
1.6	
1.5	
1.4	
1.3	
1.2	1
1.1	0
1.0	18
0.9	35
0.8	25568
0.7	22367778
0.6	248
0.5	
0.4	
0.3	
0.2	
0.1	

SULFUR DIOXIDE ALONE

1.7	7
1.6	
1.5	
1.4	
1.3	145
1.2	
1.1	78
1.0	125778
0.9	0123334456678
0.8	0011233444556777788999
0.7	0112224457778889999
0.6	0233456777789
0.5	113445666799
0.4	27788999
0.3	8
0.2	
0.1	

Fig. 1. Effects of a variety of exposures to O_3, SO_2, and NO_2 alone or in combinations on plant vegetative growth. The ratio of treatment to control values for total biomass at the end of the experimental growth period is plotted as a stem and leaf diagram for all exposures including combinations (Fig. 1A) and for O_3, SO_2, and NO_2 alone (Fig. 1B). Ratios exceeding 1.00 indicate growth stimulation, those less than 1.00 indicate growth suppression. The stem and leaf diagram (Tukey, 1977) essentially combines a tabulation of the data with a histogram of its distribution. The vertical array of stem values represents the histogram classes while the horizontal array of leaf values represents the individual data entries in each class. For example in Figure 1A there is a single value of 1.00 (no change in total biomass under pollution), two values of 1.01 (very slight increase in biomass under pollution), and a single value of 1.85 (marked biomass increase under pollution).

Data are summarized from recent studies on annual and perennial grasses (Ashenden, 1978, 1979; Ashenden & Mansfield, 1977; Ashenden & Williams, 1980; Ayazloo & Bell, 1981; Ayazloo et al., 1980; Crittenden & Read, 1978; Davies, 1980; Jones & Mansfield, 1982a, 1982b; Prasad & Rao, 1981), on broad-leaf crop species (Bennett & Oshima, 1976; Foster et al., 1983; Henderson & Reinert, 1979; Ogata & Maas, 1973; Reinert & Sanders, 1982; Reinert & Weber, 1980; Tingey et al., 1971; Tingey et al., 1973), on deciduous tree species (Marshall & Furnier, 1981; Shanklin & Kozlowski, 1984; Freer-Smith, 1984, 1985), and on an evergreen tree species (Farrar et al., 1977; Garsed et al., 1981).

dose-dependencies when applied to particular plant species and combinations of pollutants. The review is also not comprehensive, but concerns allocational responses in plants growing in atmospheres polluted by ozone, sulfur dioxide, or nitrogen dioxide—the principal air pollutants, with wide dispersal and substantial deleterious effects on plant metabolism (Treshow, 1984). Particularly with regard to the potential impact of air pollutants on plant-pest interactions, this review is intended to synthesize information on resource allocation that is scattered throughout recent, more comprehensive summaries of air pollution effects on plants (Koziol & Whatley, 1984; Treshow, 1984; Unsworth & Ormrod, 1983; Winner, Mooney & Goldstein, 1985).

III. Plant Growth under Pollution Stress Regimes

The concept of stress has a tangled history in plant biology. We have only fairly recently achieved a consistent and unified terminology. Levitt (1980) emphasized the essential distinction between stress and strain. *Stress* is the external condition to which a plant is subjected that induces a measurable *strain,* a deviation from normal plant function. In the present context a plant growing in an atmosphere polluted by 200 ppb SO_2 is actually under stress if, for example, its rate of photosynthesis is reduced relative to a control plant growing in an unpolluted atmosphere. Such a physiologic strain may be compensated for so that the net strain at the whole plant level is minimized or even avoided. For example, increases in total leaf area or delayed senescence of leaf tissues could conteract the effects of reduction in photosynthetic rates. Such scale-dependent responses to pollutants can easily confound discussions of pollution stress; a stress at the physiological or biochemical level is not necessarily a stress at the whole plant level. In the final analysis, it is reductions in lifetime resource accumulation which indicate that an environmental regime has actually been stressful for plant growth and reproduction. This is the case because both agronomic yield and evolutionary fitness are strongly linked to plant size, and any metabolic changes that do not ultimately affect yield or fitness are of only limited import in and of themselves.

From this whole plant perspective, not all experimental treatments intended as an air pollution stress actually induce an evident strain, such as reduced plant size, over the course of the experiment. In a sample of

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Ozone doses in these studies ranged from 30 to 400 ppb (median 250 ppb), SO_2 from 24 to 1500 ppb (median 110), and NO_2 from 30 to 300 ppb (median 110). Almost all plants were greenhouse or chamber-grown with exposure to repeated episodes of pollution during pre-reproductive growth.

24 recent investigations of plant growth responses in atmospheres polluted with O_3, SO_2, NO_2, or some combination of these gases, 14% of the putative stress regimes actually stimulated growth relative to controls (Fig. 1). On average the pollutant stress treatments did result in a 25% reduction in plant growth, and in the most severe stress regimes growth reductions were as high as 87%. These investigations included a variety of species and plant growth forms exposed to a range of pollutant concentrations broadly representative of local and regional variations in present atmospheric regimes, although data on SO_2 effects predominate (Fig. 1). The degree to which resource allocation is altered under these particular pollution regimes will be used to illustrate the quantitative component of plant allocational response to air pollution stress.

IV. Quantitative Changes in Resource Allocation

A. VEGETATIVE ORGANS—ROOT AND SHOOT

The overall impact of pollutant stress generally appears to be greater on roots than on shoot tissues (Fig. 2). The mean reduction in root biomass is 31% compared to 21% for shoot biomass during the pre-reproductive growth of the woody and herbaceous plants included among the available data. The greater suppression of root growth relative to shoot growth is more often apparent in response to either O_3 or SO_2 than to NO_2 (Fig. 2). For fumigations with O_3 alone, root biomass is reduced 34% compared to 23% for shoot biomass, for SO_2 alone 27% compared to 17%, and for NO_2 alone only 14% compared to 10%. Many additional studies, not amenable to summary in Figures 1 and 2, also support these trends in the quantitative pattern of resource allocation for the three pollutants alone and in combination.

Ozone fumigations reduced root more than shoot biomass in parsley (*Petroselinum crispum*) (Oshima et al., 1978), cotton (*Gossypium hirsutum*) (Oshima et al., 1979), bush bean (*Phaseolus vulgaris*) (Bytnerowicz & Taylor, 1983), radish (*Raphanus sativus*) (Adedipe & Ormrod, 1974; Reinert & Gray, 1981; Reinert et al., 1982; Walmsley et al., 1980), and alfalfa (*Medicago sativus*) (Tingey & Reinert, 1975), in four coniferous and five deciduous trees (Kress & Śkelly, 1982), and in three perennial grasses (Horsman et al., 1980). In pepper (*Capsicum annuum*), total biomass was suppressed under O_3 fumigation with no change in root : shoot ratio, but fruit production was reduced (Bennett et al., 1979). Similarly, O_3 alone did not differentially suppress the root- versus shoot-growth of green ash (*Fraxinus pennsylvanica*) seedlings, sugar maple (*Acer saccharum*) seedlings (Kress & Skelly, 1982), or soybean (*Glycine max*) (Tingey & Blum, 1973). Ozone exposure did suppress nodulation in both soybean

2A) OZONE, SULFUR DIOXIDE, AND NITROGEN DIOXIDE: ALONE AND IN COMBINATION

```
1.4 3
1.3 58
1.2 01                                   ROOT
1.1 266899
1.0 000112222256889
0.9 0011335679
0.8 0000112222333344455566777888888889999
0.7 001112455556677778999999
0.6 00001112333344455567777777788
0.5 1222222333455555577888
0.4 0011111112222366788889999
0.3 02245677888
0.2 01246689
0.1 35
0.0 44489
```

```
1.9 59
1.8 6
1.7 6
1.6 4
1.5 0
1.4 2
1.3 2
1.2 2                                    SHOOT
1.1 2234779
1.0 00111112233455555678899
0.9 0011111122234566677888
0.8 00011122222345555556666667778888889999
0.7 01111222223333333334445555556677777889999
0.6 111122223455666777778899
0.5 00002246666667999
0.4 0014568899
0.3 122334677888
0.2 24568
0.1
0.0
```

2B) OZONE ALONE

```
1.0 1226
0.9 3369
0.8 8
0.7 1799
0.6 004678
0.5 458
0.4 0119
0.3 78
0.2 06
0.1
0.0 4     ROOT
```

```
1.1 239
1.0 0024559
0.9 1
0.8 178899
0.7 15
0.6 157
0.5 029
0.4 0
0.3 1278
0.2 2
0.1
0.0        SHOOT
```

NITROGEN DIOXIDE ALONE

```
1.4 3
1.3
1.2 5
1.1 26
1.0 15
0.9 6789
0.8 0123
0.7 0557
0.6 37
0.5 338
0.4
0.3
0.2
0.1    ROOT
0.0
```

```
1.8 9
1.7
1.6
1.5
1.4 2
1.3
1.2
1.1
1.0 16
0.9 22366
0.8 2788
0.7 11233347
0.6 79
0.5
0.4
0.3
0.2
0.1     SHOOT
0.0
```

SULFUR DIOXIDE ALONE

```
1.3 8
1.2 01
1.1 689
1.0 0022288
0.9 00157
0.8 0012233344455556788888999
0.7 014556677899
0.6 01123334455777777778
0.5 1222255555578
0.4 0111223667888999
0.3 78
0.2 9
0.1        ROOT
0.0
```

```
1.9 5
1.8 6
1.7
1.6 4
1.5 0
1.4
1.3 2
1.2 2
1.1 247
1.0 1123358
0.9 0011111245677888
0.8 0001122223455555666666689
0.7 0222333334455556677788 9999
0.6 12223466789
0.5 004666799
0.4 5689
0.3 2
0.2
0.1         SHOOT
0.0
```

Fig. 2. Effects of a variety of exposures to O_3, SO_2, NO_2 alone or in combinations on root and shoot growth. The ratios of treatment to control values for root biomass and for shoot biomass at the end of the experimental growth period are plotted as stem and leaf diagrams for all exposures including combinations (Fig. 2A) and for O_3, SO_2, and NO_2 alone (Fig. 2B). The data base is the same as in Figure 1.

(Reinert & Weber, 1980; Tingey & Blum, 1973) and pinto bean (*Phaseolus vulgaris*) (Manning et al., 1971). Only in tobacco (*Nicotiana tabacum*) (Tingey & Reinert, 1975) and in tomato (*Lycopersicon esculentum*) (Oshima et al., 1975), did O_3 have more negative effects on shoot than on root growth. Exposure to O_3 in combination with SO_2 or NO_2 did not qualitatively change the general tendency for accumulated root biomass to be decreased proportionately more than shoot biomass (Bytnerowicz & Taylor, 1983; Kress & Skelly, 1982; Reinert & Gray, 1981; Reinert et al., 1982; Tingey & Reinert, 1975).

Additional reports also support the tendency for SO_2 to suppress root growth more than shoot growth; since 72% of the observations summarized in Figure 2 involve SO_2 fumigations, this is not surprising. Radish (Reinert & Gray, 1981; Reinert et al., 1982), alfalfa (Tingey & Reinert, 1975), bluegrass (*Poa pratensis*) (Whitmore & Mansfield, 1983), perennial ryegrass (*Lolium perenne*) (Bell et al., 1979), Scots pine (*Pinus sylvestris*) and Sitka spruce (*Picea sitchensis*) (Garsed & Rutter, 1984), all show greater suppression of roots under SO_2 exposure than roots under NO_2 or O_3. In contrast, root and shoot growth in hardwood tree species appear to be either unaffected or equally affected by SO_2 exposure (Garsed et al., 1979; Roberts, 1975). Norby and Kozlowski (1981), however, did show that the relative effects of SO_2 on root versus shoot growth was temperature dependent in white birch (*Betula papyrifera*), red pine (*Pinus resinosa*), and two *Eucalyptus* species. For example, white birch seedlings grown at 32°C after fumigation had greater suppression of root than shoot growth, but growth at 12°C resulted in a greater suppression of shoot growth. No such temperature dependence in allocation to root versus shoot was evident in radish under O_3 fumigation (Adedipe & Ormrod, 1974). In studies directly comparing the effects of O_3 and SO_2, both pollutants do generally suppress root growth more than shoot growth, but neither pollutant has a consistently greater effect on biomass or partitioning (Bytnerowicz & Taylor, 1983; Foster et al., 1983; McLaughlin & McConathy, 1983; Reinert & Gray, 1981; Reinert & Sanders, 1982; Reinert & Weber, 1980; Tingey & Reinert, 1975; Tingey et al., 1971, 1973).

Relatively few studies have analyzed biomass allocation responses to NO_2 exposure; only 27% of the observations in Figures 1 and 2 involve NO_2 fumigations. Reinert and Gray's (1981; also Reinert & Sanders, 1982) study of radish exposed to all combinations of O_3, SO_2, and NO_2 suggests that NO_2 has little if any effect on dry-matter partitioning. Similarly, in Kress and Skelly's (1982) comparison of O_3 and NO_2 effects on eight coniferous and deciduous trees, NO_2 had no differential effect on root and shoot, although there was often a modest overall suppression of growth. While green ash was unaffected, white ash (*Fraxinus americana*) was an exception, in that NO_2 markedly reduced root growth with no effect on shoot growth. From the available data, it appears that NO_2 has less effect on allocation of dry matter to root versus shoot than either SO_2 or O_3 across a range of concentrations.

The net effect of these changes in allocation priorities is to reduce the root : shoot ratio under pollution regimes, especially those involving exposure to O_3 and SO_2. The import of an altered root : shoot ratio lies in the possibility that the acquisition of carbon, energy, water, and nutrient resources will be impaired, thus aggravating deleterious effects of the pollutant itself. For example, polluted plants may be more vulnerable to drought stress since proportionately less root is available to supply water to transpiring leaves. Similarly reduced root growth makes not only acquisition of water but also nutrient resources potentially more difficult. The importance of such limitations ultimately depends on the overall balance between acquisition of resources and demand in different tissues, but in general disruption of resource acquisition will lead to reduced allocation to defense against pests and pathogens (Coley et al., 1985; T. C. R. White, 1984).

B. VEGETATIVE ORGANS—LEAF AND STEM

Since leaves account for essentially all transpiration and have higher nutrient concentrations than stem tissues, any disproportionate changes in leaf to stem biomass under pollution regimes can potentially amplify the deleterious effects of reduced root : shoot ratios. Available numeric data (Farrar et al., 1977; Freer-Smith, 1985; Garsed et al., 1981; Prasad & Rao, 1981; Shanklin & Kozlowski, 1984) show a mean 7% increase in leaf biomass and a concomitant 5% decrease in stem biomass in SO_2 fumigated plants. Similar trends are evident for white birch and pin oak (*Quercus palustris*) seedlings (Roberts, 1975) and for tobacco but not cucumber (*Cucumis sativus*) (Mejstrik, 1980). Ozone fumigation also increased leaf : stem ratio in cotton (Oshima et al., 1979), but not in pepper (Bennett et al., 1979). Bush beans grown under either SO_2 or O_3 fumigation have higher leaf biomass and lower stem biomass, but the SO_2 effect is greater; combined exposure to SO_2 and O_3 has an intermediate effect (Bytnerowicz & Taylor, 1983). The modular organization of plant growth in relation to canopy architecture (J. White, 1984) will tend to prevent extreme changes in leaf : stem ratios which might induce self-shading, but plants growing in polluted air do appear to be somewhat more leafy. This would be a reasonable compensatory response to air pollutant-induced losses in the photosynthetic capacity of leaves (Winner, Mooney, Williams & von Caemmerer, 1985). Plants with more leaves but lower leaf specific photosynthesis will, however, have lower water use efficiency and be more prone to drought stress; compensatory increases in root acquisition of water seems unlikely given the overall depression of root growth under pollution regimes. These interacting disruptions of physiological function and allocation under pollution regimes should be further investigated to determine if reductions in plant vigor ensue which could trigger release of pest or pathogen attacks.

C. REPRODUCTIVE ORGANS

Allocation to reproduction is an important consideration from both an agronomic and an evolutionary perspective, but most studies have not followed plant response to pollutants through flowering to seed maturation. Many groups of pests and pathogens attack only reproductive tissues, and depression of reproductive effort may also be indicative of serious disruption in the overall plant allocation pattern.

Ozone and SO_2 reduce flower number in *Begonia* spp. (Adedipe et al., 1972; Reinert & Nelson, 1980) and in a variety of annual bedding plants (Adedipe et al., 1972). Ozone, but not SO_2, reduces flower number in soybean (Heagle et al., 1974). Sulfur dioxide does increase the number of sterile flowers in pepper-grass (*Lepidium virginicum*), a crucifer (Murdy, 1979). In Kentucky bluegrass SO_2, but not NO_2, reduced flowering (Whitmore & Mansfield, 1983). Observed reductions in flower number probably stem from morphogenetic constraints (Watson & Casper, 1984) arising from altered allocation to vegetative tissues, although direct deleterious effects on floral function are documented (Bonté, 1982; DuBay & Murdy, 1983).

Ozone alone (Kress & Miller, 1983; Reich et al., 1982) and in combination with SO_2 (Reich et al., 1982) reduces the seed yield of soybean. Sulfur dioxide alone has been reported to have both no effect (Davis, 1972; Reich et al., 1982) and fairly marked negative effects (Amundson, 1983; Irving & Miller, 1981; Sprugel et al., 1980) on soybean seed yield. These contrasting results may reflect the confounding effects of determinate versus indeterminate flowering habits in soybean varieties. Depression of soybean yield by SO_2 in combination with NO_2 has also been reported (Amundson, 1983). Ozone reduces fruit yield in tomato (Henderson & Reinert, 1979; Oshima et al., 1975, 1977), fruit yield in pepper (Bennett et al., 1979), seed yield in wheat (*Triticum aestivum*) (Heagle et al., 1979), seed yield in snap beans (*Phaseolus vulgaris*) (Heggestad et al., 1980), and seed yield in red kidney bean (*Phaseolus vulgaris*) (Kohut & Laurence, 1983). Ozone reduces kernel numbers in maize (*Zea mays*) (Heagle et al., 1972; Heagle et al., 1979; Thompson et al., 1976). Although O_3 and SO_2 did not significantly alter total pod biomass in bush bean, photo-assimilates were retained in leaves at the expense of developing pods (McLaughlin & McConathy, 1983). In general, air pollution stress, especially in the case of ozone exposures has negative effects on the reproductive success of the herbaceous species studied thus far.

V. Qualitative Changes in Plant Tissues under Pollution Stress

The interpretation of qualitative changes in resource allocation poses an intrinsically difficult problem which is aggravated by the nature of the available data. Metabolite pools tend to be highly dynamic in stressed as well as unstressed plants, thus weakening the value of comparisons based on isolated point-in-time rather than sequential samples. Plant responses to pollution stress may, for example, involve an initial rise in a particular metabolite followed by its gradual decline, as is often the case for carbohydrates (Koziol, 1984). Heath (1984) provides a useful discussion of this problem in the context of stress effects on organic, fatty, and amino acids. Pest and pathogen interactions may easily be critical at a stage in the dynamic metabolic cycles following on stress events which is not sampled in a particular study. Given the obvious pragmatic difficulties in carrying out detailed comparative studies of metabolite pools over extended time periods, we will have to continue to depend on the limited information from the point-in-time comparisons which constitute almost all the available literature. I have tended to catalog more than synthesize this material, but this compendium should help formulate more detailed studies of the dynamics of metabolic fractions especially central to plant interactions with pests and pathogens.

A. EFFECTS ON ROOT TISSUES

Although the quantitative reductions in dry matter allocation are most marked in roots, little information is available on qualitative changes in root tissue under pollution regimes. Constantinidou and Kozlowski (1979) reported that SO_2 and O_3 alone or in combination reduced root concentrations of nonstructural carbohydrates, lipids, and proteins in seedlings of American elm (*Ulmus americana*). Jensen (1981) found reduced root carbohydrates in green ash exposed to O_3. Tingey et al. (1976) reported lower soluble sugars, starch, and phenols, but higher nitrogen in the roots of ozone fumigated ponderosa pine (*Pinus ponderosa*). The roots of red kidney bean had increased concentrations of reducing-sugars after exposure to moderate SO_2 levels but decreases with higher SO_2 doses; starch levels were essentially stable (Koziol & Jordan, 1978). Pell et al. (1980) reported potato (*Solanum tuberosum*) tubers had lower total solids and higher reducing-sugar concentrations in ozone fumigated plants, but Foster et al. (1983) found no change in tuber dry matter, sugar, or amino acid profiles in plants fumigated with either O_3 or SO_2. Tuber nitrogen concentrations did, however, decrease. Total solids were also reduced in carrot (*Daucus carota*) root but nitrogen and carbohydrates were unaltered under O_3 fumigation (Pippen et al., 1975). The implications of these changes for root-feeding herbivores or for plant-fungal interactions require direct investigation.

B. EFFECTS ON LEAF TISSUES

The most striking qualitative change in pollution stressed plants is frequently a decrease in leaf nitrogen concentrations associated with reduction in leaf protein. Decreased nitrogen concentrations after exposure to SO_2 have been reported in the leaves of soybean and pea (*Pisum sativum*) (Sardi, 1981) and in American elm seedlings (Constantinidou & Kozlowski, 1979). Ozone also decreases protein concentration in seedling elm leaves (Constantinidou & Kozlowski, 1979) and in bean (Craker & Starbuck, 1972). In white bean (*Phaseolus vulgaris* cv. Sanilac) both O_3 and SO_2 reduced leaf protein, but SO_2 had the greater effect (Beckerson & Hofstra, 1979). Exposure to NO_2 either increased leaf nitrogen in tomato plants (Troiano & Leone, 1977) or had no effect (Taylor & Eaton, 1966). The increased free amino acid concentrations evident in SO_2 fumigated bean (*Phaseolus vulgaris* var. Widusa) leaves (Godzik & Linskens, 1974), SO_2 fumigated jack pine (*Pinus banksiana*) needles (Malhotra & Sarkar, 1979), and O_3 fumigated bean (*Phaseolus vulgaris*) leaves (Tomlinson & Rich, 1967) may arise from degradation of leaf protein although other disruptions of amino acid metabolism also appear to be involved (Heath, 1984; Stewart & Larker, 1980). These decreases in leaf nitrogen will tend to make foliage less nutritious for insect herbivores (Mattson, 1980; T. C. R. White, 1984), although increased N concentrations in the phloem resulting from translocation of protein degradation products could enhance performance of sucking insects.

Leaf carbohydrate concentrations can also be altered by exposure to gaseous pollutants (Koziol, 1984). Ozone and SO_2 either alone or in combination reduced leaf nonstructural carbohydrate concentrations in seedling American elm (Constantinidou & Kozlowski, 1979). Depending on temperature regime, ozone increased or had no effect on leaf concentrations of soluble carbohydrates in radish (Adedipe & Ormrod, 1974). Reducing-sugar concentrations were increased by moderate SO_2 fumigations in jack pine (Malhotra & Sarkar, 1979) and red kidney bean (Koziol & Jordan, 1978), but at higher SO_2 doses reducing sugars decreased in the kidney bean. Starch levels in the leaves of red kidney bean followed the same trend (Koziol & Jordan, 1978). These changes in leaf carbohydrate concentrations may alter plant susceptibility to high and low sugar diseases (Vanderplank, 1984).

Other aspects of leaf quality are also altered by air pollutants, but the possible importance of these changes for plant-pest or plant-pathogen interactions is less clear. Changes in leaf mineral concentrations have been reported (Cowling & Koziol, 1982; Skärby, 1984). Concentrations of a variety of particular biochemicals ranging from vitamins to flavonoids are altered by pollutants (Skärby, 1984). Lipid metabolism is variously altered by air pollutants (Heath, 1984; Malhotra & Khan, 1984). Overall it seems likely that many of these changes will influence particular interactions between plants and pests or pathogens, but any generalizations about potential effects are unwarranted given the limited data available.

C. EFFECTS ON REPRODUCTIVE TISSUES

Very little information is available on qualitative changes in plant reproductive tissues after exposure to air pollutants. Seed had lower oil content but higher protein content after O_3 fumigation of soybean plants (Howell & Rose, 1980; Kress & Miller, 1983). Sprugel et al. (1980) reported reduction of seed protein but no change in oil content for SO_2 fumigated soybean plants. Ozone fumigation increased nitrogen in corn kernels, had no effect on tomato fruits, and mixed effects on strawberry cv. Tioga fruits (Pippen et al., 1975). The possible effects of such changes on seed-feeding herbivores and seed pathogens merits investigation.

VI. Concluding Remarks

The experimental results summarized above document both quantitative and qualitative shifts in resource allocation that occur in plants subjected to chronic, low levels of air pollution. General quantitative trends in the suppression of root growth, increased leafiness, and reduced flowering and fruiting are apparent across the diverse species and growth forms which have been investigated. A similar qualitative trend in decreased leaf nitrogen concentration exists, but in general the carbohydrate, lipid, and protein concentrations of tissues in stressed plants are not predictable. Moreover, the dose-dependence and response time of all these quantitative and qualitative changes varies with species and exposure. Certain general patterns of allocational response to air pollution stress are emerging, but further experimental work is essential to test and refine these rudimentary generalizations.

The importance of allocational changes for plant-pest and plant-pathogen interactions poses special challenges. Successful pest or pathogen attack often depends on qualitative changes in particular plant tissues, and it is these qualitative changes that are least investigated. Some may follow as consequences of altered patterns of quantitative allocation to different plant organs, and others may be either pathological consequences of the pollutant or prophylactic responses to reduce future pollution damage. Neither our understanding of these qualitative changes under pollution regimes nor their effects on plant interactions with pests and pathogens will be easily advanced by the broad comparative studies that have been summarized in this review. It is important that future work in this area include the time courses of plant growth and critical metabolite pools in relation to the performance of particular pests or pathogens on plants exposed to realistic pollutant regimes.

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