LA RELATION ENTRE L'ALLOCATION AUX COMPOSÉS SECONDAIRES ET LE TAUX DE CROISSANCE RELATIF CHEZ LES ASTERACEAE

par

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RÉSUMÉ

L'influence de la disponibilité en éléments nutritifs et de l'intensité lumineuse sur l'investissement relatif de la feuille en composés secondaires a été mis en évidence chez certaines espèces. Cependant, les études interspécifiques pertinentes sont rares et donnent des résultats contradictoires. La présente étude met l'accent sur le compromis existant entre la croissance et la production de composés secondaires, pour des plantes cultivées dans différentes conditions de disponibilité de ressources. Plusieurs hypothèses ont été testées: 1) il existe, chez les Asteracées cultivées dans des conditions optimales de luminosité et de nutrition minérale, une corrélation négative entre le taux de croissance relatif des espèces et leur production de composés secondaires; 2) chez des plantes cultivées dans des conditions suboptimales, il existe une corrélation négative entre les composés secondaires mobiles (test de toxicité des larves d'*Artemia*) et les composés secondaires immobiles (composés phénoliques); 3) les plantes cultivées en conditions optimales de nutrition mais sous faible intensité lumineuse produisent moins de composés secondaires carboniques que dans des conditions de stress nutritif et de luminosité optimale; et 4) les plantes cultivées dans des conditions optimales ont un taux de croissance élevé mais produisent moins de composés secondaires que dans des conditions de stress lumineux et nutritif. Pour tester la première hypothèse, 31 espèces d'Astéracées ont été cultivées dans un environnement contrôlé, dans des conditions optimales de lumière et de nutrition (solution hydroponique). Vingt espèces d'Astéracées, cultivées en conditions de stress nutritif mais sous une intensité lumineuse élevée, ont été utilisées pour tester la seconde hypothèse, *i.e.* l'existence d'une corrélation entre le taux de croissance relatif des espèces et leur production en composés secondaires, ainsi qu'entre les deux types de défense chimique (mobile et immobile). Afin de tester les hypothèses trois et quatre, une expérience a été réalisée avec six espèces d'Astéracées cultivées selon 11 différentes combinaisons de disponibilité en lumière et en minéraux nutritifs. De plus, deux de ces six espèces (*Chrysanthemum leucanthemum* et *Rudbeckia hirta*) ont été utilisées afin de tester l'existence de différences dans la quantité de composés

secondaires spécifiques produite (mesurée par HPLC) entre deux niveaux de disponibilité des ressources sous haute intensité lumineuse. Cette thèse a mis en évidence le fait que la disponibilité des ressources affecte la croissance et la production de composés secondaires de différentes manières chez quelques espèces d'Astéracées. Cependant, les données de cette thèse ne montrent aucun compromis entre la croissance et les défenses chimiques quand on compare les différentes espèces à l'intérieur d'une même expérience. La croissance relative et la surface spécifique des feuilles voient leur valeur moyenne diminuer dans des conditions de stress nutritif. Au contraire, le rapport racine:feuille est augmenté dans ces mêmes conditions. Comme on pouvait l'espérer, le pourcentage d'azote foliaire est réduit dans des conditions de stress nutritif. Les choses se compliquent en ce qui concerne les paramètres utilisés pour caractériser la défense chimique quand le contenu total en composés phénoliques augmente, la valeur moyenne de la toxicité diminue. Par ailleurs, aucun polyacétylène ni sesquiterpène lactone n'a été mis en évidence par HPLC dans les feuilles des deux espèces étudiées. Enfin, la quantité de pentaynène produite dans les fleurs de *Rudbeckia hirta* diminue significativement avec l'âge mais augmente significativement quand la plante est soumise à une faible disponibilité de nutriments.

ABSTRACT

Differences in resource availability have been shown to generate variation in defense chemistry in some species, but proper interspecific studies are rare and give conflicting results. This study focused on the trade-off between growth and production of chemical compounds of plants grown under different resource availabilities. I tested the hypothesis that: 1) contrasting plant species grown under controlled and enriched environmental conditions will show a negative correlation between their relative growth rates and their secondary compounds; 2) there is a negative correlation between mobile defenses (measured by the toxicity bioassay) and immobile defenses (measured by total phenol concentration) of plants grown under suboptimal environmental conditions; 3) plants grown under light-stressed conditions but optimal nutrient conditions will produce less carbon-based secondary compounds than plants grown under nutrient-stressed conditions but optimal light conditions; and 4) plants grown under optimal environmental conditions will have a high RGR but will produce less secondary compounds than plants grown under stressful environmental conditions. Hypothesis 1 was tested experimentally using 31 species of Asteraceae grown with high levels of mineral and light resource availability under controlled conditions. Hypothesis 2 was tested in 20 species of Asteraceae by examining if there is any correlation between relative growth rate and secondary metabolism, and if there is any correlation between the type of chemical defense (mobile and immobile) in plants grown under controlled conditions of high light intensity but suboptimal levels of mineral nutrients. To test hypotheses 3 and 4, I conducted an experiment using six species of Asteraceae grown under 11 different combinations of light and mineral resources availabilities. Also, I investigated if there was any difference concerning the amount of specific secondary compounds, measured with HPLC produced by high light intensity and two levels of mineral resources availabilities in two of the six species (*Chrysanthemum leucanthemum* and *Rudbeckia hirta*). This thesis provided evidence that the resources availabilities affect the growth and the chemical parameters in different ways, but the data of this thesis shows no

trade-off between growth and chemical defense when comparing species within a given experiment. The relative growth rate and the specific leaf area are affected by reducing the mean values under nutrient stress. In contrast, the root:shoot ratio increased under such conditions. As expected, leaf nitrogen content was reduced under nitrogen stress. The complication occurs in the parameters related to chemical defense; while total phenolics content increased, toxicity decreased. Finally, I did not detect the presence of any polyacetylenes or sesquiterpene lactones by HPLC in the leaves of the two species tested. The amount of pentaynene produced in the flowers of *Rudbeckia hirta* decreased significantly with age but increased significantly when the plant was subjected to a reduced nutrient availability.

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TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CONTRIBUTION TO ORIGINAL KNOWLEDGE

1. The main contribution of this study is that it is the first to explore a wide set of species and resources availabilities, in systematic and standardized conditions, from an ecological view point, investigating if there are tradeoffs between growth parameters and chemical defenses, focusing on just the plants. This thesis contributes to a better understanding of the controversial aspects involving tradeoffs between growth and defense in different resource environments.

2. This study is the first high resource-based study to examine chemical defenses (total phenolics and toxicity) under controlled conditions in a large number of species of a single family, versus the relative growth rate (chapter II).

3. Nutrient stress conditions can change the patterns of chemical defense. This is the first study that has focused on the maintenance of patterns under an environment in which nutrient levels have been reduced, for a large number of species (chapter III).

4. Using a subset of six species from the first chapter, under controlled conditions, I investigated the possible correlations between RGR and secondary metabolism under different combinations of light intensity and nutrient levels for 6 species of Asteraceae (chapter IV). This is the largest number of species investigated under a full range of light and nutrient conditions.

5. Differences in the amount of secondary metabolism produced by differing resource availabilities have been little examined. This is the first investigation with *Chysanthemum leucanthemum* and *Rudbeckia hirta* grown under controlled conditions with different

combinations of resource availability, analyzing by HPLC sesquiterpene lactones and polyacetylenes (chapter V).

6. An original study of polyacetylenes from *Rudbeckia hirta* flowers (young and old) harvested from plants grown under controlled conditions with high light and two different nutrient availabilities was undertaken (chapter V).

GENERAL INTRODUCTION

Animal life on Earth depends on plants; without their capacity for converting carbon dioxide and water to sugars, and nitrogen to amino acids, animals, including man, could not survive. Thus, it could be argued that green plants are the most important constituents of this planet.

Herbivory is one of the most powerful ecological interactions. Plants have been subjected to intense and recurrent natural selection to reduce herbivore impact upon them and to compensate for attacks when defenses have been breached. A major determinant of survival in plants is to avoid, or reduce, herbivory. Plant properties that have led to reduction of herbivore impact include a vast array of chemicals that act as feeding deterrents or, less often, highly toxic poisons. Yet, such defensive adaptations require the same basic resources (carbon, mineral nutrients, and water) for their construction as required for growth.

Plants have evolved an enormous variety of physical and chemical properties, which are effective deterrents against herbivores. Every plant species has a suite of secondary metabolites whose primary function is defense (Coley, 1987). Therefore, if defensive options are both diverse and ubiquitous, why are some species better defended than are others? This question has generated several theories that try to explain the biology of plant defense in different ways (Feeny, 1976; Rhoades and Cates, 1976; Bryant *et al.,* 1983; Coley *et al.,* 1985; Herms and Mattson, 1992).

According to Herms and Mattson (1992) the allocation of resources by plants to chemical and structural defenses decreases growth by diverting resources from the production of leaf area and other vegetative structures. This trade-off has ecological consequences that affect the success or failure of particular resource partitioning and allocation patterns in particular

environments. Hence the dilemma of plants: They must grow fast enough to compete and ultimately reproduce, and yet maintain the physiological adaptations (defenses) necessary for survival in the presence of herbivores and pathogens.

Some researchers (Mooney and Chu, 1974; Chung and Barnes, 1980 a, b; Waring and Pitman, 1985; Bazzaz *et al.,* 1987; Chapin *et al.,* 1990) observed that when environmental conditions are favorable, vegetative growth generally receives resource priority over secondary metabolism and storage. What is the relationship between growth and defense when environmental conditions are optimal or suboptimal to various degrees? This is the basic question that motivates this thesis. Before describing the conflicting theories that have been developed to predict such partitioning it is necessary to first clarify the difference between primary and secondary metabolism, the effects of phylogeny on secondary metabolism, and how "growth" is measured.

OBJECTIVES

The spirit of this thesis was guided by a comparative approach to the study of plant chemical defense. It tries to explore a wide set of species and resources availabilities, in systematic and standardized conditions. I will try to provide enough data to understand the great diversity of patterns that I believe exist.

This thesis explores four main questions:

First, is there any correlation between relative growth rate (fast and slow growing plants) and chemical defense (total phenolics and toxicity) in 31 species of Asteraceae under controlled and enriched environmental conditions?

Second, if there is any correlation, is it maintained in an environment in which nutrient levels have been reduced?

Third, I will investigate if there is any correlation between RGR and secondary metabolism under different combinations of light intensity conditions and different level of nutrient conditions for 6 species of Asteraceae.

The last objective is to investigate if there is any difference concerning the amount of secondary metabolism produced by resource availability in *Chrysanthemum leucanthemum* and *Rudbeckia hirta*.

Are plants grown under suboptimal conditions as well defended as plants grown under optimal conditions? And if so, is there any difference in the type of chemical defense (phenolics vs. toxicity) in these environments? For example, do plants produce less carbon-based defenses under suboptimal light conditions rather than under nutrient-limited conditions?

HYPOTHESES

- There is a negative correlation between RGR of slow and fast-growing plants and their secondary compounds under controlled and enriched environmental conditions.

- There is a negative correlation between mobile defense (toxicity) and immobile defense (phenolics) (sensu Coley *et al.*, 1985) under suboptimal environmental conditions.

- Plants grown under light-stressed conditions but optimal nutrient conditions produce less carbon-based secondary compounds than plants grown under nutrient-stressed conditions but optimal light conditions.

- Plants under optimal environmental conditions have a high RGR but produce less secondary compounds than plants grown under stressful environmental conditions.

CHAPTER I

LITERATURE REVIEW

1.1 Plant metabolism

Historically, the processes of generating plant compounds have been separated into primary and secondary metabolism. However, in the light of present-day knowledge, this distinction is arbitrary, as there is no sharp division between primary and secondary metabolites (Figure 1). Secondary metabolites are now known to be very necessary to plant life, many of them providing a defense mechanism against bacterial, viral, fungal and herbivore attack analogous to the immune system of animals. The detection of a compound depends on the sensitivity of the analytical procedure, and many compounds that now seem to be confined to a particular plant will no doubt be found to be widespread as analytical techniques advance (Vickery and Vickery, 1981).

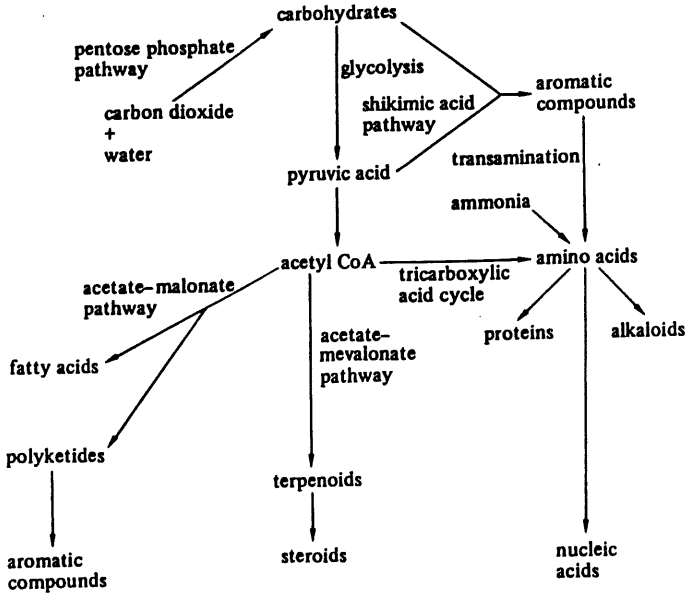


Figure 1. Biosynthetic pathways in plants (copy from Vickery and Vickery, 1981).

1.1.a Primary metabolism

Primary metabolism can be defined as all processes that are responsible for plant growth, like photosynthesis and respiration. Growth consists of cell division followed by cell enlargement, and leads to an irreversible change in plant size.

1.1.b Secondary metabolism

Vascular plants contain an enormous variety of chemical compounds, distinct from the intermediates and products of primary metabolism, which vary according to family and species. The restricted distribution of many such compounds enables them to be used as taxonomic markers, and the so-called "secondary metabolites" make a major contribution to the specific odors, tastes and colors of plants. According to Bennett and Wallsgrove (1994) in the past such secondary metabolites have been viewed as waste products resulting from " mistakes" of primary metabolism, and therefore of little importance to plant metabolism and growth. It is now known that such a view is misguided, and that many secondary products are key components of active and potent defense mechanisms - part of the age-long "chemical warfare" fought between plants and their pests and pathogens.

Secondary metabolites have a great variety of roles, in addition to pest and pathogen defense (Seigler and Price, 1976; Seigler, 1977). For instance these compounds may be involved in carbon and/or nutrient storage (Selmar *et al.,* 1988; Harborne, 1990), protection from UV radiation (Rhoades, 1977; Lee and Lowry, 1980), drought resistance (Rhoades, 1977; Meinzer *et al.*, 1990), protection of roots from acidic and reducing environments (Kimura and Wada, 1989) attraction of pollinating organisms (Rhoades, 1979), allelopathic

interactions with other plants (Inderjit, 1996), and probably many others. Any given compound may well have several such roles (Bennett and Wallsgrove, 1994).

In addition, a single metabolite or class of metabolites present in a plant will not comprise the only defense system. A wide variety of defense-related compounds may be present - in particular tannins, polyphenols, proteases and chitinases are very widely distributed even in species, which contains other major secondary metabolites such as cyanogenic glucosides, glucosinates, alkaloids, etc. There are also physical defense mechanisms such as secondary thickening of leaves, thorns and barbs, cuticular waxes, leaf hairs, and other structural factors known to protect plants (Royle, 1976; Kollatakudy and Koller, 1983). Secondary metabolites very often have a role (or roles) in plant/environment interactions, sometimes a major or dominant role, but they are not the only factors involved (Bennett and Wallsgrove, 1994).

The distribution of a secondary metabolite within a plant, both between tissues and during growth and development, is rarely uniform. According to the review of Bennett and Wallsgrove (1994) many compounds are synthesized by, and accumulate in, young developing tissues, particularly leaves, or in reproductive tissues such as flowers and seeds. There appear to be many examples of secondary metabolites providing protection for young tissues, becoming less abundant and important as the tissue ages (Dement and Mooney, 1974; Cates and Rhoades, 1977; Mauffette and Oechel, 1989; Fujimori *et al.*, 1991).

1.1.c Types of plant secondary compounds

Secondary compounds emerge from a tremendous diversity of biochemical backgrounds (Swain, 1974). They exhibit great diversity in their physical and chemical properties, in the relations of the pathways that produce them to fundamental metabolic pathways, and in the

ways in which they exert toxic effects on biological systems (Swain, 1977). Given the diversity in chemical properties alone, it would be very surprising if there did not exist some sort of partitioning of the function of defense between the various classes of secondary compounds (McKey, 1979). Contrarily to the majority opinions, Gottlieb (1990) demonstrate that the secondary metabolites are equally essential to plant life, because they also adapt an organism (plant) to herbivore pressure, but their protective functions are accidental, rather than original or predestined. In this section, I will describe briefly some secondary compounds, that are studied, in general, in research looking for tradeoffs between plant growth and secondary compounds production.

Phenolic Compounds:

The term "phenolic" is used to define substances that possess one or more hydroxyl (OH) substituents bonded onto an aromatic ring (Figure 2). The natural plant phenolics arise biogenetically from two main pathways: the shikimate pathways, which directly provide phenylpropanoides such as the hydroxycinnamic acids and coumarins; and the polyketide (acetate) pathway, which can produce simple phenols and also many quinones.

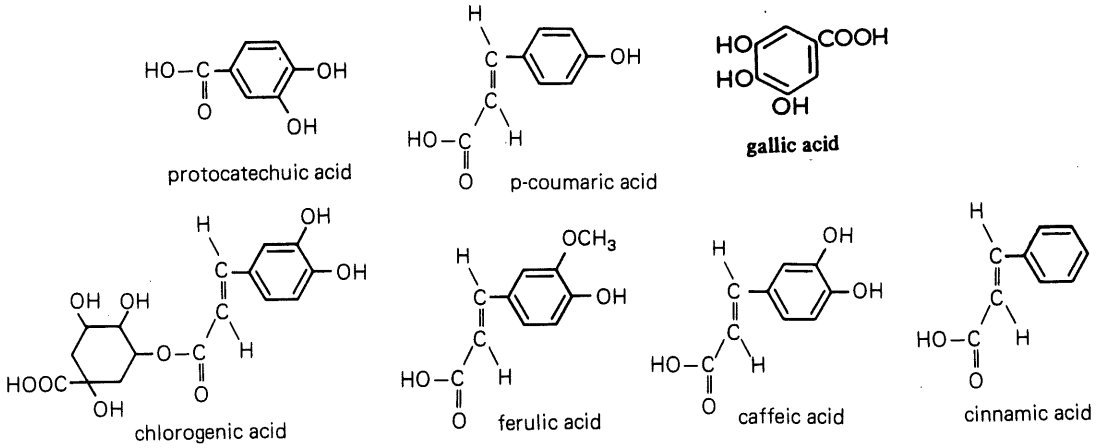


Figure 2. Structures of phenolic acids often found in plants.

Phenolics can play a role in virtually any interaction a plant can have with its environment, biotic or abiotic. In terms of the biotic environment, these interactions may be as allelopathic or feeding deterrents against herbivores (Appel, 1993; Waterman and Mole, 1994). In fact, phenolics were believed to be the most important chemical defense against herbivores (Whittaker and Feeny, 1971; Rhoades, 1979). This point of view was based in several studies showing the effect of tannins on the herbivores (Feeny, 1968, 1970; Rhoades, 1977; McKey *et al.*, 1978). So far as the ecology of plant phenolics is concerned, plant-herbivore interactions are the most widely studied interactions, which these chemicals mediate. A key factor in the development of this topic has been the considerable headway made with two very general groups of proximate assay techniques, those for "total phenolics" and "tannins" (Waterman and Mole, 1994).

Terpenoids:

Terpenoids are the most ubiquitous and structurally diverse class of natural products. Common plant terpene constituents include the monoterpenes, iridoids, abscisic acid, gibberellins, steroids, cardiac glycosides, saponins and carotenoids (Figure 3). The biosynthetic basis for the terpene nomenclature is determined by the number of five-carbon isoprene units incorporated into the carbon skeleton (Gershenzon and Croteau, 1991). Three such isoprene units linked covalently yield a sesquiterpene. The biosynthetically simplest sesquiterpene is farnesyl pyrophosphate (Figure 4), an unsaturated linear molecule which feeds into several alternative pathways, generating the major subclasses of sesquiterpenes (Seaman, 1982).

The terpenoids are distinguished from other classes of secondary metabolites by their common origin from mevalonate and isopentenyl pyrophosphate and by their broadly lipophilic nature (Gershenzon and Croteau, 1990). Characteristic features of the lower

terpenoids are their volatility and intensely pungent odors; mono and sesquiterpenoids are the most common components of flower scents and fragrances. Chemically, terpenoids are usually cyclic, unsaturated hydrocarbons, with varying degrees of oxygenation in the substituents groups (alcohols, aldehyde, lactone, etc.) attached to the basic skeleton (Harbone, 1990).

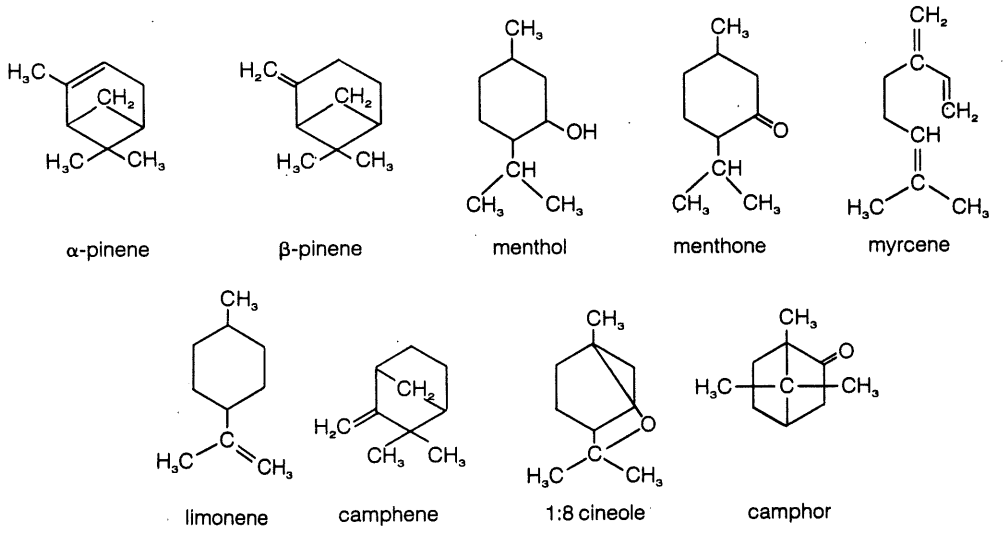


Figure 3. Structures of some terpenes

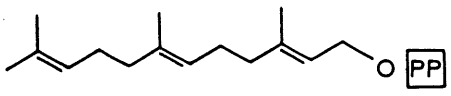


Figure 4. Structure of farnesyl pyrophosphate.

Alkaloids:

The alkaloids are a diverse collection of compounds whose only molecular similarity is the presence of nitrogen (Figure 5). Those compounds occurring in plants can be divided into the true alkaloids, the protoalkaloids and the pseudoalkaloids, according to their molecular structure and biosynthetic pathways (Vickery and Vickery, 1981).

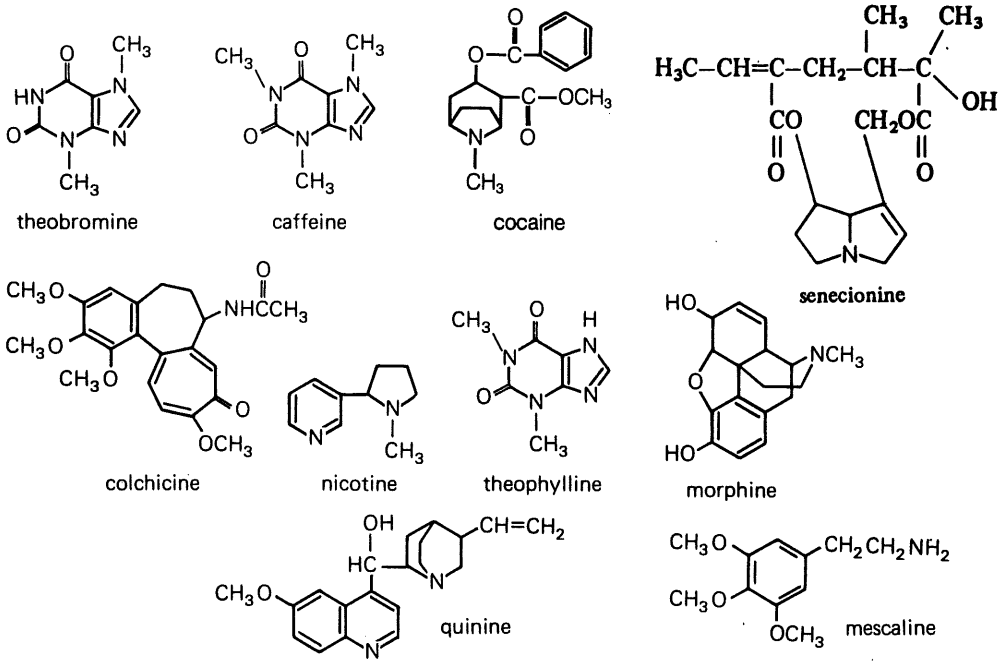


Figure 5. Structures of some representative alkaloids.

Several suggestions have been made concerning the function of alkaloids in plants, and it seems probable that these are useful to the plant in several ways. As with other toxic secondary metabolites, the main function of alkaloids is probably to protect the plant against predators (Petterson *et al.* 1991).

All alkaloids have some physiological action, generally on the central nervous system (Robinson, 1979). Alkaloid-containing plants probably cause more stock loss throughout the world than any other type of poisonous plants. Plants responsible for most stock poisoning on a worldwide scale are *Senecio* and *Crotalaria* species, yew and green potatoes (Mattocks, 1972).

1.2 Taxonomy and secondary compounds

The types of secondary compounds found in a species are strongly determined by its evolutionary history. Unlike the products of primary metabolism that are common to all plants, the secondary metabolic profile of different plant species varies considerably, reflecting evolutionary history through taxonomic relationships (Gottlieb, 1989, 1990; Harborne, 1990). It is important, when comparing different species to do the comparison between species having broadly similar chemical defenses. I choose the family Asteraceae, because (a) it is a monophyletic group and therefore all of these plants share a common ancestry, (b) the dominant class of secondary compounds in this family are sesquiterpene lactones, other terpenes and polyacetylenes, and finally, there are a large number of species within the Asteraceae. The following paragraphs describe this family and its characteristics.

1.3 Asteraceae Family

1.3.a Taxonomic aspects

The Asteraceae make up one of the largest and most successful flowering plant families, consisting of 12-17 tribes, approximately 1,100 genera, and 20,000 species (Cronquist,

1981). It is generally accepted that the Asteraceae are a "natural" family with well established limits and a basic uniformity of floral structure imposed on all members (Heywood *et al.*, 1977). A combination of specialized floral characters (capitula, reduced and modified floral parts, inferior ovaries, basal and erect ovules, and syngenesious anthers) supports the monophyly of the family (Palmer *et al.,* 1988). Recent classifications (Dahlgren, 1980; Cronquist, 1981) have emphasized the distinctness of the family by placing it in a monotypic order at the most advanced position in the Dicotyledonae. Although there is some controversy concerning the age of the family (Turner, 1977), fossil evidence (Cronquist, 1977; Muller, 1981) and biogeographical considerations (Raven and Axelrod, 1974) suggest that the Asteraceae originated in the middle to upper Oligocene (30 million years ago) and subsequently underwent rapid and extensive diversification.

1.3.b Chemical aspects

Several classes of plant compounds are characteristic of this family, notable the terpenoid-based sesquiterpene lactones, the fatty acid derived polyacetylenes and the polysaccharide fructans. The Asteraceae, in fact, are exceptionally rich, both in the range of secondary compounds present and also in the numbers of complex structures known of any one class (Heywood *et al.,* 1977). Furthermore the family is very distinctive in its chemical attributes. Although no single class of constituent is unique to the family, the Asteraceae are unlike any other family in the array of characteristic constituents.

Many of the substances elaborated by the family are toxic or show other significant physiological activity. The rich accumulation of essential oils and other terpenoids in certain composites is responsible for the use of various members such as tansy (*Tanacetum vulgare*) for flavoring foods or liqueurs (Heywood *et al.*, 1977). Terpenoids and certain phenolic constituents are also responsible for the value of many Asteraceae in pharmacology and

medicine. When considering the economic value of plants of the Asteraceae, it must be pointed out that the useful plants are to a considerable extent counter-balanced by the large number of weeds in the family. Indeed, there are few families with such an abundance of weedy members, many of which are extremely successful and have spread throughout the temperate areas of the world. The success of these weeds stems mainly from the development of biological features, which ensure both survivals under adverse environmental conditions and also a high reproductive rate. Chemical factors are, nevertheless, important in Asteraceae weeds in providing protection from over-grazing.

The family is chemically very distinct (Mabry and Bohlmann, 1977). Inulin-type fructans, seed oils sometimes containing characteristic fatty acids, bitter sesquiterpene lactones, pentacyclic triterpene alcohols, accumulation of large amounts of derivatives of caffeic acid, of flavones and of methylated flavonols and a total lack of true tannins and of iridoid glycosides were especially mentioned. Acetylenic compounds, not reported from the tribes Senecioneae and Cichorieae, and essential oils, not accumulated by latex-bearing Cichorieae, were likewise considered to belong to the chemical make-up of the family Asteraceae (Hegnauer, 1977). The following paragraphs will describe the major groups of secondary compounds studied in the Asteraceae at the present time.

Sesquiterpene lactones

Sesquiterpene lactones are colorless, often bitter-tasting, lipophilic constituents, which are the most characteristic single group of chemicals known in the Asteraceae. They are present mainly in leaf tissues and can constitute up to 5% of the dry weight (Heywood and Harborne, 1977). They have been detected in all the tribes except the Tageteae. A number are toxic to livestock and their major role in the ecology of the family seems to be as a deterrent to mammalian herbivores (Rodriguez, 1983; Harborne, 1988). The presence of sesquiterpene

lactones in the Asteraceae is often associated with a bitter taste, and it is likely that this repellent taste response acts as a signal to protect the plants from being heavily grazed. They also have insecticidal activity (Marles *et al.*, 1994). Furthermore, the lactones are not only feeding toxins in the case of mammals but they also cause allergic contact dermatitis (Rodriguez *et al.*, 1976).

Picman (1986) in her review demonstrated that sesquiterpene lactones display a variety of activities against numerous types of organisms (Figure 6). This suggests that the individual lactones from this group of secondary plant metabolites may play a role in defense of plants against pathogens, herbivorous insects and mammals, and in competition with other plants. Sesquiterpene lactones form one of the largest group of cytotoxic and anti-tumor compounds of plant origin. Anti-bacterial, anti-fungal activity, anti-protozoan activity, activity against human and animal parasites (including intermediate hosts) are other tribes of biological activity.

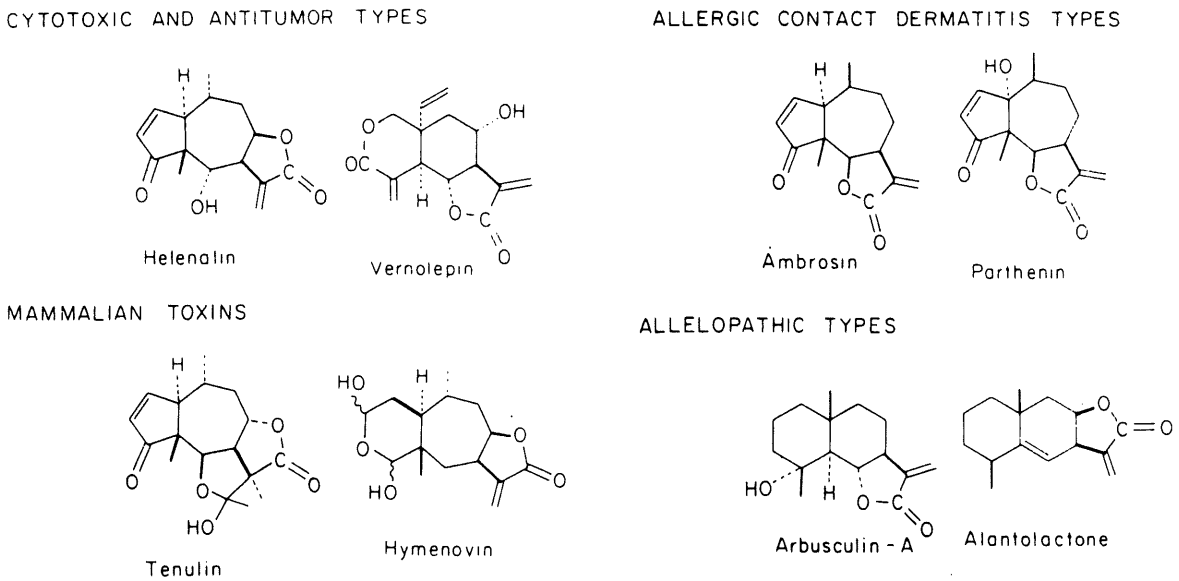


Figure 6. A few of the many sesquiterpene lactones known to exhibit various types of biological activities (copy from Mabry and Gill, 1979).

Triterpenes

Asteraceae are triterpene accumulators. Monols and diols of the oleanol, ursanol, and lupeol type are most characteristic of the family. They occur free or, more frequently, esterified with acetic acid or fatty acids in the lipid fractions of roots, stems, flowers and fruits and, in Cichorieae, in lattices (Hegnauer, 1977). The co-occurrence of the monols and diols represent a metabolic trend of the family as a whole. The synthesis of triterpene acids, saponins and rare triterpenoids, such as shionone, may become taxonomically useful in future at the generic and tribal levels.

Acetylenic compounds

These reactive substances have been found in roots, flowers and/or leaves of the great majority of the composites that have been surveyed. According to Arnason *et al.* (1992) there are 700 known polyacetylene compounds (Figure 7), which are characteristic of the Asteraceae, but are also found in several other families, but so far phototoxic polyacetylenes have not been recorded from the other families. Acetylenic compounds are much more labile than most other plant substances and they can only be isolated successfully from fresh plant material. Just as with other classes of secondary metabolites, a hierarchy can be discerned in acetylene production. Synthesis of acetylenes is a characteristic of the family as whole and distinct patterns may be attributes of tribes and lower systematic categories. These general trends, however, are often considerably upset by certain deviating taxa (Cichorieae and Senecioneae). The causes of this variation and versatility in secondary metabolism are generally unknown, but are most probably the consequences of selection. An ecological function of many polyacetylenes is suggested by the nematicidal action and the antibiotic properties of carlina oxide and the alexin-like behavior of the safflower (*Carthamus tinctorius*) acetylenes (Hegnauer, 1977). The fast acting poison ichthyothereol of

Ichthyothere terminalis (Spreng.) Malme (Chin *et al.*, 1965) and *Clibadium silvestre* (Aubl.) Baill. (Gorinsky *et al.*, 1973) may be toxic for many organisms other than fishes.

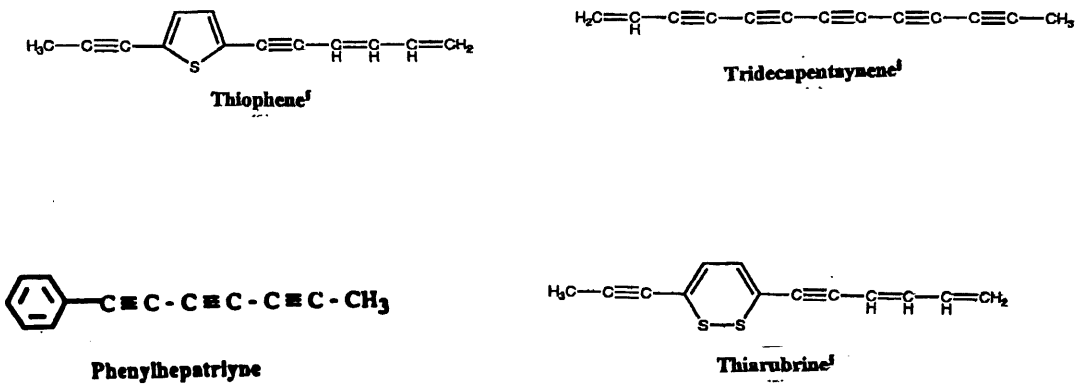


Figure 7. Structures of some polyacetylene compounds.

Alkaloids and alkaloid-like compounds

According to Hegnauer (1977), the Asteraceae is considered as a group in which alkaloids are not rare. At the same time he affirms that evidence suggests alkaloid patterns are characteristic of species, genera or tribes rather than of the family as a whole. Probably the most well known alkaloid present in this family is pyrrolizidine of Senecioneae and Eupatorieae. Pyrrolizidine alkaloids are so effective as mammalian toxins that about 50% of all cattle deaths due to plant poisoning (Heywood and Harborne, 1977), and occasionally of humans (Mattocks, 1972), are the result of ingestion of these particular alkaloids. Hegnauer (1977) lists some species in which alkaloids or alkaloid-like compounds where found.

1.4 What is RGR and how is it measured?

Growth analysis is often used as a tool to obtain insight into the functioning of a plant. Growth could be defined as any type of change that occurs in an essential feature of life, like the capacity to change in size, mass, form and/or number (Chiariello *et al.,* 1991). Ecological studies examine growth in two different, but complementary, ways. The first emphasizes productivity and views growth as the change in mass of live biomass through time. The second emphasizes demographic processes and views growth as the difference between the production of new biomass units, or "modules" (such as leaves, stems, twigs, roots) and the death or loss of old modules. Absolute growth during a time interval can be calculated by simple subtraction: biomass or module number at the end of the interval minus at the beginning. This absolute growth rate is rarely used because it is so strongly influenced by plant size.

The fundamental parameter of traditional growth analysis is the relative growth rate (RGR), also termed specific growth rate, which is the instantaneous rate of increase relative to the productive mass of the plant. It measures the mass of new biomass produced per unit of time by a given mass of pre-existing biomass, and is therefore analogous to a compound interest rate. Introduced as the "efficiency index" by Blackman (1919), RGR provides one of the most ecologically significant and useful indices of plant growth.

Specific leaf area (SLA) is the ratio of leaf area to leaf dry weight. It varies considerably between environments and species and is plastic within individuals. In particular, SLA (like the root:shoot ratio) decreases with increasing light intensities and changes in this attribute are diagnostic of shading.

One of the characteristics in which species of different habitats vary is their growth potential. When grown under optimum conditions, plant species from fertile, productive habitats tend to have inherently higher relative growth rates (RGR) than species from less favorable environments even when plants are grown under optimum conditions and free of competition (Christie and Moorby, 1975; Grime and Hunt, 1975; Poorter and Remkes, 1990; Lambers and Poorter, 1992; McKenna, 1995). Under these conditions, fast-growing species produce relatively more leaf area and less root mass, which greatly contributes to their larger carbon gain per unit plant weight. They have a higher rate of photosynthesis per unit leaf dry weight and per unit leaf nitrogen, but not necessarily per unit leaf area, due to their higher leaf area per unit leaf weight. Fast-growing species also have higher respiration rates per unit organ weight, due to demands of a higher RGR and higher rate of nutrient uptake. However, expressed as a fraction of the total amount of carbon fixed per day, they use less in respiration (Lambers and Poorter, 1992).

Fast-growing species have a greater capacity to acquire nutrients, which is likely to be a consequence, rather than a cause, of their higher RGR. There is no evidence that slow-growing species have a special ability to acquire nutrients from dilute solutions, but they may have special mechanisms to release nutrients when these are sparingly soluble (Lambers and Poorter, 1992).

Lambers and Poorter (1992) have analyzed variation in morphological, physiological, chemical and allocation characteristics underlying variation in RGR, to arrive at an appraisal of its ecological significance. When grown under optimum nutrient conditions and moderately low light intensity (300 $\mu mols/m^2/s$), fast growing species contain higher concentrations of organic nitrogen and minerals. According to those researchers the lower specific leaf area (SLA) of slow-growing species is at least partly due to the relatively high concentration of cell-wall material and quantitative secondary compounds, which may

protect against detrimental abiotic and biotic factors. As a consequence of a greater investment in protective compounds or structures, the rate of photosynthesis per unit leaf dry weight is less, but leaf longevity is increased according to Lambers and Poorter (1992). There is, however, little experimental evidence of this, and is one of the questions explored in this thesis.

1.5 The Dilemma of Plants: Growth and Defense.

The idea that a plant must accept tradeoffs because it must allocate limited resources among growth, reproduction, and defense has been central to ecological and evolutionary theories (Feeny, 1976; Rhoades and Cates, 1976; Krischik and Denno, 1983; Coley *et al.,* 1985; Herms and Mattson, 1992; Tuomi, 1992; Frank, 1993). If a plant allocates a greater proportion of resources to defense, then less should be available for growth and/or reproduction. The concept of costs and benefits of defense has been central to hypotheses that postulate variations in defense investment associated with successional status (Cates and Orians, 1975), soil quality (Janzen, 1974), plant "apparency" (Feeny, 1976), leaf lifespan (Janzen, 1974; Stanton, 1975), environmental variations facing a single species (Cates, 1975), and intraplant distribution (Orians and Janzen, 1974; Rhoades and Cates, 1976).

Some of the literature published until now have considered the costs of defense on a whole-plant basis, i.e. direct carbon costs of construction of the molecules and the cost of maintenance of the cellular machinery needed to construct them, and indirect costs, which involves the reduction in plant growth at some future time because of the allocation of carbon to defense in the present. Givnish (1986) affirms that plants should be defended more heavily in unproductive habitats or in slow-growing forms, in which a leaf is more costly to replace, in terms of nutrients or the photosynthetic period needed to repay its construction cost. According Jong (1995) defense (secondary compounds) is costly because it diverts

assimilates from growth, reducing the inherent growth rate of the plant. Table 1 shows that the costs of the biosynthesis of a gram of defensive chemicals range from the same as, or up to twice as much as the mean cost of construction of a gram of leaves. A large investment in costly reduced compounds may thus affect the plant's growth rate and vitality (Baas, 1989).

Table 1. Mean costs of construction of leaves and of various secondary compounds (after Gulmon & Moony, 1986). Copy from Baas 1989.

Type	Compound	Formula	Cost ($g\ CO_2/g$)	Content (% leaf wt)	Plant
leaves			1.93-2.69		Shrub species
phenolic resin	diplacol	$C_{22}H_5O_7$	2.58	29%	*Diplacus aurantiacus*
cyanogenic glycoside	prunasin	$C_{14}H_{17}NO_6$	2.79	6	*Heteromeles arbutifolia*
alkaloid	nicotine	$C_{10}H_{14}N_2$	5	0.2-0.5	*Nicotiana tabacum*
long-chain hydrocarbon	2-tride-canone	$C_{13}H_{26}O$	4.78	0.9-1.7	*Lycopersicum hirsutum*
terpenes	camphor	$C_{10}H_{16}0$	4.65	1.3	*Salvia melifera*

Gershenzon (1994) agrees that the costs to produce secondary compounds are more expensive than those to produce primary compounds and affirms that terpenoids are more expensive to manufacture per gram than most other primary metabolites (Table 2), but that the maintenance of this particular compound pool is probably inexpensive because there is no evidence that substantial quantities of terpenes are lost as a result of metabolic turnover, volatilization, or leaching. From studies on cost/benefit relations, little direct correlation seems to exist between investment in defense compounds and benefits to the plant. Other factors could be influencing the production of the secondary compounds.

Table 2. Average substrate and cofactor costs for terpenoids and various other classes of plant primary and secondary metabolites (Gershenzon, 1994).

		Cost (g glucose/g)	
Class	N	Mean	Range
Terpenoids	23	3.18	1.99-3.54
Primary metabolites			
Fatty acids	2	3.10	3.01-3.18
Amino acids	20	2.09	1.23-2.82
Nucleotides	4	1.59	1.27-1.80
Carbohydrates	5	1.07	1.00-1.11
Organic acids	4	0.73	0.61-0.87
Secondary metabolites			
Alkaloids	5	3.24	2.89-3.62
Other nitrogen-containing compounds	8	2.27	1.70-2.83
Phenolics	9	2.11	1.28-3.39

The evolutionary response of plants to herbivores is also strongly influenced by other selective pressures in the plant's environment, such as nutrient availability. Studies of the resource availability hypotheses have tended to contrast the defense capacities of the plant species growing in two different resource states (McKey *et al.,* 1978; Bryant and Kuropat, 1980; Coley, 1983; Newberry and de Foresta, 1985; Baldwin and Schultz, 1988). However, in most natural communities, individuals within a population of plants may often experience a wide range of different levels of resource availability (Grime, 1979; Keddy, 1989). Differences in resource availability have been shown to generate variation in defensive chemistry within a single species (Waterman *et al.,* 1984; Larsson *et al.,* 1986; Bryant *et al.,* 1987 b; Shure and Wilson, 1993). Such variation in defensive chemistry, even on a small spatial scale, may influence host selection and subsequent success of insect herbivores (Zangerl and Berenbaum, 1993). Therefore, it is important to understand how a range of resource availabilities influences phenotypic variation in plant allocation to defensive chemistry.

In recent years, much attention has been focused on the mechanisms by which the environment may alter the plant's production of chemical defenses, and thereby alter the susceptibility to herbivores (Mattson, 1980; Bryant *et al.,* 1983; Mooney *et al.,* 1983; Tuomi *et al.*, 1984). Carbon/nutrient balance is viewed as a key to understanding why plant susceptibility changes under different growing conditions. We might expect that carbon-based defensive chemicals (e.g. phenols, terpenes, acetylenes) should be scarce in plants subjected to reduced carbon uptake or very high respiration, where a low carbon/nutrient ratio would result. On the other hand, plants provided with adequate light, even when subjected to suboptimal nutrient availability, should exhibit a high carbon/nutrient ratio and resistance to herbivory (Bryant *et al.,* 1983).

Plants growing under nitrogen-limiting conditions generally have a slower growth rate than those growing under nitrogen-rich conditions. Comparable loss of leaf nitrogen to herbivores by nitrate-limited and nitrate-rich plants presumably has a greater impact on the growth of nitrogen-limited plants. Carbon supply does not limit plant growth under low nitrate conditions and subsequently, increased quantities of carbon-based defenses should be selected for as nitrate availability decreases (Janzen, 1974; McKey *et al.*, 1978; Bryant *et al.*, 1983; Coley *et al.*, 1985; Mihaliak and Lincoln, 1985).

A negative correlation between two traits can be generated in two general ways. One possibility is that there is no genetic link between the two traits, but each responds in an opposite way to some common environmental change. The other possibility is that the negative correlation is generated by the physiology or morphology of the plant even when the environment is constant. This second possibility is a "genetic" correlation and provides an operational definition of a "trade-off". The existence of a trade-off between growth and defense has generated some controversy. Even if some studies have found a negative correlation between RGR and the attack by herbivores (Coley, 1983; Sheldon, 1987), others (Meijden *et al.*, 1988; McCanny *et al.*, 1990) did not find any correlation, and still others (Denslow *et al.*, 1987, 1990; Briggs and Schultz, 1990) show a positive correlation between the two variables.

How may resource availability constrain secondary metabolism and, thereby, plant defensive responses? How may resource availability constrain the costs of defense and under what conditions can this be considered to indicate a negative genetic correlation between defense and growth?

A study that can provide answers to such questions should have a number of attributes. First, it should include a number of different species that differ both in their growth potentials and

in their production of secondary metabolites. This is important because the ecological questions refer to general responses, not responses limited to any particular species. Second, the study species should share a common known phylogenetic history. This is important because the types of secondary compounds produced by a species are strongly constrained by its evolutionary history. Third, the variation in resource availability should be imposed through a controlled randomized experiment in order to separate genetic and environmental correlations. Fourth, the range of resource availabilities should be sufficient to detect any non-linear responses by either growth or nutrient availabilities.

Few studies have examined how a range (i.e., more than two levels) of a resource affects allocation to defensive chemistry and growth-related characteristics (Mihaliak and Lincoln, 1985; Waring *et al.,* 1985; Shure and Wilson, 1993). Furthermore, few studies have examined how two resources, simultaneously manipulated influence the allocation by plants to secondary chemicals (Larsson *et al.,* 1986; Bryant *et al.,* 1987 a, b; Dudt and Shure, 1994).

In this project my focus is on plants, not on the response of herbivores or pathogens to the plants. I report results from 32 wild herbaceous species of the family Asteraceae that evaluate how they allocate resources to defensive chemistry versus growth when grown over a range of resource availabilities. All experiments were performed under controlled environmental conditions.

1.6 Plant-herbivore defense theories

1.6.1 Apparency Theory

Feeny (1976) and Rhoades and Cates (1976) presented the major theory for the last 21 years to explain defensive differences among species. This "apparency theory" suggests that some species are poorly defended because they are sufficiently rare (in either time or space) that they escape discovery by herbivores. This hypothesis predicts that only species, which are easily found by herbivores, need to invest in defenses. The theory implies that species should have similar rates of damage in the field, with some species (unapparent) minimizing damage by escaping and others (apparent) by chemical defenses.

Feeny (1976) based his studies on patterns of interaction between herbivorous insects and oak trees (*Quercus robur*) and various crucifer species. He concluded that tannins represent the major chemical defense of mature oak leaves while glucosinolates represent the primary chemical defense of crucifers. Based on these findings he elaborated some hypotheses. First, he distinguished chemical defenses as two differents kinds: "qualitative" (for instance glucosinolates, which are present and effective, even in small concentrations, against non-adapted insect species) and "quantitative" (for instance tannins, which are dosage-dependent). But, the major goal of his hypotheses was the prediction that "the susceptibility of an individual plant to discovery by its enemies may be influenced not only by its size, growth, form and persistence, but also by the relative abundance of its species within the overall community". According to their susceptibility to be found, Feeny divided the plants into two groups: "apparent" and "unapparent". Feeny (1976) defined the "apparency" of an individual plant to its enemies as determined both by its genotype, reflected in various adaptations such as growth form and secondary chemistry, and also by various environmental influences which act on the phenotype. "Apparency" is also dependent upon various characteristics of

the microenvironment and of the community as a whole. Such characteristics include the nature of neighboring plants, the population density of the plant's own species and the species, numbers, and host-finding adaptations of all relevant herbivores and pathogens in the community. It is clear that "apparency" is difficult to measure in any objective way.

In the same year, Rhoade and Cates published an analogous theory that emphasized the " predictability" and "availability" of the plant or plant tissue as a food resource to herbivores. They assumed that plant defenses are costly to the time and energy budget of plants and concluded that the observed distribution of toxic and digestibility-reducing defensive systems, both between leaves of different stages of maturity and between plant species, can be explained in terms of greater investment in chemical defense for "predictable" plants and tissues than for ephemeral plants and tissues. Since the probability of escape, particularly escape from specialist herbivores, is high for ephemeral plants and ephemeral leaf tissues, according to Rhoade and Cates (1976), they are defended by a cheap, divergent, toxic chemical defense affording some protection against generalist herbivores. The probability of escape is low for predictable plants and predictable plant tissues which thus utilize a more costly convergent digestibility-reducing chemical defense, effective against both specialist and generalist herbivores. They believe that predictable plants utilize toxins in their ephemeral tissues and generalized digestibility-reducing systems, particularly tannins, in their predictable leaf tissues. Finally, ephemeral plants utilize toxins in their ephemeral tissues and are postulated to utilize specific digestive enzyme inhibitors, in their mature leaves.

Table 3 summarizes the apparency theory based on the characteristics of "apparent" and " unapparent" plants. Coley (1983) found no evidence to explain the observed differences in defense for tropical trees. She found no evidence that supposedly "unapparent" pioneers escape discovery by herbivores more than the persistent species do. As an alternative to the apparency theory, Coley proposed a new one (termed the resource availability theory).

According to Futuyma (1983) there is no evidence that genetic changes in plants and insects are highly coupled as would be suggested by the term "arms race" of the apparency theory. He affirms that the diversity among the secondary plant compounds would result from broad-spectrum adaptations of plants to a very large suite of enemies, including vertebrate herbivores and pathogens, rather than from plant-insect coevolution.

Table 3. Growth habitats, type of growth and defense-type of unapparent and of apparent plants (based on Gershenzon 1984).

"unapparent" plants	"apparent" plants
- adapted to favorable growth conditions	- constantly or temporarily environmentally stressed: nutrient deficiency; water stress (arid regions, salinity, extreme temperatures)
- growth limited by photosynthetic light	- light generally not growth limiting
-growth is highly related to increase in photosynthetic tissue	- growth highly related to the formation of secondary compounds
- defense: small amounts of toxins	- large amounts of quantitative defense compounds

1.6.2 Optimal Defense Hypothesis (OD)

The OD hypothesis predicts a negative relationship between growth and defense. This hypothesis argues that allocation to defense by any given plant can only be understood in terms of the herbivore pressure experienced by that plant over evolutionary time (McKey, 1974; Rhoades, 1979). For this hypothesis defenses are always costly, that is, any carbon allocated to defense is removed from a pool of carbon that the plant could partition for growth, and that there are no internal physiological constraints on how a plant may allocate fixed carbon (Rhoades, 1979).

1.6.3 Resource Availability Theory

Coley *et al.* (1985) proposed, as an alternative to the apparency theory that plant species differ in their defenses because they differ in their intrinsic rate of growth. They assume that in a world without herbivores, the maximum potential growth rates would be determined by the resource availability in the environment (modified slightly by allocation patterns of individual species). Inherent growth rates of plants may influence the type of defense as well as the amount. Because of the increased conservation of resources, slow-growing plants of resource-limited environments have longer-lived leaves than fast-growing species (Table 4). According to them, intrinsically slow growth rates are thought to favor selection for high amounts of defense, because the opportunity costs of defense are relatively low, and the potential impact of herbivory is extremely high. The type of defense is also thought to be influenced by growth characteristics of the species, specifically the average leaf lifetime (McKey, 1984; Coley *et al.*, 1985). Long leaf lifetimes are thought to favor selection for immobile defenses such as tannins and lignins, large molecular weight compounds which are metabolically inactive (Coley *et al.*, 1985). Immobile defenses do not have the continued metabolic cost of turnover, but they have large initial construction costs, and cannot be

reclaimed upon leaf senescence (McKey, 1979, 1984; Coley *et al.*, 1985). Coley *et al.* (1985) preferred the terms "mobile" and "immobile" defenses as opposed to "quantitative" and " qualitative" because the latter implies two distinct modes of action against herbivores, and these have not been well supported. The terms "mobile" and "immobile" defenses refer to physiological properties of the defenses in plant and encompass a continuum of metabolic activity and mobility (Coley *et al.*, 1985).

Table 4. Characteristics of inherently fast-growing and slow-growing plant species (Coley *et al.*, 1985).

Variable	Fast-growing species	Slow-growing species
Growth characteristics		
Resource availability in preferred habitat	high	low
Maximum plant growth rates	high	low
Maximum photosynthetic rates	high	low
Dark respiration rates	high	low
Leaf protein contents	high	low
Responses to pulses in resources	flexible	inflexible
Leaf lifetimes	short	long
Successional status	often early	often late
Antiherbivore characteristics		
Rates of herbivory	high	low
Amount of defense metabolites	low	high
Type of defense (sensu Feeny)	qualitative (alkaloids)	quantitative (tannins)
Turnover rate of defense	high	low
Flexibility of defense expression	more flexible	less flexible

The cost of defense by immobile compounds is therefore independent of leaf lifetime and would be most cost-effective in long-lived leaves (Figure 8). Shorter leaf lifetimes would favor defense by low molecular weight mobile compounds such as alkaloids, cardiac glycosides or monoterpenes (Feeny, 1976). Since these compounds have rapid turnover rates, they must be continually synthesized. The cost of defense therefore accumulates over the entire leaf lifetime (Coley *et al.*, 1985).

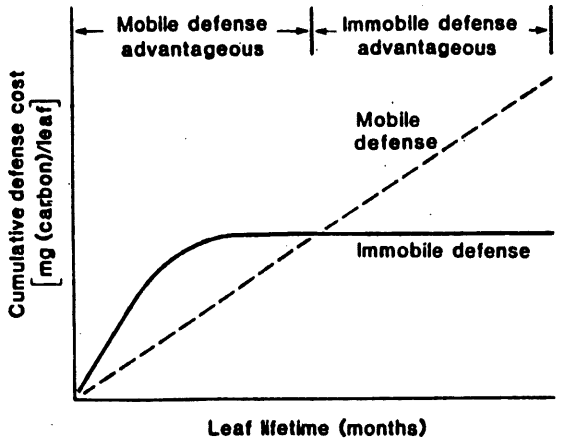


Figure 8. The cost of defending a leaf according to the mobile or immobile defenses (Coley *et al.*, 1985).

In summary, Coley *et al.* (1985) predicts that species adapted to low-resource habitats will have intrinsically slow growth rates, and therefore high amounts of defense and low rates of herbivore damage. However, a given defense level will mean a larger opportunity cost for fast-growers, since any resources allocated to defense translate to a greater reduction in growth for fast than slow-growers (Coley *et al.*, 1985; Gulmon and Mooney 1986). Therefore, it may be that fast-growers (with low defense levels but high opportunity costs) and slow-growers (with high defense levels but low opportunity costs) suffer relatively similar defense related growth reductions (Coley, 1988).

1.6.4 The Carbon/Nutrient Balance Hypothesis (CNB)

This theory was introduced at about the same time by Bryant *et al.* (1983), Waterman *et al.* (1984) and Gershenzon (1984). It is based on the influence of the abiotic habitat on the carbon/nutrient balance of the plant. The carbon/nutrient balance of plants is regarded as an important factor in the defensive chemistry and the palatability of plant tissues to herbivores.

In their carbon/nutrient hypotheses, Bryant *et al.* (1983) suggest that resources present in excess of growth demands are put into defense. For example, in sunny conditions within limiting nutrients, carbon will be relatively in excess and carbon-based defenses such as tannins and terpenoids will increase. Conversely, in shaded conditions, carbon-based defenses decrease. Analogous patterns are predicted for nitrogen-based defense and nitrogen availability.

The CNB hypothesis predicts that concentrations of carbon-based secondary metabolites (e.g. terpenes, phenolics, and other compounds that have only C, H and O as part of their structure) will be positively correlated with the carbon/nutrient (C/N) ratio of the plant. Conversely, concentrations of nitrogen-based secondary metabolites (e.g. alkaloids, nonprotein amino acids, cyanogenic compounds, proteinase inhibitors, and others having N as part of their structure) are predicted to be inversely correlated with C/N ratio of the plant (Bryant *et al.*, 1983).

According to Bryant *et al.* (1983), moderate nutrient deficiency limits growth rate more than photosynthetic rate. Hence, nutrient-deficient plants are assumed to accumulate carbohydrates, increasing the C/N ratio within the plant. Carbohydrates accumulated in

excess of growth requirements are allocated to C-based secondary metabolites. In contrast, increased nutrient uptake in fertile soils is predicted to decrease the C/N ratio within the plant; C-based secondary metabolism is predicted to decline as growth receives allocation priority. As other factors begin to limit growth, nitrogen assimilated in excess of growth requirements may be allocated to production of N-based secondary metabolites (Bryant *et al.,* 1983).

According Bryant *et al.* (1983) light intensity can also affect the C/N balance within the plant, and consequently secondary metabolism. Shade decreases C/N ratio of plants by limiting carbon assimilation more than nutrient uptake. Concentrations of C-based secondary metabolites decline as limited available carbon is allocated to growth. Nitrogen assimilated in excess of growth requirements, however, may be diverted to N-based secondary metabolic pathways. On the other hand, increased light intensity is predicted to increase net photosynthesis, thereby increasing the C/N ratio within the plant, and concentrations of C-based secondary metabolites. Concentrations of N-based secondary metabolites are predicted to decline as N is allocated to photosynthetic and growth processes (Bryant *et al.,* 1983).

Baas (1989) proposed to extend the carbon/nutrient balance theory to all other processes that affect the carbon status or nutrient availability to the plant. He named "carbon/nutrient cycle theory" (CNC-hypothesis). He predicted that the main significance of secondary compounds is their regulatory and selecting role in the often multitrophic (sym)biotic interaction of host plant and their dependent heterotrophic organisms.

1.6.5 Growth-differentiation balance (GDB)

The growth-differentiation balance hypothesis was first developed by Loomis (1932, 1953) and later elaborated by Lorio (1986) and Herms and Mattson (1992) for application to plant-insect herbivore systems. The GDB hypothesis provides a framework for predicting how plants will balance allocation between differentiation-related process over a range of resource environments. Loomis defined "growth" as the process of cell division and cell elongation that results in an irreversible increase in size, and "differentiation" as the process that leads to and enhances morphological and metabolic features of cells or tissues. Differentiation processes typically occur after cell expansion has occurred. Examples of differentiation-related products are: lignification, cuticle production, trichome production, and secondary metabolism leading to products such as alkaloids, phenolics, and terpenes (Loomis, 1932, 1953). Specifically, the GDB hypothesis makes the following predictions: (1) plants experiencing very low levels of resources should be limited in both growth and photosynthetic capability, and therefore exhibit both low biomass gain and low secondary-metabolite concentration (Herms and Mattson, 1992). At low resource levels, plants must maintain baseline metabolic and growth processes to survive (Figure 9). Therefore, limited resources may be preferentially shunted into these processes, resulting in a lower relative allocation to secondary chemicals compared to plants growing in higher resource conditions (Waring and Pitman, 1985); (2) plants experiencing intermediate resource availability will have high concentrations of secondary metabolites, but an intermediate level of biomass accumulation (Figure 9), relative to plants experiencing higher or lower levels of resources (Loomis, 1932, 1953). The GDB hypothesis predicts this pattern at intermediate levels of resource availability because growth (through cell division and enlargement) is inhibited by relatively small shortages of resources, whereas net photosynthesis is less sensitive to the same level of resource limitation (Chapin, 1980; Dietz 1989; Körner, 1991; Luxmoore, 1991). Therefore, secondary metabolites, a product of photosynthesis, will tend to accumulate in plants that are photosynthesizing at high levels but also experiencing growth

inhibition due to moderate resource shortage. Thus, defenses produced from the excess pool of carbon are "cost-free" because they are constructed of carbon that the plant is unable to allocate to growth anyway; (3) finally, plants experiencing high resource availability will not be limited in photosynthesis or growth and, therefore, growth processes receive allocation priority for resources, decreasing the relative availability of carbon for the support of secondary metabolism and structural reinforcement (Figure 9) (Loomis, 1932; Herms and Mattson, 1992). Hence, within a population, the fastest growing plants will be the least resistant to (but perhaps the most tolerant of) herbivores (Bryant *et al.*, 1983; Mihaliak and Lincoln, 1985; Larsson *et al.*, 1986).

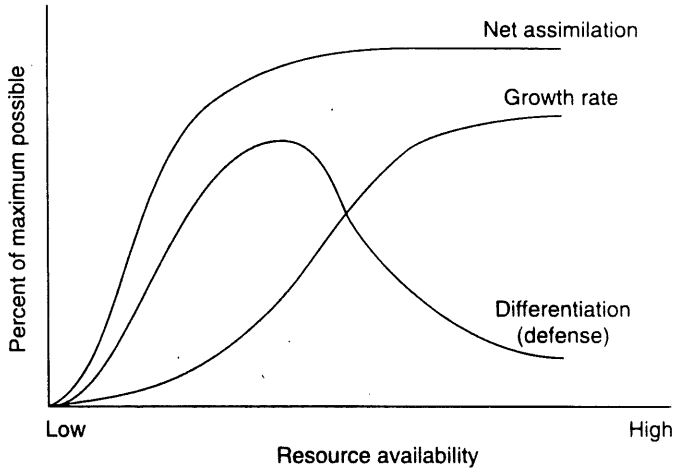


Figure 9. The relationships among resource availability, assimilation, growth and differentiation (copy from Herms and Mattson, 1992).

In fact, none of these theories have really ever been resoundingly rejected; they all more-or-less coexist, by virtue of supportive evidence in some system or other and because of the difficulty of translating the theoretical concepts into measurable variables. Studies of plant-herbivore interactions are in a sense unique in the field of chemical ecology; no other area is quite so rife with speculative theory (Berenbaum, 1995).

The relative importance of consumer selection pressure in determining patterns of production of secondary compounds varies with the theory. Coley *et al.* (1985) suggest that resource availability and the concomitant growth rate of a plant, more than its potential risk of herbivory or its historical association with herbivores, determine the type and quantity of chemical defenses in plants; while "the predictability of a plant in time and space may influence the degree of herbivore pressure it should be included as a complementary factor", rather than as the sole driving force in the evolution of chemical defenses and their allocation patterns. Bryant *et al.* (1983) suggest that carbon and nutrient availability alone can determine patterns of chemical defense allocation; according to this hypothesis, "environmental variations that cause changes in plant carbohydrate status will lead to parallel changes in levels of carbon-based secondary metabolites" (Reichardt *et al.,* 1991).

1.7 Different theories in relation to my experiment

From the time of the first review articles on plant chemical defenses (Whittaker and Feeny, 1971), workers in this field have emphasized that there is a sensitive balance between the adaptive advantage conferred by herbivore-deterrent chemical and the metabolic cost that its production imposes on the plant. Whittaker and Feeny (1971) postulated that patterns of variation in the importance of (a) herbivore pressure and (b) metabolic costs of chemical defense would be reflected by variation in the amounts of defensive substances produced. This same kind of balance has been visualized by Jazen (1969), Feeny (1970), Jones (1972), Rehr *et al.* (1973) and Levin (1976). The concept of costs and benefits of defense has been central to hypotheses that postulate variations in defense investment associated with successional status (Cates and Orians, 1975), soil quality (Janzen 1974), plant "apparency" (Feeny, 1976), leaf lifespan (Janzen 1974; Stanton, 1975), environmental variations facing a

single species (Cates, 1975; Jing and Coley, 1990), and intraplant distribution (Orians and Janzen,1974; Rhoades and Cates, 1976).

While the concept of costs and benefits of defense has stimulated the formulation of useful hypotheses and this concept has received support from such empirical studies have been carried out (e.g., Cates and Orians, 1975; but see Otte, 1975; McKey *et al.*, 1979), there is a lack of studies that present careful quantitative models of costs, benefits, and the outcome of conflicts between the two. There are just statements about the patterns of variation of costs and of benefits. There has been no assessment, for example, of the ratio of increasing benefit to increasing cost when the concentration of a toxic compound is increased. How many resources are saved from herbivory when a given amount of resources are used to synthesize defense chemicals? If resources are expensive for plants growing on poor soils, why should they be spent on defense? The answer must be that the cost of defense is relatively low compared to the cost of herbivory where the plant to be not defended. What determines the point when further investment in defense is not rewarded by commensurate benefits? For plants growing on rich soils, if defenses are cheap, why not possess them in abundance? The point is that predictive power of current formulations is greatly limited by their distinctly qualitative character. Prediction of gross differences between light-gap and understory species, for example, is about the limit of precision allowed by existing models.

1.8 Relation between evidence and theories

Selective forces imposed by herbivores will certainly form a major influence on the evolution of patterns of toxic-compound allocation. However, defense compounds emerge from the internal physiology of the plant, and the importance of their metabolic behavior within the plant has not been sufficiently appreciated in existing concepts about their distribution within plants.

Investigations involving phenolics have been critical to the development of apparency theory (Feeny, 1976; Rhoades and Cates, 1976) and resource allocation ideas (Coley *et al.,* 1985). Mole and Waterman's (1988) appreciation of co-evolution, induced defenses in plants and cyclic play-herbivore dynamics has also been dependent on work with phenolics, as well as Schultz and Baldwin (1982), Lindroth and Baltzli (1986) and Schafer *et al.* (1989).

Most specific studies of modes of action of plant chemicals have concentrated on one herbivore and one chemical interaction, but since plants synthesize a wide variety of different chemicals, and synergism is such a common phenomenon in biology, we are still far from understanding the complex ways that plant chemistry influences herbivory (Levin, 1976).

Herms and Mattson (1992) have framed a comprehensive analysis of plant defense theory in terms of tradeoffs. Their major premise is that this trade-off is made at the physiological level of resource allocation to either defensive structures and chemicals or to vegetative and reproductive growth. In this respect, their work further elaborates resource allocation based theory (Bryant *et al.*, 1983; Coley *et al.*, 1985). But, Herms and Mattson (1992) are not alone in considering tradeoffs involving plant defense (Cates and Orians, 1975; Levin, 1976). The idea seems to be widely accepted although the evidence for their existence is extraordinarily scant. Furthermore, the current evidence for tradeoffs derives from studies made at different organizational levels, which are difficult to integrate as support for the theories of Bryant *et al.* (1983) or Herms and Mattson (1992) which are specifically physiological and resource based.

In studies at the phenotypic level, Rehr *et al.* (1973) have reported a negative relationship between chemical defense (cyanogenic glycosides) and pugnacious ant mutualists in an interspecific study of South American *Acacia.* Bjorkman and Anderson (1990) have also reported negative relations between defense related traits in an intraspecific study of *Rubus*

bogotensis. In neither case do these studies address the physiological level on which Herms and Mattson (1992) predicate their ideas. There is even contradictory phenotypic evidence from Steward and Keeler (1988) who failed to find defense related tradeoffs in an interspecific study of *Ipomoea*.

The available genetic evidence also provides poor support for the idea that plant defense and growth are negatively correlated via tradeoffs based on limited resources. For example, Hanover (1966) showed a negative phenotypic correlation between growth and terpenoid content in *Pinus monticola* but the heritability of terpenoid content was high while the heritability for growth was not statistically different from zero. From these data it cannot be inferred that there is a trade-off on the formal constraint of limiting resources. In such a case growth and terpenoid content should be tightly coupled, generating similar heritabilities. Two other examples where resource allocations to alternative traits must have been made on a non-limiting pool of resource are the trade-off of a reproductive growth versus cyanogenisis in *Trifolium repens* (Kakes, 1989) and that between yield and nicotine content in tobacco (Vandenberg and Matzinger, 1970). In tobacco, a negative genetic correlation between nicotine content yield was overcome via breeding to increase nicotine content with no loss in yield.

One study that does directly address the physiological level is that of Briggs and Schultz (1990) who examined tradeoffs involving growth, reproduction and defense in *Lotus corniculatus* (Leguminosae). For Mole (1994) the results of this study are equivocal because experimental manipulations of plant carbon resources produced unexpected changes in leaf nitrogen and reproductive output as well as leading to changes in the level of one chemical but not another. The lack of other appropriate empirical evidence for tradeoffs at the physiological level seems to be because many studies have focused directly on the defensive traits themselves, to the exclusion of traits with which they may trade off. It is also the case

that such studies have focused on the allocation of resources rather than addressing the critical issue of whether the allocation is of limiting resources.

At present there is a critical need for ecological studies of tradeoffs made by comparing individuals within populations or by comparisons of individuals drawn from populations exhibiting different levels of defense, or by comparisons of the largest number of species as possible. Such studies need to be carefully controlled to assess resource acquisition and use. They also need to be replicated in several different resource environments.

The goal of this project is to give a contribution to understand better whether or not there are tradeoffs between growth and defense in different resource environments.

CHAPTER II

INTERSPECIFIC COMPARISONS OF PLANT TOXICITY AND PRODUCTION OF PHENOLICS IN RELATION TO PLANT GROWTH RATE UNDER OPTIMAL CONDITIONS OF LIGHT AND MINERAL NUTRIENTS.

2.1 INTRODUCTION

In recent years, a body of theory has developed that relates defense allocation to resource availability and the indirect cost of defense (Bryant *et al.* 1983; Coley 1983, 1988; Coley *et al.* 1985; Chapin *et al.* 1986; Gulmon and Mooney 1986; Bazzaz *et al.* 1987) as previously discussed in chapter I. The essence of the hypothesis is that selection in resource-rich habitats favors plants with high growth rates. High growth rates are achieved by producing inexpensive leaves that can be quickly and economically replaced as the canopy moves higher. In contrast, plants in resource-poor habitats are characterized by slow growth and long-lived leaves. Leaf replacement is much more costly in these habitats and therefore defense investments must be higher to avoid leaf losses (Fritz and Simms, 1992; Simms, 1992). Moreover, because selection in resource-rich habitats favors plants with high growth rates, the indirect cost of defense, resulting in reduced growth rates, would place defended plants at a competitive disadvantage compared to undefended plants. Tradeoffs between defense and productivity are generally assumed to exist in crop systems (Bottrell and Adkisson, 1977; Zangerl and Bazzaz, 1992). The trade-off between growth and defense presumably exists because secondary metabolism and structural reinforcement are physiologically constrained in dividing and enlarging cells, since they divert resources from the production of new leaves. Hence the dilemma of plants: they must grow fast enough to

compete, yet maintain the defenses necessary to survive in the presence of pathogens and herbivores (Herms and Mattson, 1992). To evaluate the resource availability/defense hypothesis, studies in controlled conditions are needed that measure defense (toxicity) as a function of resource availability.

The objective of this chapter is to describe the interspecific relationship between RGR and plant chemical defenses under conditions of high levels of resource availability in 31 species of Asteraceae, under controlled conditions.

2.2 MATERIALS & METHODS

2.2.1 The species

The family Asteraceae consists of over 20,000 species, having a cosmopolitan distribution (Gleason and Cronquist, 1991). It is a monophyletic group and therefore all of these plants share a common ancestry (Cronquist, 1981). I worked with 31 different species from 7 tribes (Table 5). This study is restricted to herbaceous species that inhabit open sunny habitats such as meadows, waste places, roadside, riverbanks and stream banks. Of the 31 species, there are 2 biennial, 9 annual and 20 perennial growth forms (Marie-Victorin, 1964). These species display a variability in growth rate as well as physical and chemical defenses (Heywood *et al.*, 1977, 1978). The Asteraceae, in fact, are exceptionally rich, both in the range of secondary compounds present and also in the numbers of complex structures known of any one class (Heywood *et al.*, 1977). In this project I concentrated on chemical defenses.

2.2.2 Seed collection and storage

Seeds were collected from wild populations across southwestern Quebec during the summer of 1994. The seeds were stored in paper bags in a refrigerator at 4°C prior to germination.

2.2.3 Germination conditions

The experiment was conducted from February 1995 until April 1995 under controlled conditions in a Conviron (PGW36) growth chamber at McGill University, Montreal, Quebec.

Table 5. List of species used in this study and their taxonomic affiliations.

Tribe		Genus	Species	Author
Anthemideae		*Achillea*	*millefolium***	L.
		Artemisia	*vulgaris**	L.
		Chrysanthemum	*leucanthemum***	L.
		Matricaria	*matricarioides***	Less (Porter)
		Tanacetum	*vulgare**	L.
Astereae		*Erigeron*	*canadensis**	L.
		Solidago	*canadensis**	L.
		S.	*graminifolia*	(L.) Salisb.
Cichorieae		*Cichorium*	*intybus***	L.
		Hieracium	*aurantiacum**	L.
		H.	*venosum*	L.
		H.	*vulgatum**	Fries
		Lactuca	*biennis*	(Moench) Fern.
		L.	*canadensis**	L.
		L.	*muralis*	L.
		Lapsana	*communis**	L.
		Leontodon	*autumnalis**	L.
		Sonchus	*asper*	(L.) Hill
		Taraxacum	*officinale**	Weber
		Tragopogon	*pratensis**	L.
Cynareae	Carduinae			
		Arctium	lappa*	L.
		A.	*minus***	(Hill) Bernh
		Cirsium	*arvense*	L.

Centaureinae				
		Centaurea	*nigra*	L.
Eupatorieae	Eupatoriinae			
		Eupatorium	*maculatum*	L
		E.	*rugosum*	Houtt.
Heliantheae	Coreopsidinare			
		Bidens	*cernua**	L.
		B.	*frondosa*	L.
	Helianthinae			
		Rudbeckia	*hirta***	L.
	Galinsoginae			
		Galinsoga	*ciliata*	(Raf.) Blake
Senecioneae		*Senecio*	*vulgaris*	L.

Note: * means species used in chapter III; ** means species used in chapter III and IV.

Wild plant species may differ substantially in their germination rates and percentages. To reduce this variation, I estimated the germination rates and percentages for each species prior to the experiment. The results of these trials are given in the Appendix 1. These trials allowed me to estimate the amount of time required for each of the species to germinate so that germination dates could be better synchronized to take place during a 1 week period.

2.2.4 Growth of the seedlings

Seeds were germinated on wet filter paper in distilled water in petri dishes at room temperature. Within 2-3 days of germination, seedlings were transplanted individually into

separate small blocks of rock wool (2 x 2 x 4 cm^3). Rock wool was chosen because it is commonly used in hydroponic culture. Rock wool is a mineral fiber, sterile and inert without phytotoxic substances (Anonymous, 1993-1994). Rock wool was used as a support medium. To minimize algae growth and reduce evaporation, aluminum foil was placed around each seedling on the upper surface of the rock wool. Plants were supplied with a photosynthetic photon flux density (PPFD) of 500 $\mu mol/m^2/s$ (provided by a combination of fluorescent tubes (Sylvania cool white VHO, 240 W) and incandescent bulbs (Phillips 60 W lamps)) for 16 hours each day. This provided a daily integrated photon flux of 28.8 $moles/m^2$. The temperature was maintained at 25°C day and 20°C night and the relative humidity was 80%.

2.2.5 Hydroponic system

The hydroponic system chosen was an aerated standing nutrient solution (Benton Jones, 1983). The hydroponic system consisted of 15 poly-ethylene containers (36 x 36 x 30 cm^3). Each container was divided in 144 compartments (2.5 x 2.5 x 21.5 cm^3) using poly-ethylene sheets. There was therefore approximately 10 cm of undivided space at the bottom of each container, thus allowing free circulation of the hydroponic solution between compartments. The four corner compartments of each container were used to introduce aeration tubes and to monitor the temperature, pH and nitrate daily. Therefore each container held 140 plants. Each compartment contained a block of wool rock (2 x 2 x 4 cm^3) which functioned as a support medium. Aquarium pumps were used to aerate and circulate the solution inside of each container. Each container was filled with 30 L of modified Hoagland solution (Hoagland & Arnon, 1950 as given in Table 6). This solution has a nitrogen concentration of 8 mM (6mM NO_3^- plus 2 mM NH_4^+). The solution was topped up daily with the same solution as required to compensate for water loss due to evaporation and transpiration. The nutrient solution in each container was completely renewed every week; the pH of a freshly prepared solution was 6.1. The pH and the nitrate concentration was monitored daily with a NO_3 selective

electrode (model 800522 Orion Research Inc. Boston, Mass) for re-adjustment. Nitrate standards were prepared prior to the experiment and daily nitrate and pH measurements were recorded (Appendix 2 and 3).

Table 6. Composition and concentration of modified Hoagland solution.

Stock solution	Solution
Macronutrient	ml/L
1M $Ca(NO_3)_2.4H_2O$	3
1M $MgSO_4.7H_2O$	2
1M KH_2PO_4	5
1M $NH_4H_2PO_4$	2
Micronutrient	g/L
$MnSO_4$	1.37
$ZnSO_4.7H_2O$	0.22
H_3BO_3	2.87
$Na_2MoO_4.H_2O$	0.02
$CuSO_4$	0.05
1 ml of micronutrient stock/L solution	
$FeSO_4.7H_2O$	5
EDTA	7
2 ml of Iron-EDTA stock/L solution	

2.2.6 Plant harvests

The experiment was in the form of randomized blocks. Each container formed one block. The 140 individuals were randomly assigned to positions within each container. One plant per species per container was randomly chosen for each harvest period (therefore 15 plants per species per harvest). For each species, 15 randomly chosen plants were harvested at 14, 21, 28 and 35 days after transplanting into the hydroponic system. Of these 15 plants, a sufficient number were randomly chosen for the bioassay, which required 1 g fresh weight. The remaining plants, varying from 5 to 13 per harvest date (Appendix 4), were used to estimate growth rate. At each harvest, plants were separated into leaves, stem, bud flowers or flowers, seeds (when they are present) and roots. Roots were separated at the base of each plant and washed free of rock wool with tap water. All plant parts were blotted dry with paper towels and fresh weights were measured. Leaf blades and flowers were placed in a plant press and roots and stems were placed in paper bags. These were allowed to dry at 80°C in a forced air drying oven to a constant dry weight for a minimum period of 48 hours.

2.2.7 Measurements of plants

Dry weights of all plant parts were measured to the nearest 0.0001 g. Leaf area of the upper leaf surface of each plant was measured using an image analyzer (AgVision, Decagon Devices, Inc. Pullman, Washington) (Appendix 4).

2.2.8 Phytochemical analyses

2.2.8.1 Extraction and Bioassay of Plant Chemical Toxicity:

Many of the secondary compounds produced by the Asteraceae are toxic or show other significant physiological activity (Heywood *et al.* 1977). A bioassay (Arnason *et al.* 1991) using brine shrimp larvae (nauplii of the genus *Artemia* sp.) was used to measure the chemical toxicity of the extracts of each species. Brine shrimp, a small marine crustacean, was used because it presumably has not evolved any defense against the terrestrial plant toxins. In fact, brine shrimp are not natural pests of plants, so they provided a convenient invertebrate assay (Alkofahi *et al.*, 1989).

I- Preparations of Brine Shrimp:

a) Brine solution was prepared using 76 g of sea salt (Tropic Marine) in 2 liters of distilled water. The pH of the solution was adjusted to 7.6 using HCl (1N). The brine solution was filtered through Whatman N° 1 filter paper using a Buchner funnel and aspiration. 1000 ml of this solution was poured into an Erlenmeyer flask for hatching of the eggs and the other 1000 ml was reserved to be used later (see section IIIa).

b) The first Erlenmeyer flask, containing 100 mg of brine shrimp eggs, was placed in a controlled temperature room (25 °C day- 20 °C night) under incandescent bulbs (Phillips 60 W lamps) for 24 hours. The Erlenmeyer flask was covered with plastic wrap and an air hose was inserted to aerate the solution gently. The brine shrimps (*Artemia* sp.) were ready to be used 4 days later.

II- Plant extraction:

a) Fresh tissues (bulked by species for each harvest period) were placed in 95% ethanol for a minimum 24 h period after weighing. This resulted in a general extraction of secondary compounds. Leaves, stems and roots were analyzed separately whatever sufficient fresh biomass was available. Sometimes more than one individual was necessary for 1 g fresh weight.

b) The tissue samples were homogenized with the aid of "Polytron" to increase the efficiency of the extraction process. These extracts were filtered through Whatman N° 1 filter paper using a Buchner funnel and aspiration.

c) The residue was obtained after evaporation of the ethanol in vacuum and then brought back into solution in 50% ethanol to achieve a ratio of 1 ml solvent per 1 g (fresh weight) of tissue. The final extract solutions were stored in a freezer at -4°C prior to bioassay to avoid loss of solvent volume.

III- Brine Shrimp Bioassay

a) In small test tubes (10 ml) were added 4 ml of brine solution (1000 ml brine solution which was reserved, see section Ia).

b) Serial logarithmic dilutions (1/10 dilution) of the extract solutions were prepared in their solvent: 1 µl of the extract solution plus 99 µl solvent; 10 µl of the extract solution plus 90 µl solvent; 100 µl of the extract solution plus 0 µl solvent. Controls were prepared using 0 µl of

the extract solution plus 100 µl solvent (controls). Geometric dilutions were sometimes used in order to more accurately bracket the lethal concentration. Controls were always included.

c) After mixing the brine solution and the sample dilutions using a vortex, 1 ml of brine with nauplii was added. An average of 50 nauplii per treatment were used. Therefore, the final volume within each test tube was 5.1 ml.

d) The rack of test tubes was covered with a piece of plastic wrap to prevent significant evaporation and placed under constant light intensity in the controlled temperature room.

e) The number of dead nauplii after 24 hours was counted with the aid of a dissecting microscope and phage typing grid dishes. Moribund nauplii (only slight uncoordinated twitching with no propulsion) were counted as dead.

f) After the number of dead had been counted, 1 ml of methanol or ethanol was added to each vial. After 1 h all nauplii were dead, and the total number was determined and the LC_{50} (concentration needed for 50% mortality) was calculated using logistic regression, PROC LOGISTIC (SAS Institute Inc., 1990).

2.2.8.2 Tissue preparation for nitrogen and phenolic measures:

Dried above-ground material was bulked per species per harvest per treatment and ground in a Brinkman mill to pass a 500 µm mesh and dried again at 80°C for a minimum 24 hours prior to use in the total phenolic and nitrogen analyses.

2.2.8.3. Total phenolics analyses

The conceptual basis of the measurement of total phenolics is to quantify the total concentration of phenolic hydroxyl groups present in the extract being assayed, irrespective of the particular molecules in which they occur (Waterman and Mole, 1994). The method used in this project of quantitative analysis for total phenolics is a modification of the Price and Butler method (Price and Butler, 1977, 1978). The method exploits an oxidation-reduction reaction in which the phenolate ion is oxidized. The ferric ions are reduced to the ferrous state and detected by the formation of the Prussian Blue complex ($Fe_4[Fe(CN)_6)]_3$) with a potassium ferricyanide-containing reagent.

Extracts were prepared by maceration of 0.5 g of ground dried tissue in 10 ml of methanol (8% concentrated HCl in methanol) in test tubes at room temperature for 1 hour. The tissue material and the extractant were initially mixed in a vortex for 2 min. This procedure improved the results of extraction. After 1 hour of maceration, the samples were centrifuged at 1150 RPM (712.5 xg) for 2 min. 250 µl of the supernatant was added in exactly 25 ml of deionized water (50 ml test tubes) and mixed. 3 ml of ferric chloride reagent (0.1M solution of ferric chloride ($FeCL_3$) in 0.1 M hydrochloric acid) was then added and mixed. After 3 min, 3 ml of potassium ferricyanide reagent (0.008 M $K_3Fe(CN)_6$ in deionized water) was added and mixed. After a further 15 min, the absorbance was read at 720 nm on a spectrophotometer. A blank was used to zero the spectrophotometer after the correct time and before measurement of the sample. The blank consisted of all the reagents including the solvent in which the sample was dissolved, with the reagents being added at the proper time and in proper sequence. Price and Butler (1977) note that methanol-containing solvents have a slight effect on the reaction of ferric choride and that they need therefore to be present in the blank. Since values were calibrated using gallic acid, units are percent phenolic content (g/g) in gallic acid equivalents (% GAE). When plant material was sufficient, 3 replicates of

each sample were analyzed. Some dilutions were done if necessary. Leaves, stems and roots (and flowers as present) were analyzed separately. Total plant concentrations were calculated by multiplying the dry weight proportion of each tissue type by its phenolic content.

2.2.8.4. Nitrogen analyses

The organic nitrogen (micro-Kjeldahl N) content of dried and ground samples was determined by digesting plant material in sulfuric acid and a mixture of potassium sulfate and selenium oxychloride as a catalyst (Lang, 1962), followed by Nesslerization (Middleton, 1960). Test tubes (15 x 125 mm) contained 0.5 g of ground dried sample plus 200 µl of the digestion solution were placed in a heat block (200 °C). The digestion solution is a mixture of potassium sulfate, oxychloride selenium, distilled water, sulfuric acid (96 %) and cupric sulfate. The temperature was increased until 310-320 °C and maintained constant for 1 hour. After 1 hour in this temperature, the test tube was placed in room temperature for 10 min. One ml of distilled water was added in each tube and mixed with the vortex. 500 µl was transferred to another test tube (16 x 10 mm). 700 µl of distilled water was added and mixed. 3 ml of solution of tartaric acid in deionized water was added and mixed. 2.5 ml of the solution of gum Arabic (prepared with gum Arabic, distilled water, 0.2 % of Nessler reactive and 0.72 % NaOH (1.4N) filtered through Whatman N° 42 filter paper using a Buchner funnel and aspiration) was added and mixed. Finally, 2.5 ml of the Nessler reactive was added and mixed. The Nessler reactive is a mixture of mercury (II) iodide and potassium iodide and NaOH (4N). The reaction takes 30 min in complete darkness. After Nesslerization the absorbency was read at 500 nm on a spectrophotometer (Milton Roy, Spectronic 1001 Plus, Rochester, NY). A blank was used to zero the spectrophotometer after the correct time and before measurement of the sample. Values were calibrated using ammonium sulfate; units are percent nitrogen content relative to tissue dry weight. Two test tubes containing ground leaves of *Citrus* sp. (NBS - Standard Reference Material, 1572 Citrus Leaves, US

Department of Commerce, National Bureau of Standards, Washington, DC - 20234) were used for each digestion series as standard tissue material. When plant material was sufficient, 3 replicates of each sample were analyzed. Some dilutions were done if necessary. Leaves, stems and roots were analyzed separately.

2.2.9 Growth analyses

The relative growth rate (RGR, g/g/day) of each species was estimated as the slope of the linear regression of the natural logarithm of seedling dry weight on time. Units are grams of new biomass produced per gram of pre-existing biomass per day (g/g/day). Thus, RGR was a mean taken over the 14, 21, 28 and 35 days growth period.

Specific leaf area (SLA, leaf area:leaf dry weight (cm^2/g)) data of each plant were transformed to their natural logarithms to stabilize variance. The data were then pooled for each species and each harvest, and the means of the natural logarithms were back transformed to their exponential (Appendices 4 and 5).

Root:shoot ratios (g/g), calculated from the arithmetic means of root and shoot biomass at each harvest occasion, were instantaneous values (Appendices 4 and 5).

2.2.10 Statistical analyses

a) Growth analyses

All data were analyzed using the Spearman correlation and/or the general linear model (GLM) procedure in the SAS statistical package (SAS, Inc. 1990). The trends in the relationships between the parameters were plotted using Sigma Plot (Jandel Scientific, 1994).

b) Phytochemical analyses

Bioassay of Plant Chemical Toxicity

The mean of measurable toxicity (LC_{50}; µg/ml) in the brine shrimp test was calculated using probit test of the SAS statistical package (SAS, Inc. 1990). These values were then transformed to their inverse (1/ LC_{50}) (Appendix 5). Thus, larger values indicate a greater toxicity and therefore a lower concentration needed to produce 50% mortality within 24 hours. Spearman correlations were used to study the relationship between the variables.

Total Phenolics Analyses

The dry-weight percent of soluble phenolics of each species for each harvest date were transformed to their natural logarithms to stabilize variance, and the data were then subjected to correlation analyses (Spearman correlation) to compare with the growth parameters (RGR,

SLA, root:shoot) and/or chemical parameters (total nitrogen in plant and/or total nitrogen in leaf, toxicity).

Nitrogen Analyses

I prepared a calibration curve using ammonium as a standard based in concentration of 0.1 to 0.001 mM nitrogen. The curve was used to determine the % nitrogen (g/g, dry weight) separately for leaves, stems and roots for each species and harvest date. Therefore individuals of a given species and harvest date were pooled together. The total plant nitrogen was calculated by multiplying the proportional biomass in each tissue type by its % nitrogen, and adding the three tissues types together.

2.3 RESULTS

2.3.1 General Observations

2.3.1.1 Seedling establishment and plant growth

I tested the germination rates of approximately 45 wild herbaceous species of the Asteraceae. Of these, the seeds of 31 species provided a sufficient number of healthy seedlings for use in this experiment (Appendix 1). The following species were not used in any of the experiments due to poor germination rates or excessive mortality rates: *Anaphalis margaritaceae, Aster umbellatus, Gnaphalium ulginosum and Prenanthes alba.* Seedlings that died due to transplanting shock during the first week of the experiment were replaced. For these individuals, the replacement date was counted as day 1. Those seedlings (13.2%) that died subsequent to the first week were discarded and not replaced.

Five of 31 species flowered and 2 species produced seeds during this experiment. *Galinsoga ciliata* plants flowered during the third week of the experiment and one week later produced seeds. One *Sonchus asper* plant produced seeds during the last week of the experiment. The others species that flowered were *Bidens frondosa, Leontodon autumnalis* and *Matricaria matricarioides. Bidens frondosa* was the highest species at 1.2 m at 28 days. Seedlings did not show signs of chlorosis or necrosis during the growth period. Cotyledons of most of the species died during the experiment. Therefore, cotyledons were not included in the dry weight or the surface area measurements.

2.3.1.2. Growth conditions

The nutrient solution was monitored daily for changes in pH and nitrate concentrations. The lowest and highest pH levels were 5.1 to 6.0 during the experimental period with most values being close to 5.5. Since these pH values were within the acceptable range, they were not adjusted. The lowest and highest concentration of nitrate in the solution during the experimental period ranged from 5.2 to 10.0 millimoles with most values to 7.9 millimoles. A record of the daily changes in NO_3 and pH of the solution are given in the Appendix 3. Samples of the hydroponic solution were taken for each container weekly. I measured the toxicity of these samples using the brine shrimp bioassay. The values of the measurable toxicity for the hydroponic samples were not different from the controls. This means that there were no detectable secondary compounds diluted in the hydroponic solution.

2.3.2 Means and Variances of Measured Variables: growth and phytochemical parameters

The full data set of the 31 species investigated in this study is given in Appendices 4 and 5. Table 7 gives the mean relative growth rates (RGR) from day 14 to day 35 as well as the mean of measurable toxicity ($1/LC_{50}$; µg/ml) in the brine shrimp test and the mean total soluble phenolics (% phenolic GAE (g/g)) for each harvest day.

Growth parameters:

The mean relative growth rates (RGR) varied 2.1-fold between the slowest (*Bidens cernua*, RGR= 0.108 g/g/day) and the fastest growing species (*Artemisia vulgaris*, RGR= 0.226

g/g/day). The specific leaf area (SLA) varied 3.7-fold between 128.074 to 478.533 $cm^2\ g^{-1}$ for *Centaurea nigra* and *Erigeron canadensis*, respectively.

The means of the root:shoot ratios varied 4.7-fold for the four harvest dates. *Hieracium vulgatum* had the lowest root-shoot ratio (0.231 $g\ g^{-1}$) while *Solidago graminifolia* had almost the same proportion of production of root biomass per shoot biomass (1.097 $g\ g^{-1}$). There were no species that produced substantially more root biomass than shoot biomass. This is an indication that the plants did not experience shading that was able to affect their development. The means of the root:shoot ratios were 0.44, 0.43, 0.47 and 0.53 for the first to fourth harvest dates, respectively.

Phytochemical parameters:

Tissue nitrogen concentration varied 1.86-fold between 3.28% to 6.12% for *Actium minus* and *Bidens frondosa*, respectively. The mean of total phenolic concentrations varied 3.5-fold between 0.55 to 1.90 % GAE (g/g) for *Senecio vulgaris* and *Lactuca muralis*, respectively. The means of measurable toxicity ($1/LC_{50}$; μg/ml) in the brine shrimp test varied 133-fold between 0.01 to 1.33 μg/ml for *Bidens frondosa* and *Sonchus asper*, respectively.

2.3.3 Variation of total phenolics and toxicity in relation to taxonomic or ecological classifications and tissue type

In order to determine if the phenolic concentration and brine shrimp toxicity varied between species or between tribes (see classification on Table 5), I conducted a nested ANOVA using the GLM procedure of SAS (SAS Institute Inc., 1990) in which the four harvest periods

where nested within the species from which the measures came (this served as the error variance) and species were nested within the taxonomic tribe to which they belong. There were significant differences in both total phenolic concentration ($p < 0.0001$) and in measured toxicity ($p = 0.02$) between tribes and also between the different species within each tribe for total phenolic concentration ($p < 0.0001$). There may be marginally significant differences between the different species within each tribe for measured toxicity ($p = 0.05$).

Table 7. Relative growth rate (RGR), means of measurable toxicity (LC_{50}; µg/ml) in the brine shrimp test and means of total soluble phenolics (% phenols GAE (g/g)) by harvest day (14, 21, 28 and 35 post-germination) of 31 species of Asteraceae grown under controlled conditions of temperature (25 °C), RH (80%), light intensity (500 µmol/m^2/s PAR) and photoperiod (16 h/day) in a full-strength Hoagland hydroponic solution.

Tribe Subtribe Species	RGR (g/g/day)	Toxicity ($1/LC_{50}$; µg/ml) Harvest day					Total Phenolics [GAE (g/g)] Harvest day				
		14	21	28	35	(X)	14	21	28	35	(X)
Anthemideae											
Achillea millefolium	0.175	0.100	0.167	0.143	0.333	0.186	1.26	0.47	0.47	0.64	0.71
Artemisia vulgaris	0.226	0.027	0.045	0	0	0.018	0.92	0.65	0.67	0.59	0.71
Chrysanthemum leucanthemum	0.151	0.050	0.019	0.250	0.059	0.095	0.68	0.67	0.58	0.64	0.64
Matricaria matricarioides	0.130	0.025	0.021	0.034	0.036	0.029	0.67	0.64	0.58	0.56	0.61
Tanacetum vulgare	0.178	#	0.333	0.015	0.056	0.135	0.79	0.53	0.96	0.89	0.79
Astereae											
Erigeron canadensis	0.165	0.026	0.167	0.043	0.033	0.067	0.70	1.05	0.95	0.79	0.87
Solidago canadensis	0.182	0.048	0.045	0	0.143	0.059	0.62	0.63	0.81	0.60	0.66

S. graminifolia	0.151	0.037	0.032	0.043	0.024	0.034	0.62	0.64	0.54	0.77	0.64
Cichorieae											
Cichorium intybus	0.141	0.014	0.016	0.016	0	0.012	0.81	0.89	0.46	0.49	0.66
Hieracium aurantiacum	0.157	0.048	0.026	0.022	0.059	0.039	0.68	0.83	0.81	1.0	1.29
H. venosum	0.147	#	0.033	0.020	0.025	0.02	0.69	0.68	1.1	0.75	0.81
H. vulgatum	0.179	0.010	0.048	0	0.031	0.022	1.3	1.1	1.0	1.7	0.84
Lactuca biennis	0.146	0.018	0	0.033	0.024	0.019	1.0	0.92	0.97	#	0.96
L. canadensis	0.172	0.015	0.016	0.012	0	0.011	0.87	0.78	0.70	0.88	0.81
L. muralis	0.133	0.026	0.037	0.042	0	0.026	1.5	1.5	2.1	2.5	1.9
Lapsana communis	0.206	0.038	0	0.056	0	0.024	1.1	1.2	0.84	1.1	1.05
Leontodon autumnalis	0.114	0.100	0	0	#	0.033	0.84	0.52	0.45	0.68	0.62
Sonchus asper	0.177	0.200	0.091	0.021	5	1.33	1.0	0.95	0.57	0.54	0.77
Taraxacum officinale	0.156	0.143	0.125	0.011	0.010	0.072	1.0	0.74	0.73	1.0	0.88
Tragopogon pratensis	0.163	0.036	0.017	0.033	0	0.022	0.77	0.82	0.70	0.55	0.71
Cynareae											
Carduinae											
Arctium lappa	0.110	0.059	0.053	0	0	0.028	0.82	0.66	0.80	1.4	0.92
A. minus	0.141	0	0.015	0	0.059	0.019	0.58	0.81	0.74	0.69	0.71
Cirsium arvense	0.116	0.034	#	0	0	0.013	0.62	0.61	0.61	0.56	0.60
Centaureinae											
Centaurea nigra	0.152	#	0.020	0.026	0.053	0.033	1.2	1.3	1.4	1.3	1.3

Eupatorieae											
Eupatoriinae											
Eupatorium maculatum	0.191	#	#	0	0.045	0.023	#	1.2	1.2	1.4	1.27
E. rugosum	0.210	0.063	0.024	0.030	0.071	0.047	0.84	1.7	1.6	1.3	1.36
Heliantheae											
Coreopsidinare											
Bidens cernua	0.108	0.063	0.067	0.053	0.333	0.129	0.74	0.72	0.56	0.56	0.65
B. frondosa	0.191	0	0	0	0	0	1.0	0.97	0.79	0.80	0.89
Helianthinae											
Rudbeckia hirta	0.221	0.014	0.020	0	0.038	0.018	0.75	1.5	1.0	0.71	0.99
Galinsoginae											
Galinsoga ciliata	0.156	0.036	0	0.022	0.042	0.033	0.55	0.75	0.59	0.44	0.58
Senecioneae											
Senecio vulgaris	0.130	0.250	0.143	0.034	0.091	0.13	0.61	0.65	0.44	0.48	0.55

Note: # represents missing data; 0 represents no measured toxic in the brine shrimp test.

However, one can conceive of other classifications beside a taxonomic one. For instance, the study species were either annuals, biennials or perennials. I therefore repeated the above nested ANOVA by nesting species within the appropriate life history type of each. There were no significant differences in the mean values of either total phenolic concentration or measurable toxicity between the three life history groups, but clear differences in the mean values of these two variables (total phenolic concentration, $p< 0.0001$ and measurable toxicity, $p= 0.02$) among species of the same life history type.

Finally, it is conceivable that the amount of chemical protection may be affected by the type of morphological defenses of a particular species. I therefore nested each species within one of three types of physical defense (hairs, spines or both). There was marginally significant differences between these three groups in terms of the total phenolic concentrations of their tissues ($p= 0.05$), but no differences were detected in terms of measurable toxicity. In both cases, there were significant differences ($p< 0.01$) between species within each physical protection type.

Total phenolics differed significantly between leaves and roots based on a paired t-test. The average total leaf phenolic concentration was 0.93% while the average for roots was 0.53%. There were not enough tissues to allow a separation of measured toxicity into root and leaf tissues.

2.3.4 Relationships between total phenolics, toxicity and growth

Figure 10 illustrates the relationship between the average total phenolics content and the average RGR. There was a positive non-parametric correlation between the average total phenolic content per species and its average RGR ($r_s= 0.40$, $p= 0.03$) as well as with leaf

phenolic content (r_s= 0.47, p= 0.007) but not with root phenolic content (r_s= 0.20, p= 0.28). Therefore, species with more phenolic compounds in their tissues (especially their leaves) tended to have higher RGR values as well, but there was no relationship between RGR and phenolic content after controlling for differences in root:shoot partitioning.

There was no significant relationship between mean RGR values of these species and the mean measurable toxicity of their tissues (r_s= 0.12, p= 0.53). The mean tissue nitrogen content was negatively correlated with the mean tissue phenolic content (r_s= -0.42, p= 0.02; Figure 11) but this trend was diluted when looking only at leaf tissues (r_s= -0.31, p= 0.09) or only at root tissues (r_s= 0.18, p= 0.32). Finally, the mean measurable toxicity values per species were never significantly related to either total phenolic or nitrogen concentration, measured on a whole-plant basis or separated into leaf and root tissues.

The Spearman correlation coefficient between the mean relative growth rates (RGR) from day 14 to day 35 and mean SLA was weak, positive but non-significant (r_s= 0.14, p= 0.45) as was the correlation between mean RGR and average root-shoot partitioning (r_s= 0.16 p= 0.38), while the correlation between SLA and root-shoot was weak, negative and non-significant (r_s= -0.14, p= 0.14).

There was a strong and highly significant negative correlation between RGR and plant nitrogen content (r_s= -0.39, p= 0.0001; Figure 12).

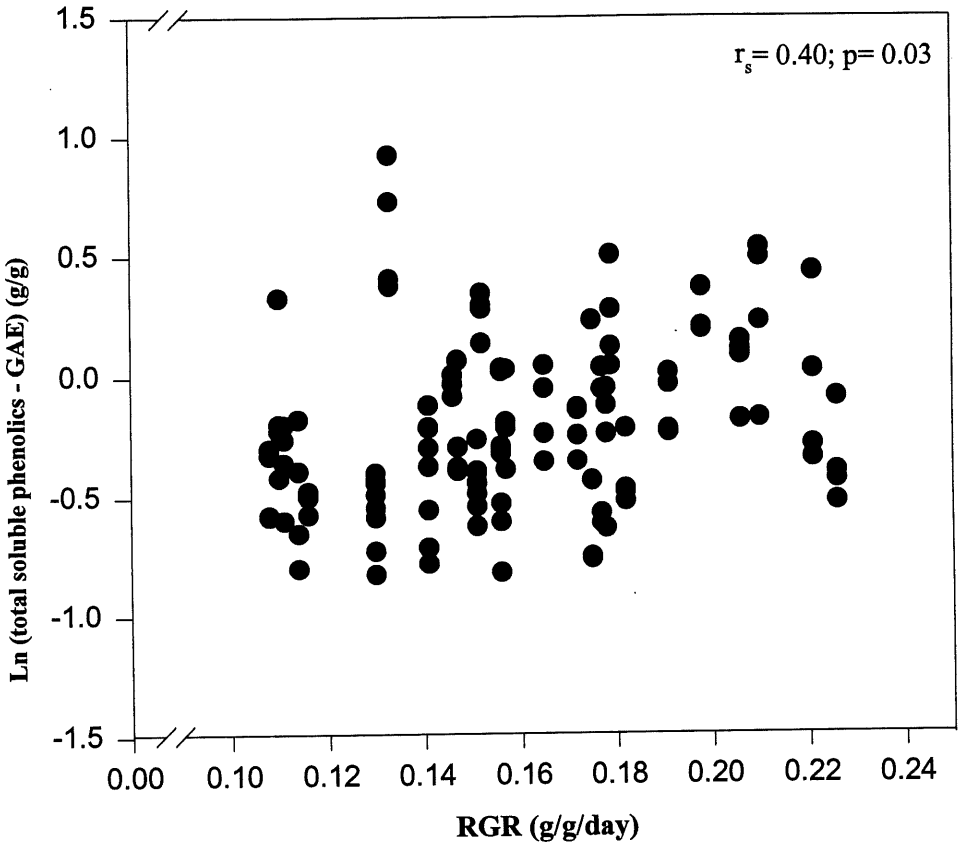


Figure 10. Relationship between means of RGR (g/g/day) and means of total soluble phenolics (% phenolic GAE (g/g)) for 31 species of Asteraceae grown under controlled conditions of temperature (25 °C), RH (80%), light intensity (500 μ mol/m^2/s PAR) and photoperiod (16 h/day) in a full-strength Hoagland hydroponic solution.

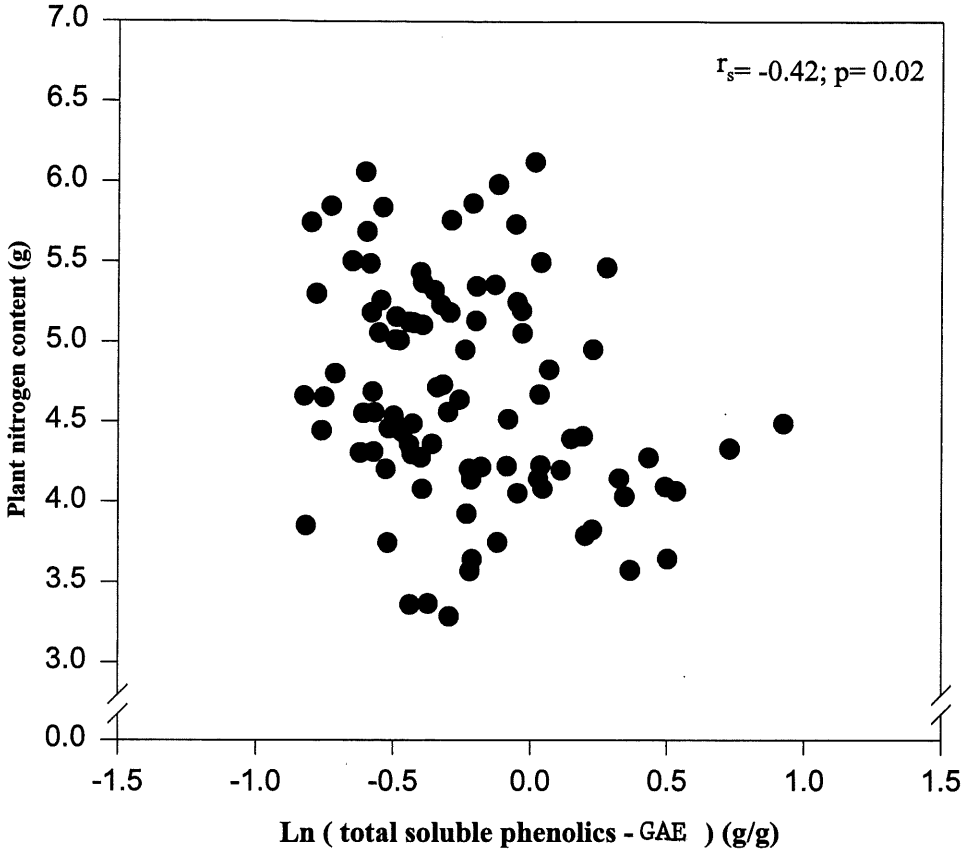


Figure 11. Relationship between means of total soluble phenolics (% phenolic GAE (g/g)) and means of leaf Nitrogen content (%) for 31 species of Asteraceae grown under controlled conditions of temperature (25 °C), RH (80%), light intensity (500 μ mol/m^2/s PAR) and photoperiod (16 h/day) in full-strength Hoagland hydroponic solution.

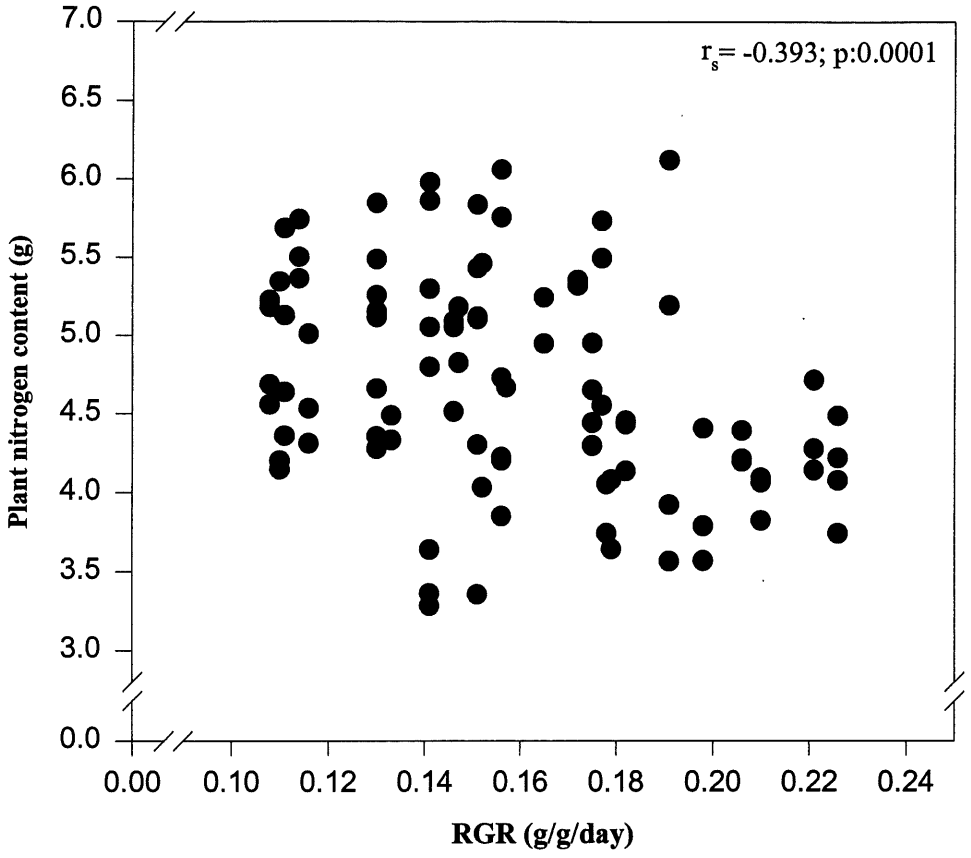


Figure 12. Relationship between means of RGR (g/g/day) and means of leaf Nitrogen content (%) for 31 species of Asteraceae grown under controlled conditions of temperature (25 °C), RH (80%), light intensity (500 μmol/m^2/s PAR) and photoperiod (16 h/day) in full-strength Hoagland hydroponic solution.

2.4 DISCUSSION

This study combines a wide set of species and non-limiting resources availabilities, in systematic and standardized conditions. In this chapter I tested if there is any correlation between relative growth rate (fast and slow growing plants) and chemical defense (phenolic and toxicity) in 31 species of Asteraceae under controlled and enriched environmental conditions. It represents the most detailed and extensive interspecific test to date of the relationship between these variables.

Although most of the defense theories emphasize a trade-off between relative growth rate and chemical defense (Rhoades 1979; Mattson, 1980; Bryant *et al.*, 1983), there are few published papers evaluating a range of species under controlled conditions (e.g. Niemann *et al.*, 1992; Rousi *et al.*, 1996). The lack of appropriate empirical evidence for tradeoffs at the physiological level seems to be because many studies have focused directly on the defensive traits themselves, to the exclusion of traits with which they may trade off (i.e. growth rate, seed production, etc.). For plants growing on rich soils, if defenses are cheap, why not possess them in abundance? It is therefore important to be able to quantitatively relate a cost in terms of reduced growth with the benefit in terms of increased tissue toxicity.

At present there is a critical need for ecological studies designed in a hierarchical manner by measuring tradeoffs made by comparing individuals within populations or by comparisons of individuals drawn from populations exhibiting different levels of defense, or by comparisons of the largest number of species as possible. Such studies need to be carefully controlled to assess resource acquisition and use. They also need to be replicated in several different resource environments. For instance, in this chapter I tested the largest number of species grown under controlled conditions to date and I will discuss whether or not there is any trade-off between growth and chemical defense. In chapter III, I will compare the relationship

between these two variables under nutrient stress. In chapter IV, I will investigate if there is any trade-off when the plants grow under a range of different levels of light intensity (carbon) and nutrient (nitrogen) but using a smaller number of species. Finally, in chapter V, I provide exact estimates of one type of secondary compound but based on only one species and two levels of mineral nutrient concentrations.

Reproduction may affect allocation to secondary compounds. The nutrient levels in the Hoagland solution and the light intensity (500 $\mu mol/m^2/s$) were favorable to reproduction of three fast-growing species (*Galinsoga ciliata* (RGR= 0.156 g/g/day), *Sonchus asper* (RGR= 0.177 g/g/day- produced flowers within 35 days) and *Bidens frondosa* (RGR= 0.191 g/g/day - produced bud flowers within 33 days). *Galinsoga ciliata* produced flowers within 19 days and seeds 33 days from germination. Yet two slow-growing species reproduced during the last week of the experiment (*Matricaria matricarioides* (RGR= 0.130 g/g/day - produced flowers within 33 days) and *Leontodon autumnalis* (RGR= 0.114 g/g/day - produced bud flowers within 33 days).

According to Bloom *et al.* (1985) generally the total allocation of resources to reproduction is much greater in resource-rich than in resource-poor environments, and this further increases the cost of resource use in resource-rich environments. Herms and Mattson (1992) predicted that the allocation of resources by plants to chemical and structural defenses decreases growth by diverting resources from the production of leaf area and other vegetative structures. This predicted trade-off has ecological consequences that affect the success or failure of particular resource partitioning and allocation patterns in particular environments. Hence the dilemma of plants: they must grow fast enough to compete and ultimately reproduce, and yet maintain the physiological adaptations (defenses) necessary for survival in the presence of herbivores and pathogens. So according to this premise, the species that produce flowers divert resources from growth and chemical defense towards reproduction. In other words, I would expect

flowering plants to produce less chemical toxicity because the carbon and nutrient cost of producing reproductive structures is generally high due to their high concentration of nitrogen, phosphorus, and lipids. This trade-off does not exit for all species in my experiment even when they were grown under non-limiting resources.

Galinsoga ciliata, at the beginning of flowering, produced no detectable toxicity in the brine shrimp test, but increased the amount of soluble phenolics (21 days, see Table 7). These observations are supported by Briggs' and Schultz' (1990) studies. They studied ecological trade-offs between growth, reproduction and both condensed tannins and cyanogenic glycosides in *Lotus corniculatus*. These authors hypothesize that if competition between defense and primary metabolism exists, defense production costs should be reflected in trade-offs with other plant functions, such as growth and reproduction. They found that chemical defense was depressed when plants produced fruits.

Some researchers (Mooney and Chu, 1974; Chung and Barnes, 1980 a, b; Waring and Pitman, 1985; Bazzaz *et al.,* 1987; Chapin *et al.,* 1990) observed that when environmental conditions are favorable, vegetative growth generally receives resource priority over secondary metabolism and storage. This is not true for *Sonchus asper*, the species having the highest toxicity (1.33 μg/ml) and also one of the highest relative growth rates and producing only a moderate amount of soluble phenolics (0.77 % GAE). Furthermore, *Bidens frondosa*, the only species with no detectable toxicity in the brine shrimp test over the four harvest periods, and producing only a moderate amount of soluble phenolics (0.89 % GAE) also had one of the highest relative growth rates. In fact, in this experiment with non-limiting nutrients, *Bidens frondosa* is the only species that fit with the previously references.

According to Grime and Hunt's (1975) classification, twenty of my 31 species had a high relative growth rate (i.e. > 0.143 day $^{-1}$). Herms and Mattson (1992) in developing the growth-

differentiation hypothesis describes growth-dominated plants as plants corresponding to the competitive and ruderal strategies of Grime (1977, 1979). These plants inhabit resource-rich environments, grow rapidly, possess low quantitative levels of chemical defenses, and are often characteristic of early stages of secondary succession. On the other hand, differentiation-dominated species inhabit resource-limited environments, grow slowly, possess high levels of defenses, and often occupy late-successional sites (Grime, 1979; Coley *et al.,* 1985; Huston and Smith, 1987; Taylor *et al.*, 1990). The slow-growing species *Leontodon autumnalis* and *Matricaria matricarioides* did not follow this behavior. They produced low amounts of soluble phenolics (0.62 and 0.61 % GAE, respectively) and presented low levels of toxicity (0.033 and 0.029 μg/ml).

Selective forces imposed by herbivores will certainly have a major influence on the evolution of patterns of toxic-compound allocation. However, defense compounds emerge from the internal physiology of the plant, and the importance of their metabolic behavior within the plant has not been sufficiently appreciated in existing concepts about their distribution within plants.

A negative correlation between two traits can be generated in two general ways. One possibility is that there is no genetic link between the two traits, but each responds in an opposite way to some common environmental change. The other possibility is that the negative correlation is generated by constraints inherent in the physiology or morphology of the plant even when the environment is constant. This second possibility is a "genetic" correlation and provides an operational definition of a "trade-off". The existence of a trade-off between growth and defense has generated some controversy. Even if some studies have found a negative correlation between growth and the attack by herbivores (Coley, 1983; Sheldon, 1987), others (Meijden *et al.,* 1988; McCanny *et al.*, 1990) did not find any

correlation, and still others (Denslow *et al.,* 1987, 1990; Briggs and Schultz, 1990) show a positive correlation between the two variables.

Herms and Mattson (1992) have framed a comprehensive analysis of plant defense theory in terms of tradeoffs. Their major premise is that this trade-off is made at the physiological level of resource allocation to either defensive structures and chemicals or to vegetative and reproductive growth. In this respect, their work further elaborates resource allocation based theory (Bryant *et al.*, 1983; Coley *et al.*, 1985). But, Herms and Mattson (1992) are not alone in considering trade-offs involving plant defense (Cates and Orians, 1975; Levin, 1976). The idea seems to be widely accepted although the evidence for their existence is extraordinarily scant. Furthermore, the current evidence for tradeoffs derives from studies made at different organizational levels, which are difficult to integrate as support for the theories of Bryant *et al.* (1983) or Herms and Mattson (1992) which are specifically physiological and resource based.

Investigations involving phenolics have been critical to the development of apparency theory (Feeny, 1976; Rhoades and Cates, 1976) and resource allocation ideas (Coley *et al.,* 1985). This is probably due to the fact that a simple chemical assay of total phenolics exists while similar assays for other types of secondary compounds do not. I have tried to get around this practical problem by using the toxicity assay but it is important to remember that most studies refer to "secondary compounds" but in practice only measure phenolics. Mole and Waterman' s (1988) appreciation of co-evolution induced defenses in plants and cyclic play-herbivore dynamics has also been dependent on work with phenolics, as well as Schultz and Baldwin (1982), Lindroth and Baltzli (1986) and Schafer *et al.* (1989). So far as the ecology of plant phenolics is concerned, plant-herbivore interactions are the most widely studied interactions which these chemicals mediate.

My findings indicate that there is a positive, rather than negative, correlation between the average total phenolic content per species and its average RGR as well as with leaf phenolic content. Therefore, species with more phenolic compounds in their tissues (especially their leaves) tended to have higher RGR values as well, but there was no relationship between RGR and phenolic content after controlling for differences in root:shoot partitioning. This is the opposite of what the growth/defense tradeoff predicts. Furthermore there was no significant relationship between the mean RGR of species and the mean measurable toxicity of their tissues. Therefore my experimental results do not support the claim that species with more chemical defenses tend to have lower relative growth rates when comparisons are made under constant environmental conditions.

Most specific studies of modes of action of plant chemicals have concentrated on one-herbivore and one chemical interaction, but since plants synthesize a wide variety of different chemicals, and synergism is such a common phenomenon in biology, we are still far from understanding the complex ways that plant chemistry influences herbivory (Levin, 1976).

Published tests of the growth/defense tradeoff have been contradictory. Rousi *et al.* (1996) studied growth and hare resistance of one-year-old seedlings of ten birch (*Betula* ssp) species under two fertilization treatments (fertilized, unfertilized) crossed with two shade treatments (shade- 25% of outdoor irradiance (211 ± 27 μmol/s/m^2) and no shade (398 ± 55 μmol/s/m^2). For the fertilization treatment the seedlings were watered during one month with a 0.1 % fertilizer containing 19.4 % nitrogen. For the following two weeks the fertilizer was changed by reducing the nitrogen to 10.9 % and during the last week no nitrogen was included in the fertilizer composition. For the control treatment (unfertilized) the plants were simply watered without any fertilizer addition. The plants were grown under greenhouse conditions without any control of humidity or temperature. These authors could not find measurable tradeoffs between the resistance of one-year-old seedlings and their growth rate, neither for the

cafeteria test nor the field feeding experiment. Neither was the resistance of faster growing species more plastic than that of slower growing species (cf. Coley *et al.*, 1985; Herms and Mattson, 1982).

McCanny *et al.*, (1990) studied the resource availability hypothesis of antiherbivore defense with 42 emergent wetland plant species and they too found no correlation between food quality based on a standard corn agar diet to which different amounts of extracted secondary compounds had been added and the maximum relative growth rates of these plants as seedlings. The experiment by McCanny *et al.*, (1990) was based on a tissue collection, which means that leaf samples were collected in the field and secondary compounds were extracted in 95% ethanol. The plants were collected along different fertility gradients. For the smaller species, leaf tissue from many individuals was pooled to make the necessary amount. The authors tested the chemical defense based on a bioassay test using *Ostrinia nubilalis*, a generalist insect herbivore. For the maximum relative growth rate, the plants were grown from seed in a greenhouse receiving natural light intensities and uncontrolled conditions of temperature and humidity. This method was described in an another experiment (Shipley and Peters, 1990).

Sheldon (1987) and Coley (1988) have demonstrated that the rapidly growing plant species in their experiments were the preferred foods of generalist herbivores. By contrast, the results of McCanny *et al.* (1990) and those of van der Meijden *et al.* (1988) show no such relationship.

Coley (1988) studied growth, herbivory and defenses for 41 tree species in a lowland rainforest. Growth was quantified as the annual increase in height, and as the annual production of leaf area for an average of 10 individuals of each species. The author did not know the age of the plants, but she used plants growing in light gaps 1-2 years old. It means that the plants differed in age. Total phenolic, condensed tannins, fiber content, leaf

toughness, and pubescence were determined in order to analyze the defense against herbivores. Also, herbivory was determined in the field on marked leaves as the rate of insect damage for 3-week periods during the dry, early wet and late wet seasons (Coley 1982, 1983). According to the author this gives an estimate of the average annual rate of herbivory in terms of the percentage of leaf area eaten per day. Coley (1988) affirms that these experiments provide the most complete data set to date for testing the theories of plant defense. Since this was a field experiment, it is possible (see chapters III, IV and V) that both growth rate and defense chemicals were simply responding independently to different resource supplies. Also, she did not take into account the life history of the species, neither did she mention if the herbivory test ran in the same year that the growth rate measurements were taken, nor if she used the same individuals to measure the defense characteristics, growth rate and herbivory. Coley (1988) found a negative correlation between growth rates as estimated simply by the increase of leaf area or branch length and the estimate of defense investment which was obtained by constructing an index which was a linear combination of fiber, tannin, toughness and pubescence ($r= -0.69$, $p< 0.001$). For some reason she did not present the data of total phenolics and it is not possible to know the relative importance of the leaf attributes in determining herbivore choice. The author also found a significant positive correlation between growth and herbivory ($r= 0.52$, $p< 0.001$), also "suggesting that faster-growers were more poorly defended". Note that such crude measures of growth potential can be very misleading. First, the compound nature of growth means that growth rate must be expressed as a measure relative to initial size. Second, fluctuating environments will cause large differences in the relative allocation to leaves, stems and roots (see chapters III and IV) and so increases in leaf area cannot be used to measure the growth potential. Leaf lifetimes were positively correlated with the concentrations of immobile defenses (condensed tannin). In agreement, other studies in a variety of environments have also found that fast-growing species are less defended and more heavily attacked by herbivores than slow-growing ones, and that immobile defenses are common in longer-lived leaves (Feeny, 1976; Rhoades and

Cates, 1976; McKey *et al.*, 1978; McKey 1979, 1984; Bryant and Kuropat, 1980; McKey and Gartlan, 1981; Bryant, 1987).

Sheldon (1987) studied the influence of herbivorous snails (*Physa gyrina*) on 14 freshwater macrophyte species growing in the laboratory. According to the author, the plants had growth rates ranging from 1-10% per day in the absence of herbivores. Therefore, when the plants were grown with four different densities of herbivorous snails, species that grew fastest in the absence of herbivores were the most negatively influenced by grazing. In the food choice tests, snails typically preferred the plant species that grew fastest in the absence of herbivores. This, by itself, cannot be interpreted as evidence that such plant species were better defended; the result may be either because the fast-growing species were more poorly defended or because they were more nutritionally valuable, since both attributes can affect herbivore choice. The author conducted a study to determine primary plant growth rates under laboratory conditions. The growth rate was estimated based on the wet mass in which a piece of macrophyte of 1g wet mass grew during 10 days and after being reweighed. The same procedure was done in the presence of snails.

As I have mentioned previously, my results did not support the claim that there is a negative trade-off between growth rate and production of secondary compounds. However my experiment was done under controlled conditions, thus excluding the possibility that the correlations were generated by common responses to differing environments, using a range of 31 wild species grown under high nutrient and light availabilities.

Despite much research on plant defenses, evidence for significant defensive costs has been shown in only a few species. In white pine, above-ground growth is negatively correlated with alpha-pinene and with total monoterpene content (Hanover, 1966). In ten wild and cultivated varieties of tobacco, leaf production is inversely related to nicotine content

(Vandenberg and Matzinger, 1970), but leaf production is a poor measure of whole-plant relative growth rate, for the same reasons as already discussed. In clover, cyanide-producing morphs have lower vegetative and sexual reproduction than acyanogenic morphs (Fould and Grime, 1972). In a study of wild ginger (Cates, 1975), unpalatable morphs produced more seeds than palatable morphs if herbivorous slugs were present, but fewer if they were absent. In a tropical tree, *Cecropia peltata*, rates of leaf production were significantly negatively correlated with tannin concentration ($r = -0.52$, $p < 0.001$) suggesting according to Coley (1986) that there is a significant cost to tannin production which reflected in reduced leaf production. However, again leaf production in the field is a poor measure of a whole-plant cost to defense.

The available genetic evidence also provides poor support for the idea that plant defense and growth are negatively correlated via tradeoffs based on limited resources. For example, Hanover (1966) showed a negative phenotypic correlation between growth and terpenoid content in *Pinus monticola* but the heritability of terpenoid content was high while the heritability for growth was not statistically different from zero. From these data it cannot be inferred that there is a genetic trade-off on the formal constraint of limiting resources. In such a case growth and terpenoid content should be tightly coupled, generating similar heritabilities. Two other examples where resource allocations to alternative traits must have been made on a non-limiting pool of resources are the trade-off of a reproductive growth versus cyanogenisis in *Trifolium repens* (Kakes, 1989) and that between yield and nicotine content in tobacco (Vandenberg and Matzinger, 1970). In tobacco, a negative genetic correlation between nicotine content yield was overcome via breeding to increase nicotine content with no loss in yield, thus contradicting the claim that there is a necessary physiological trade-off between growth potential and production of nicotine.

One study that does directly address the physiological level is that of Briggs and Schultz (1990) who examined tradeoffs involving growth, reproduction and defense in *Lotus corniculatus* (Leguminosae). For Mole (1994) the results of this study are equivocal because experimental manipulations of plant carbon resources produced unexpected changes in leaf nitrogen and reproductive output as well as leading to changes in the level of one chemical but not another. The lack of other appropriate empirical evidence for tradeoffs at the physiological level seems to be because many studies have focused directly on the defensive traits themselves, to the exclusion of traits with which they may trade off. It is also the case that such studies have focused on the allocation of resources rather than addressing the critical issue of whether the allocation is of limiting resources.

The mean tissue nitrogen content was negatively correlated with the mean tissue phenolic content (r_s= -0.42, p= 0.02) but this trend was diluted when looking only at leaf tissues (r_s= -0.31, p= 0.09) or only at root tissues (r_s = 0.18, p= 0.32). These results are well supported by the literature (Phillips and Henshaw, 1977; Bryant *et al.*, 1983; Clausen *et al.*, 1987; Kainulainen *et al.*, 1996; but see Hendry *et al.*, 1994). One contradictory result is presented in Hendry *et al.* (1994) who determined the concentration of phenols (orto-dihydroxyphenol) and soluble protein in seeds of 81 species. These authors found a high positive correlation (r_s = 0.61, p< 0.001) between these two variables.

Phillips and Henshaw (1977) observed that nitrogen inhibits accumulation of phenolics in plant cell culture. According to Phillips and Henshaw (1977) there was also a strong and highly significant negative correlation between RGR and plant nitrogen content, which according to the authors provides evidence of the general inverse relation between nitrogen, enhanced growth, and phenolic production. Although this may be true, it is not at all obvious what relation a growth rate on callus tissue would have with the normal relative growth rate of a real plant.

Bryant *et al.*, (1987) studied the effects of nitrogen fertilization upon the concentration of nitrogen, condensed tannin and phenolic glycoside of young *Populus tremuloides* leaves. They found that an increase in nutritional value was correlated with an increase in the concentration of leaf nitrogen and a reduction in the concentrations of leaf total phenols, condensed tannins and phenolic glycosides. Note, however, that these results cannot differentiate between a necessary physiological link between the two variables and simply a common effect of nitrogen fertilization on both variables.

Kainulainen *et al.*, (1996) studied the effects of nitrogen fertilization on secondary chemistry of *Pinus sylvestris*, a species adapted to grow under nutrient-poor sites. These authors found that the total nitrogen concentration of needles was significantly increased with higher fertilization. By contrast, concentrations of foliar monoterpenes and total phenolics decreased with elevated nitrogen availability. Again, the same distinction must be made between a necessary physiological linkage and common response to changing soil fertility.

It therefore seems that there is no interspecific trade-off between growth rate and chemical defense when species are grown under the same environmental conditions and when growth is measured on whole plants and standardized for different initial plant sizes. Those studies who did report such a correlation either obtained their data from field-growth plants that differed in light and soil environments or failed to measure whole-plant growth rate. On the other hand, my results were obtained from plants grown in controlled conditions without limiting supplies of nitrogen and our measure of growth (RGR) was based on whole plants. The carbon/nitrogen theory (Bryant *et al.*, 1983; Waterman *et al.*, 1984; Gershenzon, 1984) implies that the tradeoff of these species with carbon-based secondary compounds should be seen when growth is limited more by nutrient supply that by light. This possibility is explored in the next chapter.

CHAPTER III

INTERSPECIFIC COMPARISONS OF PLANT TOXICITY AND PRODUCTION OF PHENOLICS IN RELATION TO PLANT GROWTH RATE UNDER CONDITIONS OF NUTRIENT STRESS

3.1 INTRODUCTION

As discussed previously, the idea that a plant must allocate limited resources among growth, reproduction, and defense has been central to ecological and evolutionary theories (Feeny, 1976; Rhoades and Cates, 1976; Krischik and Denno, 1983; Coley *et al.,* 1985; Herms and Mattson, 1992; Frank, 1993). If a plant allocates a greater proportion of resources to defense, then less is available for growth and/or reproduction. The concept of costs and benefits of defense has been central to hypotheses that postulate variations in defense investment associated with successional status (Cates and Orians, 1975), soil quality (Janzen, 1974), plant "apparency" (Feeny, 1976), leaf lifespan (Janzen, 1974; Stanton, 1975), and environmental variations, although most studies have involved only intraspecific comparisons. The evolutionary response of plants to herbivores is also strongly influenced by other selective pressures in the plant's environment, such as nutrient availability. Plants growing under nitrogen-limiting conditions generally have a slower growth rate than those growing under nitrogen-rich conditions (Chapin, 1980). Comparable loss of leaf nitrogen to herbivores by nitrate-limited and nitrate-rich plants presumably has a greater impact on the growth of nitrogen-limited plants. Carbon supply does not limit plant under low nitrate conditions and subsequently, increased quantities of carbon-based defenses should be selected for as nitrate availability decreases (Janzen 1974; McKey *et al.*, 1978; Bryant *et al.*,

1983; Coley *et al.*, 1985; Mihaliak and Lincoln, 1985). Since defensive compounds in the Asteraceae are primarily carbon-based, one might therefore expect that when these plants are provided with high levels of light intensity but reduced levels of mineral nutrients, the "excess" carbon would result in increased levels of tissue toxicity and increased production of phenolic compounds.

Furthermore, if there is a tradeoff between growth and defense, one might expect that this would be most pronounced under such environmental conditions, as predicted by the carbon/nutrient theory (see page 32).

In this chapter, the primary objective was to investigate if there is any correlation between relative growth rate (RGR - fast and slow growing plants) and secondary metabolism (soluble phenolics and toxicity) in 20 species, under controlled conditions of high light intensity but suboptimal levels of mineral nutrients. The second objective of this chapter was to determine how the growth and chemical variables change, and whether the patterns of correlations between the variables change, under such conditions relative to those provided to the plants in chapter II. In other words, I compared the results of the previous chapter (non-limiting nutrient conditions) with the results of the present chapter (stress nutrient condition).

3.2 MATERIALS & METHODS

3.2.1 Seed collection and storage

This chapter uses 20 different species of which all but *Tussilago farfara* are the same as those used in chapter II (Table 5). Seeds of the following seventeen species came from the same populations as used in chapter II, *Achillea millefolium, Arctium lappa, A. minus, Artemisia vulgaris, Bidens cernua, Erigeron canadensis, Hieracium aurantiacum, H. vulgatum, Lactuca canadensis, Lapsana communis, Matricaria matricarioides, Rudbeckia hirta, Solidago canadensis, Tanacetum vulgare, Taraxacum officinale*, and *Tragopogon pratensis*. Seeds of the following three species came from populations in the local Sherbrooke area during the summer of 1996: *Chrysanthemum leucanthemum, Cichorium intybus* and *Leontodon autumnalis*. Seeds were stored as described in chapter II.

3.2.2 Germination conditions

The experiment was conducted under controlled conditions in a Conviron growth chamber (PGW36) at the Université de Sherbrooke, Sherbrooke, Québec. The germination rates and percentages were estimated for each species prior to the experiment. The results of these trials are given in the Appendix 6. These trials allowed me to estimate the amount of time required for each of the species to germinate, so that germination dates could be better synchronized to take place during a 1 week period.

3.2.3 Growth of the seedlings

Seeds were germinated on wet filter paper in distilled water in petri dishes at room temperature. Within 3 days of germination, seedlings were transplanted individually into 1 L pots filled with silica sand (40 mesh) and moistened immediately with distilled water. These 1 L containers were placed randomly in 24 rows of 15 columns (400 pots) in the larger main reservoir of the growth chamber. Plants were supplied with a photosynthetic photon flux density (PPFD) of 450 $\mu mol/m^2/s$ fluorescent lamps and incandescent bulbs (Phillips 40 and 100 W lamps) for 16 hours a day. This provided a daily integrated photon flux of 25.92 $moles/m^2$. The temperature was maintained at 24 °C day and 20 °C night and the relative humidity was 80 %.

3.2.4 Nutrient delivery system

The nutrient delivery system consisted of a 200 L external nutrient holding tank filled with a 1/8 full-strength modified Hoagland solution (Table 8). Three times a day, the solution was pumped into a main reservoir in the growth chamber in which the pots were housed. The solution was allowed to saturate the silica sand via perforations at the base of each pot. Once saturated, the solution drained out of the pots and the reservoir by gravity into a holding tank. These pots held approximately 300 ml of solution at field capacity. The returning solution was filtered though cheesecloth and activated charcoal (to remove organic molecules) and recirculated into the external holding tank.

Table 8. Composition and concentration of modified Hoagland solution

Stock solution	g/L	vol. to 200 L (ml)
Macronutrient		
KNO_3	101.1	66.6
$Ca(NO_3)_2.4H_2O$	236,0	50.0
$MgSO_4.7H_2O$	246.0	67.0
KH_2PO_4	136.0	33.32
$(NH_4)_2SO_4$	100.0	16.6
Micronutrient		33.32
$MnSO_4.H_2O$	1.53	
$ZnSO_4.7H_2O$	0.21	
H_3BO_3	2.87	
$Na_2MoO_4.2H_2O$	0.02	
$CuSO_4$	0.06	
FeEDTA		50.0
$FeSO_4.7H_2O$	5	
EDTA	7.5	

3.2.5 Nutrient solution

A 1/8 full-strength modified Hoagland solution was prepared from distilled water and stock standards. Its composition is given in Table 8. The pH was adjusted daily to 5.5 and the nitrate concentration was monitored daily with a NO_3 selective electrode (model 800522

Orion Research Inc. Boston, Mass) for re-adjustment. Nitrate standards were prepared prior the experiment and daily nitrate and pH measurements were recorded (Appendix 7). The 200 L nutrient solution in the holding tank was completely replaced each week from distilled water and stock standards. The pH of a freshly prepared solution was 5.5. Thus, the molarity of nitrogen in this experiment (1mM) was 8 times less than that in chapter II.

3.2.6 Plant harvests

For each species, 5-12 randomly chosen plants were harvested at 20 days and 3-8 randomly chosen plants were harvested at 40 days after transplanting into the hydroponic system for the growth analysis. Five randomly chosen plants of each species were harvested at 40 days for the bioassay, which required 1 g fresh weight (they were bulked individually, if the plant material was sufficient). At each harvest, plants were separated into leaves, stems and roots. Roots were separated at the base of each plant at ground level and washed free of sand with tap water. All plant parts were blotted dry with paper towels and fresh weights were measured. Leaf blades were placed in a plant press and roots and stems were placed in paper bags. These were allowed to dry at 80°C in a forced air drying oven to a constant dry weight for a minimum period of 48 hours.

The measured growth and phytochemical parameters are as described in chapter II. One exception was that the bioassay for measurable toxicity was done independently for each individual, rather than being bulked by species by harvest day, except for *Erigeron canadensis* and *Rudbeckia hirta.* For these two species more than one plant was necessary to obtain 1 g fresh material.

3.3 RESULTS

3.3.1. Growth conditions

The nutrient solution was monitored daily for changes in pH and nitrate concentrations. The pH levels fluctuated daily from 5.66 to 6.85 during the experimental period. However, the pH was adjusted daily to 5.5 with dilute H_2SO_4. The concentration of nitrate in the solution was close to 1.0 millimol. A record of the daily changes in NO_3 and pH of the solution is given in the Appendix 7.

3.3.2 Means and variances of measured variables and comparisons with non-limiting nutrients.

The full data set of the 20 species investigated in this study are given in Appendices 8a and 8b. Table 9 gives the mean relative growth rates (RGR), mean of measurable toxicity ($1/LC_{50}$; μg/ml) in the brine shrimp test and mean total soluble phenolics (% phenols GAE (g/g)) for each harvest date.

Growth parameters:

The mean relative growth rates (RGR) varied 2.5-fold between the slowest (*Hieracium aurantiacum*, RGR= 0.073 $gg^{-1}day^{-1}$) and the fastest growing species (*Tanacetum vulgaris*, RGR= 0.182 $gg^{-1}day^{-1}$). Thus, the mean RGR (0.12 $gg^{-1}day^{-1}$) was reduced by 25 % relative to the first experiment with non-limiting nutrient concentrations (0.16 g $g^{-1}day^{-1}$). Figure 13 plots the mean RGR values for the 19 species common to both experiments. It is clear that

the growth rate was reduced when the nutrient solution was diluted approximately 8 times with the exception of four species (*Chrysanthemum leucanthemum*, *Cichorium intybus*, *Leontodon autumnalis* and *Tanacetum vulgaris*) whose RGR values were essentially the same. One explanation could be that the seeds of three of these species used in the second experiment came from different populations than those used in the first experiment, except the seeds of *Tanacetum vulgaris* ($(RGR_1\text{-}RGR_2) = -0.004$ $gg^{-1}day^{-1}$) that came from the same population. The seeds of the other 15 species common to both experiments came from the same populations as those used in chapter II.

The specific leaf area (SLA) varied 2.2-fold between 121.057 to 269.047 cm^2 g^{-1} for *Tragopogon pratensis* and *Lactuca canadensis*, respectively. Thus, the mean SLA (188.214 cm^2 g^{-1}) was reduced by 32 % relative to the first experiment with non-limiting nutrient concentrations (273.984 cm^2 g^{-1}). Figure 14 plots the mean SLA values for the 19 species common to both experiments.

The means of the root:shoot ratios varied 3.98-fold for the two harvest dates. *Achillea millefolium* had the highest production of root biomass per shoot biomass (3.27g g^{-1}) while *Bidens cernua* had the lowest ratio (0.823 g g^{-1}). The means of the root:shoot ratios were 1.86 and 1.83 for the first and second harvest dates, respectively. Thus, the mean root:shoot ratios (1.836 g g^{-1}) was increased by 320 % relative to the first experiment with non-limiting nutrient concentrations (0.436 g g^{-1}). Figure 15 plots the mean root:shoot ratios values for the 19 species common to both experiments.

Table 9. Relative growth rate (RGR- g/g/day), measurable toxicity ($1/LC_{50}$; µg/ml) in brine shrimp test and total soluble phenolics (% phenols GAE (g/g)) of 20 species of Asteraceae under controlled conditions of temperature (25 °C), RH (80 %), light intensity (450 µmol/m^2/s PAR) and photoperiod (16 h/day) in hydroponic solution (1/8 dilute).

Tribe	Subtribe	Species	RGR (g/g/day)	Toxicity ($1/LC_{50}$; µg/ml) Day 40	Total Phenolics (GAE (g/g) 20	40
Anthemideae		*Achillea millefolium*	0.03	0.049	1.45	1.43
		Artemisia vulgaris	0.123	0.034	0.69	1.33
		Chrysanthemum leucanthemum	0.172	0.01	1.01	1.06
		Matricaria matricarioides	0.112	0.01	0.65	0.77
		Tanacetum vulgare	0.182	0.047	2.11	1.37
Astereae		*Erigeron canadensis*	0.140	.013	1.41	1.26
		Solidago canadensis	0.166	.015	0.66	1.43
Cichorieae		*Cichorium intybus*	0.159	0.01	0.62	0.81
		Hieracium aurantiacum	0.073	0.01	0.81	1.30
		H. vulgatum	0.134	0.01	0.81	1.62
		Lactuca canadensis	0.077	0.01	0.71	0.80

	Lapsana communis	0.121	0.026	1.14	0.99
	Leontodon autumnalis	0.161	0.01	0.63	0.84
	Taraxacum officinale	0.085	0.01	1.18	1.18
	Tragopogon pratensis	0.076	0.01	0.88	0.77
Cynareae					
Carduinae					
	Arctium lappa	0.079	0.01	0.79	1.29
	A. minus	0.075	0.01	0.63	1.21
Heliantheae					
Coreopsidinare					
	Bidens cernua	0.107	0.024	0.77	2.43
Helianthinae					
	Rudbeckia hirta	0.147	0.01	0.73	1.56
Senecioneae					
	Tussilago farfara	0.151	0.074	0.67	1.12

Phytochemical parameters:

Leaf nitrogen concentrations varied 6.17-fold between 0.728 to 3.166 % for *Lapsana communis* and *Artemisia vulgaris*, respectively. Nitrogen in leaves was proportional to the concentration of the nutrient solution between the two experiments as we can see in Figure 16. Thus, the mean leaf nitrogen concentrations (1.642 %) was reduced by 69 % relative to the first experiment with non-limiting nutrient concentrations (5.291 %).

Mean total phenolics varied 2.5-fold between 0.706 to 1.738 (% GAE) for *Matricaria matricarioides* and *Tanacetum vulgaris*, respectively. Thus, the mean total phenolics of the first experiment with non-limiting nutrients (0.781 % GAE) was increased 25 % relative to a mean value of 1.046 % GAE in this experiment with limiting nutrient concentrations. Figure 17 plots the mean total phenolics ratios values for the 19 species common to both experiments.

Means of measurable toxicity ($1/LC_{50}$; μg/ml) in the brine shrimp test varied 7-fold between 0.01 to 0.07 μg/ml. The mean of measurable toxicity (0.017 μg/ml) in this experiment with reduced nutrient supply was decreased 47 % relative to the first experiment with non-limiting nutrients (0.032 μg/ml). Figure 18 plots the means of measurable toxicity in the brine shrimp test values for the 19 species common to both experiments. Although all species used in the nutrient stress experiment had detectable levels of toxicity in the brine shrimp test when grown with non-limiting nutrients (see chapter II), twelve of the twenty species (*Arctium lappa*, *A. minus*, *Chrysanthemum leucanthemum*, *Cichorium intybus*, *Hieracium aurantiacum*, *H. vulgatum*, *Lactuca canadensis*, *Leontodon autumnalis*, *Matricaria matricarioides*, *Rudbeckia hirta*, *Taraxacum officinale* and *Tragopogon pratensis*) had toxicity levels below the detectable limit (0.01 μg/ml) under nutrient stress

conditions. *Tussilago farfara* was the most toxic species (0.07 μg/ml) in the second experiment.

Table 10 gives the means over all 19 species common to both this experiment and that in chapter II for RGR, SLA, root:shoot ratios, leaf nitrogen content, total phenolics and measurable toxicity in the brine shrimp test. A paired t-test showed that each variable in table 10 differed between the two experiments. Compared to the values obtained under non-limiting nutrients, RGR was reduced by 25 %, SLA by 32 %, leaf nitrogen content by 69 % and, measurable toxicity in the brine shrimp test by 46 %, while root:shoot ratios increased by 320 % and total phenolics by 25 %. Despite these changes in means, there were significant correlations between the values of these variables measured for each species over the two experiments (table 10).

3.3.3 Relationship between total phenolics, toxicity, tissue nitrogen and growth

I did not find any correlation between the average values of RGR, total phenolics, measurable toxicity and tissue nitrogen concentrations for the 20 species studied in this nutrient-stress experiment. The only significant correlation was between average phenolic concentration over the two harvest dates (20 and 40 days) and average measurable toxicity of the plant at day 40 (r_s= 0.817, p= 0.0001). In other words, those species with more total phenolics averaged over the harvest period had tissues that were more toxic at day 40. This correlation was rather complicated. The correlation between the two variables was not significant if comparisons were done only for day 40 (i.e. total phenolic concentration at day 40 was not related to measurable toxicity at day 40). In other words, the significant correlation was generated by total phenolic concentration before day 40: plants that had higher total phenolic concentrations earlier during the experiment had higher toxicity at day 40 when this measure was taken.

Table10. The means of relative growth rate (RGR), the means of specific leaf area (SLA), the means of root:shoot ratio, the means of leaf nitrogen content, the means of measurable toxicity (LC_{50}; μg/ml) in the brine shrimp test and means of total soluble phenolics (% phenolic lights GAE (g/g)) of 19 species of Asteraceae. Plants grown under non-limiting nutrient conditions and a light intensity of 500 μ mol/m^2/s PAR versus plants grown under nutrient stress conditions (1/8 dilution) and a light intensity of 450 μmol/m^2/s PAR. Both experiments ran under controlled conditions of temperature (25 °C), RH (80 %), and photoperiod (16 h/day).

Variables	Non limiting nutrients	Limiting nutrients
RGR**	0.159 (0.036)	0.121 (0.037)
SLA*	274.0 (87.426)	188.2 (39.852)
Root:Shoot*	0.436 (0.103)	1.836 (0.687)
Leaves nitrogen*	5.3 (0.830)	1.642 (0.659)
Total phenolics**	0.781 (1.225)	1.046 (1.301)
Toxicity**	0.032 (0.033)	0.017 (0.013)

* means p>0.0001

** means p> 0.002

There was a significant negative correlation between the natural logarithm of total soluble phenolics and SLA (r_s= -0.461; p= 0.0027). The mean of leaf nitrogen content was negatively correlated with the mean of the natural logarithm of total soluble phenolics (r_s= -0.475; p= 0.04) and with the measurable toxicity (1/LC_{50}; μg/ml) in brine shrimp test (r_s= -0.525; p= 0.02).

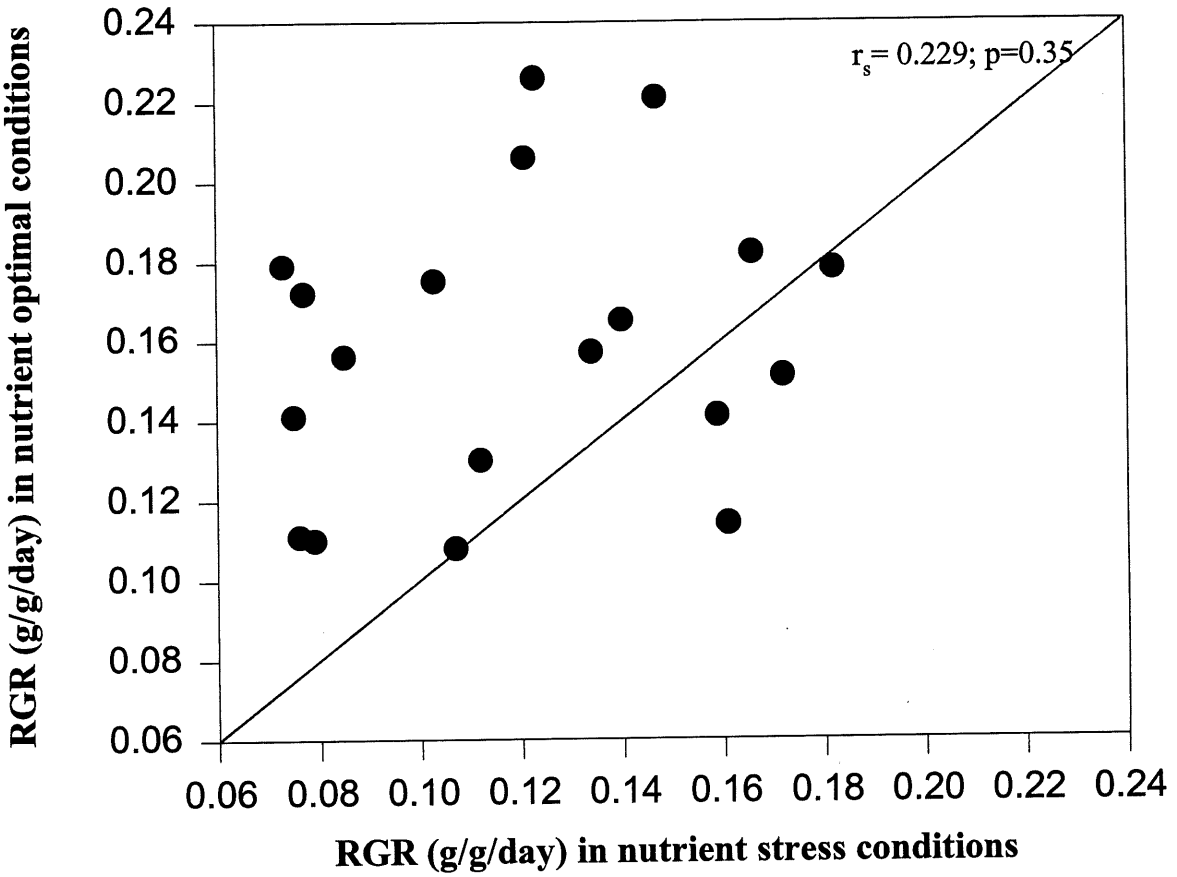


Figure 13. Relationship between means of RGR (g/g/day) of 19 species of Asteraceae. Plants grown under optimal nutrient condition (light intensity (500 μmol/m^2/s PAR) in full-strength Hoagland hydroponic solution) versus plants grown under nutrient stress conditions (light intensity (450 μmol/m^2/s PAR) in a diluted Hoagland hydroponic solution (1/8 dilute)). Both experiments ran under controlled conditions of temperature (25 °C), RH (80 %), and photoperiod (16 h/day). The solid line represents a 1:1 relationship.

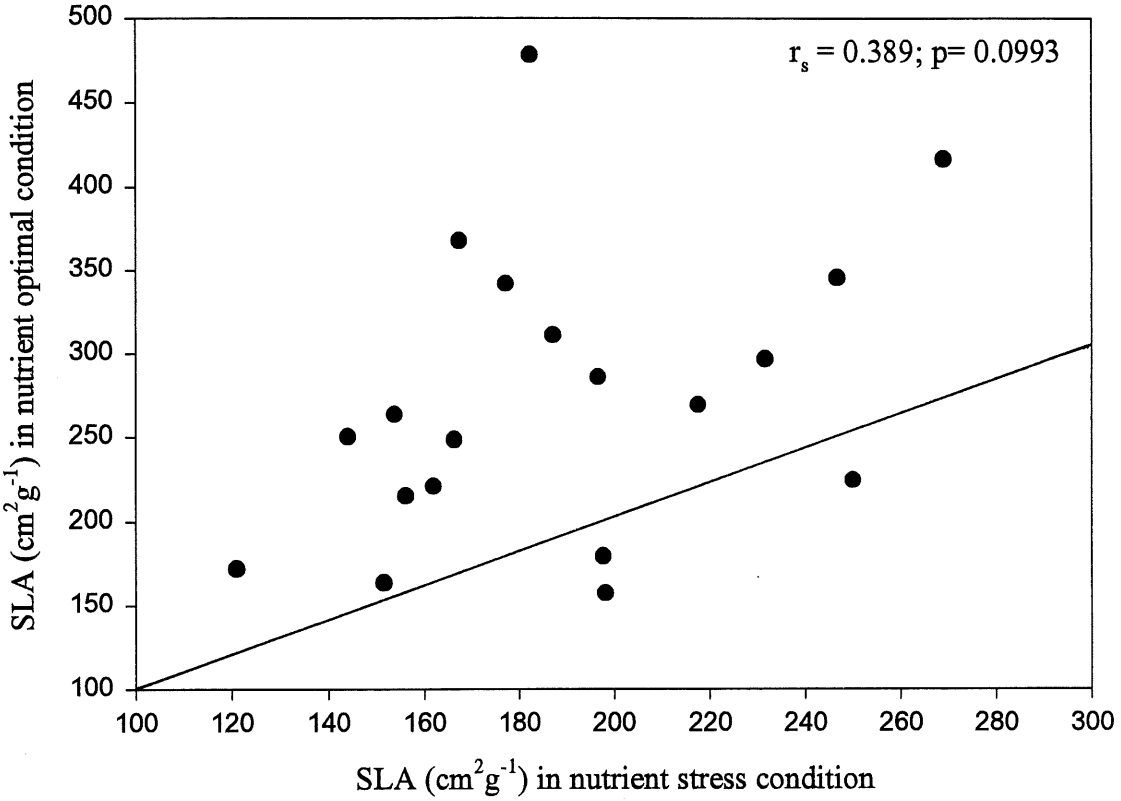


Figure 14. Relationship between means of SLA (cm^2g^{-1}) of 19 species of Asteraceae. Plants grown under optimal nutrient condition (light intensity (500 μmol/m^2/s PAR) in full-strength Hoagland hydroponic solution) versus plants grown under nutrient stress conditions (light intensity (450 μmol/m^2/s PAR) in a diluted Hoagland hydroponic solution (1/8 dilute)). Both experiments ran under controlled conditions of temperature (25 °C), RH (80 %), and photoperiod (16 h/day). The solid line represents a 1:1 relationship.

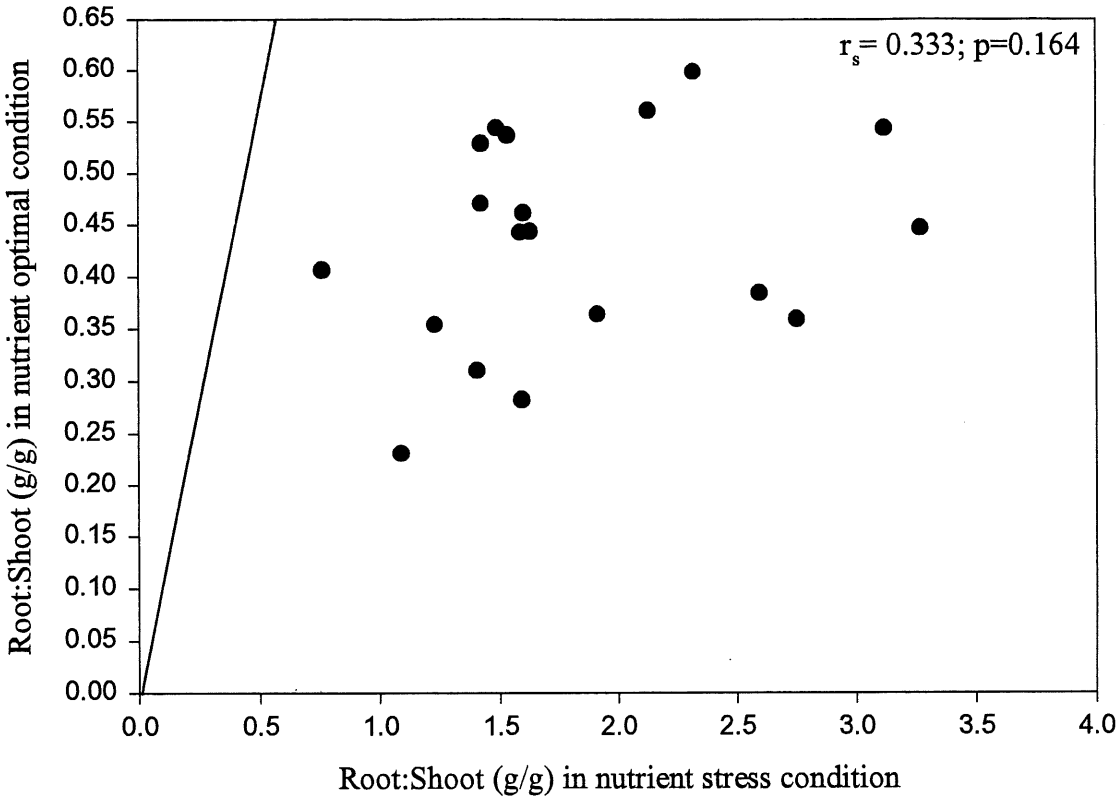


Figure 15. Relationship between means of root:shoot ratios (g/g) of 19 species of Asteraceae. Plants grown under optimal nutrient conditions (light intensity (500 μmol/m^2/s PAR) in full-strength Hoagland hydroponic solution) versus plants grown under nutrient stress conditions (light intensity (450 μmol/m^2/s PAR) in a diluted Hoagland hydroponic solution (1/8 dilute)). Both experiments ran under controlled conditions of temperature (25 °C), RH (80 %), and photoperiod (16 h/day). The solid line represents a 1:1 relationship.

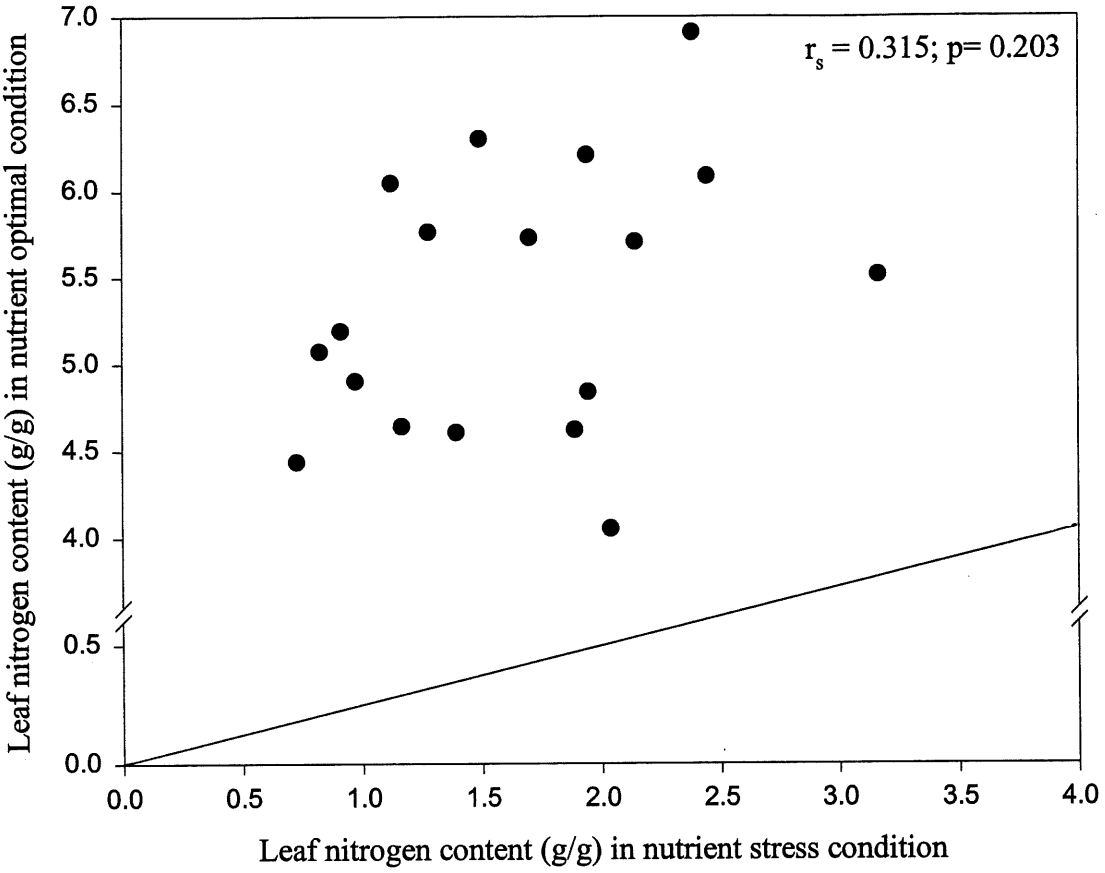


Figure 16. Relationship between means of leaf nitrogen content (%) of 19 species of Asteraceae. Plants grown under optimal nutrient conditions (light intensity (500 μ mol/m^2/s PAR) in full-strength Hoagland hydroponic solution) versus plants grown under nutrient stress conditions (light intensity (450 μmol/m^2/s PAR) in a diluted Hoagland hydroponic solution (1/8 dilute)). Both experiments ran under controlled conditions of temperature (25 °C), RH (80 %), and photoperiod (16 h/day). The solid line represents a 1:1 relationship.

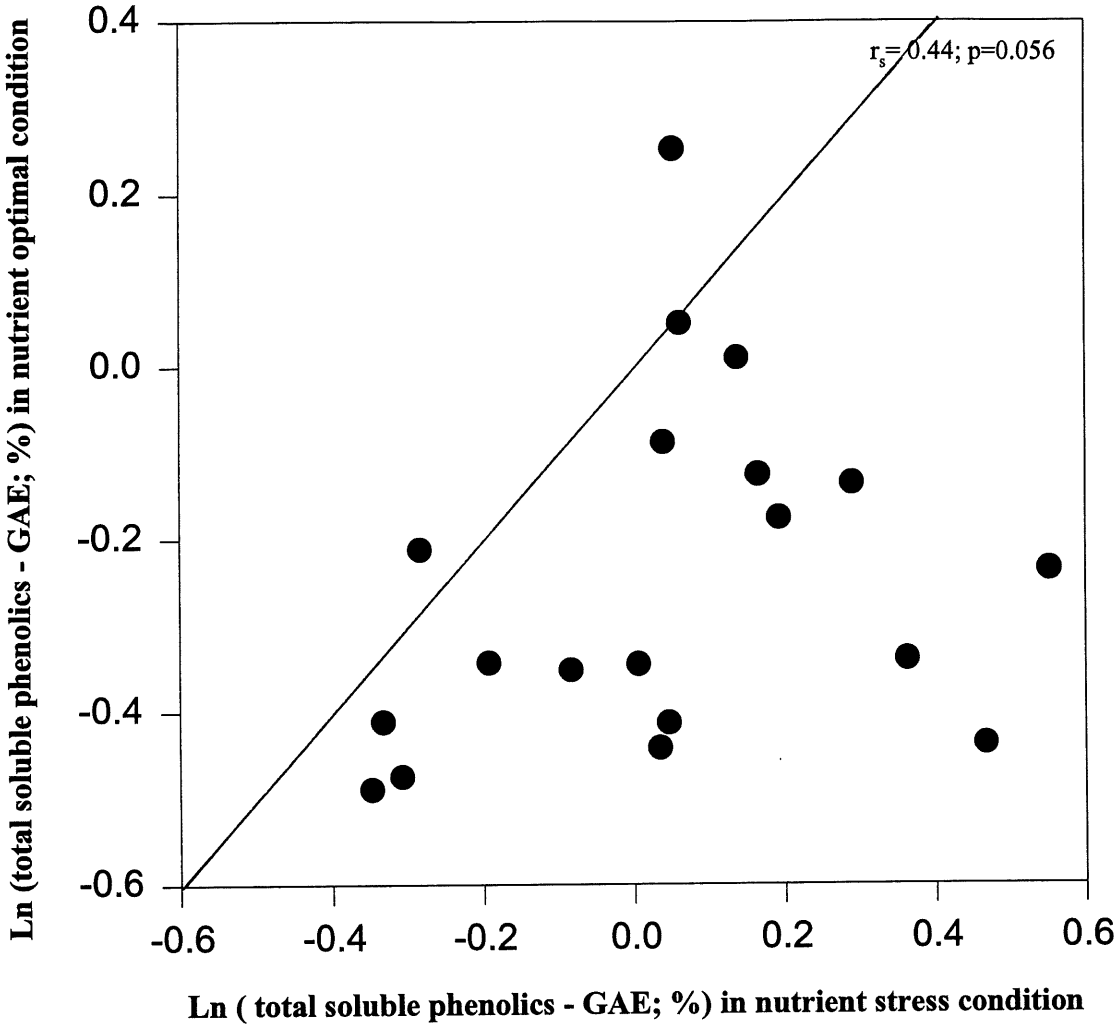


Figure 17. Relationship between means of total soluble phenolics (GAE - g/g) of 19 species of Asteraceae. Plants grown under optimal nutrient conditions (light intensity (500 μmol/m^2/s PAR) in full-strength Hoagland hydroponic solution) versus plants grown under nutrient stress conditions (light intensity (450 μmol/m^2/s PAR) in a diluted Hoagland hydroponic solution (1/8 dilute)). Both experiments ran under controlled conditions of temperature (25 °C), RH (80 %), and photoperiod (16 h/day). The solid line represents a 1:1 relationship.

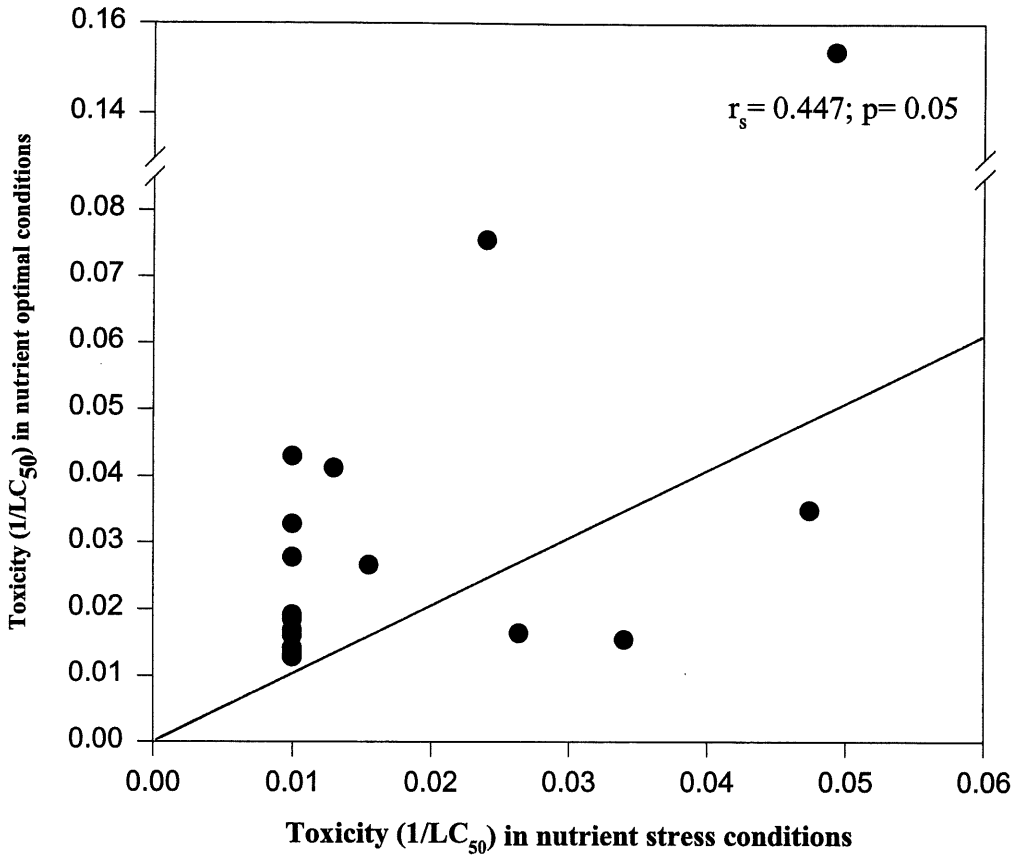


Figure 18. Relationship between means of measurable toxicity (1/LC_{50}; µg/ml) in brine shrimp test for 19 species of Asteraceae. Plants grown under optimal nutrient conditions (light intensity (500 µmol/m^2/s PAR) in full-strength Hoagland hydroponic solution) versus plants grown under nutrient stress conditions (light intensity (450 µmol/m^2/s PAR) in a diluted Hoagland hydroponic solution (1/8 dilute)). Both experiments ran under controlled conditions of temperature (25 °C), RH (80 %), and photoperiod (16 h/day). The solid line represents a 1:1 relationship.

3.4 DISCUSSION

In this chapter, the primary objective was to investigate if there is any correlation between relative growth rate (RGR - fast and slow growing plants) and the production of secondary compounds related to defense (soluble phenolics and toxicity) in 20 species, under controlled conditions of high light intensity but suboptimal levels of mineral nutrients. The second objective of this chapter was to determine how the growth and chemical variables change, and whether the patterns of correlations between the variables change, under such conditions relative to those provided to the plants in chapter II. In other words, I compared the data from plants grown under non-limiting nutrient conditions versus plants grown under a 8-fold reduction in nitrogen concentrations. The reason why this second experiment was conducted is that plants growing under nitrogen-limiting conditions generally have a slower growth rate than those growing under nitrogen-rich conditions. Comparable loss of leaf nitrogen to herbivores by nitrate-limited and nitrate-rich plants presumably has a greater impact on the growth of nitrogen-limited plants. Carbon supply does not limit plants under low nitrate conditions and subsequently the carbon/nutrient theory predicts that increased quantities of carbon-based defenses should be selected for as nitrate availability decreases (Janzen, 1974; McKey *et al.*, 1978; Bryant *et al.,* 1983; Coley *et al.,* 1985; Mihaliak and Lincoln, 1985).

Before evaluating prediction, it is important to establish that the changes in the plant variables under nutrient stress are consistent with previously published results.

3.4.1 Growth responses to nutrient availability

As the results showed the mean RGR (0.12 $gg^{-1}day^{-1}$) was reduced by 25 % relative to the first experiment with non-limiting nutrient concentrations (0.16 g $g^{-1}day^{-1}$). This reduction is not surprising and can be explained in a series of experiments relating RGR to optimum and supra-optimum nitrogen supply published by Ingestad and co-workers (Ingestad, 1979; Jia and Ingestad, 1984; Ingestad and Kähr, 1985). Ingestad (1979) affirmed that growth rate was strongly and linearly correlated with the nitrogen status of the seedlings within the whole suboptimum range in a study involving *Betula verrucosa*. Jia and Ingestad (1984) showed the same relationship (regression) between relative growth rate and relative nutrient addition rate (of the hydroponic solution) in two different tree species (*Populus simonii* and *Paulownia tomentosa*). Ingestad and Kähr (1985) found the same relationship working with *Pinus sylvestris*, *P. contorta* and *Picea abies*.

The reduction of RGR under nutrient stress that was observed in my experiment is also consistent with field results. The role of low growth rates as an important factor in survival of species in soils of low fertility was proposed in earlier work by Bradshaw *et al.* (1964), Clarkson (1967) and Higgs and James (1969). According to Crick and Grime (1987) maintenance of a low growth rate is advantageous for species adapted of infertile soils for two reasons: firstly, the species have a lower nutritional demand for optimal growth, and secondly, they exhibit slower turnover rates of plant tissue and a lower risk of nutrient loss. Certainly some of the species used in this experiment (e.g. *Artemisia vulgaris, Arctium lappa, A. minus, Cichorium intybus, Solidago canadensis, Tragopogon pratensis*) are common on sandy infertile soils while others (e.g. *Achillea millefolium, Chrysanthemum leucanthemum, Leontodon autumnalis, Matricaria matricarioides, Taraxacum officinale*) are agricultural weeds typical of more fertile soils. Later, Grime (1979) and Coley (1983, 1987)

demonstrated that protection of captured resources against losses by herbivory is also prominent in many slow growing plants.

Another variable that is influenced by nutrient availability is specific leaf area (SLA). Poorter and Remkes (1990) reported a strong positive correlation between RGR and SLA. Shipley (1995) provided evidence that maximizing relative growth rate involves maximizing specific leaf area, which in turn involves maximizing leaf area with the least amount of biomass. In this nutrient stress experiment, the mean SLA (188.214 $cm^2\ g^{-1}$) was reduced by 32 % relative to the first experiment with non-limiting nutrient concentrations (273.984 $cm^2\ g^{-1}$). This reduction in SLA with decreased nutrient supplies is also well known (Lambers and Poorter, 1992). The lower relative growth rate and the lower specific leaf area could be because both parameters were affected in the same way by reduced nutrients.

In contrast to the two first variables that were reduced as the nutrient availabilities were reduced, the root:shoot ratio increased from 0.436 g g^{-1} to 1.836 g g^{-1}. These data also agree with the literature. Chapin (1980) affirms that in response to reduced nutrient status at low nutrient availabilities, reserves are allocated to root growth at the expense of shoot growth. This affirmation is supported by a number of empirical studies (Davidson, 1969; Brewster *et al.*, 1975; Christie and Moorby, 1975) which report that a 100-fold drop in availability of a limiting nutrient causes a 1.5- to 12-fold increase in root-shoot ratio, depending upon species and initial growth conditions. The high root:shoot ratio found in the field in many infertile habitats (Dennis and Johnson, 1970) is in part a phenotypic response to reduced nutrient availability (Christie and Moorby, 1975). Rapidly growing species from high-nutrient habitats show considerable phenotypic plasticity in root:shoot ratio and generally have a higher ratio at low availability and a lower ratio at a high availability than do species from a low-nutrient habitat (Christie and Moorby, 1975; Grime and Curtis, 1976).

The different partitioning is due to a homeostatic response by the plants to a resource imbalance by allocating new biomass to acquisition of the resources that most strongly limit growth (Mooney, 1972; Thornley, 1972; Chapin and Van Cleve, 1981). Nutrient stress leads to low concentrations of limiting nutrients and to accumulation of carbohydrates. Plants respond by increasing proportional allocation to root growth (Davidson, 1969; Chapin and Van Cleve, 1981), and this leads to a more favorable carbon/nutrient balance (Bloom *et al.*, 1985). At a more refined level, allocation is adjusted within roots or shoots in response to environmental stress so as to maximize efficiency for capturing the most strongly limiting resource (Bloom *et al.*, 1985).

The partitioning of resources between shoots and roots has long since been analyzed as a balance between shoot and root activity (Davidson, 1969) with the shoot providing carbon and the root providing nutrients and water. A number of mathematical models have been suggested (Thornley, 1976; Reynolds and Thornley, 1982; Johnson, 1985; Robinson, 1986), in which partitioning between shoot and root is achieved by introducing some specific partitioning function. However Ågren and Ingestad (1987) demonstrated that partitioning can be explained without resort to any extra hypothesis of resource allocation, but follows as an absolute requirement from the balance between carbon assimilating structures (shoots) and carbon utilization determined by nutrition.

3.4.2 Phytochemical parameters and nutrient availability

Leaf nitrogen content is logically dependent on nutrient availability. Here, the mean leaf nitrogen concentrations were reduced from 5.291 % to 1.642 % after 8-fold dilution of the hydroponic solution. According to Bloom *et al.* (1985), over the range of most natural conditions, increased nitrogen availability leads to parallel increases in all nitrogen-containing fractions in leaves (Van Den Driessche, 1974; Chapin and Kedrowski, 1983).

Thus, the distribution of nitrogen among the major chemical fractions differs little qualitatively either among species or in response to variations in the environment (Van Den Driessche, 1974; Chapin *et al.*, 1980; Chapin and Kedrowski, 1983).

Carbon accumulation occurs under conditions of high light, low nutrients or mild water stress (Chapin, 1980). In response to high carbon supply, organic acids increase in some species and decline in others (Dickson, 1987). Soluble phenolics and hydrolyzable tannins can increase in response to carbon surplus (Larsson *et al.*, 1986; Bryant *et al.*, 1987 a, b). Production of phenolic chemicals has also been hypothesized to be enhanced under the low productivity condition of nitrogen stress (Janzen, 1974; Bryant *et al.*, 1983). In this experiment I found an increase of 25 % in the mean total phenolics under conditions of nutrient stress. Plants in the first experiment with non-limiting nutrients had an average of 0.781 % GAE total phenolics while in this nutrient stress experiment I observed a mean value of 1.046 % GAE.

Other authors have reported the same trend for field experiments. In infertile soils (nutrient stress), plants accumulate high concentrations of carbon-rich compounds such as carbohydrate, resin and lignin but have low tissue nutrient contents (Mooney, 1972; Chapin and Van Cleve, 1981; Bryant *et al.*, 1983; Bloom *et al.*, 1985). According to Kainulainen *et al.* (1996), concentrations of foliar monoterpenes and total phenolics decreased with elevated nitrogen availability, as expected by the carbon/nutrient balance hypothesis (Bryant *et al.*, 1983). In woody plants low nutrient availability has been observed to increase (McCullough and Kulman, 1991) or to have no effects (Thorin and Nommik, 1974; Muzika, 1993) on concentrations of monoterpenes, but in terpenoid-bearing herbs low nutrient availability stimulated monoterpene formation (Mihaliak and Lincoln, 1985; Mihaliak *et al.*, 1987). The decreased concentrations of foliage phenolic compounds following nitrogen fertilization

agree with earlier studies (Bryant *et al.*, 1987; Muzika and Pregitzer, 1992; Hartley *et al.*, 1995).

Contrary to the above studies, Larsson *et al.* (1986) found different results while studying the effects of light and nutrient stress (availability) on leaf phenolic chemistry in *Salix dasyclados* (c.v. *aquatica*), in three different environmental conditions: low light (65 μmol $m^{-2}s^{-1}$) with free access to nutrients; higher light (300 μmol $m^{-2}s^{-1}$) with free access to nutrients and higher light with suboptimal nutrient supply. Their results showed an increase in relative growth rate, leaf nitrogen content and total phenolics under optimal conditions. Therefore their results demonstrated that concentrations of phenolic compounds in plants with low carbon supply were reduced more than the relative growth rate. One explanation could be that because nutrient stress generally reduces growth more than it reduces photosynthesis per se (e.g. McKey, 1979; also cf. Waring *et al.*, 1985), and thus, it has been argued that the expected surplus of carbon can lead to an accumulation of carbon-based secondary substances under such circumstances (Bryant *et al.*, 1983). On average, total amounts of phenolic compounds in the above cited studies were lower in plants grown in low light and with free access to nutrients than the other two treatments with higher light with suboptimal nutrient supply and higher light with free access to nutrients. Waring *et al.* (1985) found that RGR varied 2.3-fold between optimal conditions (14.7 % d^{-1}) and the same higher light intensity but suboptimal nutrient concentrations (6.4 % d^{-1}). As expected, the plants grown under higher light with suboptimal nutrient supply had a lower concentration of total leaf nitrogen (2.54 % dw) than plants grown in low light with free access to nutrients (3.80 % dw) or higher light with free access to nutrients (3.96 % dw).

Bryant *et al.* (1987b), studied the effects of nitrogen fertilization upon the concentration of nitrogen, condensed tannin and phenolic glycoside of young *Populus tremuloides* leaves. They found that fertilization with nitrogen increased the nutritional value of *Populus*

tremuloides leaves for *Choristoneura conflictana* larvae. This increase in nutritional value was correlated with an increase in the concentration of leaf nitrogen and a reduction in the concentrations of leaf total phenols, condensed tannins and phenolic glycosides. Their results are consistent with the prediction that the nutritional value of woody plant foliage is strongly influenced by the plant carbon-nutrient balance (Bryant *et al.*, 1983).

Thus, my results for total phenolics are also consistent with those reported in the literature. However, I did not find the same response in relation to toxicity. The mean of measurable toxicity in this experiment with 1/8 nutrient concentrations (0.017 μg/ml) was decreased 47 % relative to the first experiment with non-limiting nutrients (0.032 μg/ml). Although all species used in the nutrient stress experiment had detectable levels of toxicity in the brine shrimp test when grown with non-limiting nutrients, twelve of the twenty species (*Arctium lappa*, *A. minus*, *Chrysanthemum leucanthemum*, *Cichorium intybus*, *Hieracium aurantiacum*, *H. vulgatum*, *Lactuca canadensis*, *Leontodon autumnalis*, *Matricaria matricarioides*, *Rudbeckia hirta*, *Taraxacum officinale* and *Tragopogon pratensis*) had toxicity levels below the detectable limit (0.01 μg/ml) under nutrient stress conditions. Since defense compounds in these species (primarily different types of terpenes and acetylenes) are all carbon-based, this result is contrary to the carbon/nutrient balance hypothesis. These data could mean that under such circumstances (nutrient stress) it is cheaper to produce phenols than the other forms of chemical defense (sesquiterpenes or polyacetylenes). This possibility is derived from Bazzaz *et al.* (1987) who predict a variation in defense allocation based on costs and benefits. Chemical defenses draw from an enormous variety of compounds, which can differ in both concentration and distribution. According to Coley *et al.* (1985) defensive compounds that are mobile within the plant such as terpenes (but see Gershenzon, 1994) have a higher cost when compared to immobile defensive compounds such as phenols. Other leaf properties should have an influence on the allocation to chemical defense and the way that they respond; such properties include toughness,

cellulose content, hairs or fiber content, for example. Unfortunately, I did not measure these parameters.

According to Kainulainen *et al.* (1996), reduced nitrogen availability had effects only on the concentration of some individual secondary compounds, while others remained unaffected. This has already been observed in many studies (Muzika *et al.*, 1989; McCullough and Kulman, 1991; Reichardt *et al.*, 1991; Muzika and Pregitzer, 1992; Horner *et al.*, 1993; Muzika, 1993). In contrast, Mihaliak and Lincoln (1985) found an increased leaf mono- and sesquiterpene content with decreased nitrate availability and they claim that this is consistent with the hypothesis that increased allocation to carbon-based defense chemicals would be favored in nitrogen-poor environments.

3.4.3 Is there a trade-off between relative growth rate and chemical defense?

Chew and Rodman (1979) affirm that carbon not allocated to growth could be utilized for secondary chemical production. Is that true? Is there a trade-off between these two parameters?

Contrary of this affirmation, I found no trade-off between growth and chemical defense when comparing species within a given experiment. Similarly, although the trade-off hypothesis predicts a negative correlation between phenolics and RGR, there was a positive non-parametric correlation between the average total phenolic content per species and its average RGR (r_s= 0.40, p= 0.03) as well as with leaf phenolic content (r_s= 0.47, p= 0.007) but not with root phenolic content (r_s= 0.20, p= 0.28) for the plants grown under non-limiting nutrient conditions. However, I did not find any relation between these two variables when the plants were grown under nutrient stress experiment as Larsson *et al.* (1986) described previously.

There was no significant relationship between mean RGR of species and the mean measurable toxicity of their tissues for either the non-limiting nutrient experiment or the nutrient stress experiment. In other words, the positive non-parametric correlation between the average total phenolic content per species and its average RGR, found in the non-limiting nutrient experiment, disappears when the plants are grown under nutrient stress. Certainly one could detect a negative correlation between RGR and total phenolics when comparing data sets across the two experiments; decreasing nutrient supply levels reduced RGR and increased total phenolics. However, the fact that this negative correlation does not exist within a nutrient level means that this overall negative relationship is due to both variables responding in different ways to a change in external fertility levels, not to a necessary physiological trade-off between the two.

3.4.4 Is there a relation between leaf nitrogen and soluble phenolics?

In both experiments I found consistent results that show a negative relation between leaf nitrogen and soluble phenolics. The mean tissue nitrogen content was negatively correlated with the mean tissue phenolic content (r_s= -0.42, p= 0.02) but this trend was diluted when looking only at leaf tissues (r_s= -0.31, p= 0.09) or only at root tissues (r_s= 0.18, p= 0.32) for the plants grown under non-limiting nutrient conditions. For the nutrient stress experiment, the mean of leaf nitrogen content was negatively correlated with the mean of the natural logarithm of total soluble phenolics (r_s= -0.475; p= 0.04).

In many studies, leaf nitrogen is negatively correlated with foliage phenol concentrations (Haukioja *et al.*, 1985; Dustin and Cooper-Driver, 1992; Kainulainen *et al.*, 1996). It has also been observed that concentrations of phenolic compounds (Ross and Berisford, 1990; Sunnerheim-Sjöberg and Hämäläinen, 1992) are inversely related to tree growth although this

growth is not based on a whole plant measure and it is not generally standardized for differences in initial size.

There was no significant relation between the mean of leaf nitrogen and the measurable toxicity ($1/LC_{50}$; μg/ml) in brine shrimp test for the non-limiting nutrient experiment. However, the mean of leaf nitrogen content was negatively correlated with the measurable toxicity ($1/LC_{50}$; μg/ml) in brine shrimp test (r_s= -0.525; p= 0.02) for the nutrient stress experiment.

This negative correlation between toxicity - based on carbon containing compounds, since the Asteraceae do not generally possess nitrogen-based toxins - and leaf nitrogen shows the same statistical trend as the negative correlation between total phenolics (other carbon-based compounds) and leaf nitrogen. These two trends must not be confused however. Nutrient stress increased the concentration of the total phenolics, as predicted by the carbon/nutrient hypothesis, but decreased the toxicity of the tissues, contrary to the carbon/nutrient hypothesis. In other words, under nutrient stress all species had less toxic tissues (except *Artemisia vulgaris, Lapsana communis* and *Tanacetum vulgare,* for which the toxicity was essentially the same) and less leaf nitrogen, but those species whose toxicity was less reduced had their nitrogen concentrations more reduced. I offer the following explanation, recognizing that this must remain speculative until further studies are conducted.

It is possible that not all species were equally limited in their nitrogen demands in the nutrient-stress experiment. Those species least strongly limited had their leaf nitrogen levels least depressed and therefore their photosynthetic rates were not as strongly depressed. This allowed these species to still produce some carbon-based toxic compounds. Those species most strongly limited in the nutrient stress experiment had their leaf nitrogen levels most depressed and therefore their photosynthetic rates were more severely depressed. This

prevented these species from producing any detectable concentrations of these carbon-based toxic compounds. If this is true, then the same statistical trend between leaf nitrogen and either total phenolics or toxicity is due to different reasons. Another explanation could be the fact that different species produce different secondary compounds, so the negative correlation between toxicity and leaf nitrogen that I found for the nutrient stress experiment could be just because some of the secondary compounds respond to the nutrient treatment in different ways. This hypothesis is supported by Zangerl and Berenbaum (1987). These authors studied six furanocoumarins present in wild parsnip and showed that light and nutrient availability affected the concentration of four of the six furanocoumarins studied but in different ways.

In conclusion, the data of this chapter provide evidence that the external nutrient availability affects the growth and the chemical parameters in different ways. First, the relative growth rate and the specific leaf area are affected by reducing the mean values under nutrient stress. In contrast, the root:shoot ratio increased under such conditions. Those results are supported by the previously cited studies. As expected, leaf nitrogen content was reduced under nitrogen stress. The complication occurs in the parameters related to chemical defense: while total phenolics content increased, toxicity decreased. Since both phenolics and toxic compounds (sesquiterpenes and polyacetylenes) are carbon-based, the carbon/nitrogen balance hypothesis cannot be used to explain the contrary results based on the toxicity measure since the toxicity of most species was higher when nutrients were not limiting. I have suggested that the carbon/nutrient hypothesis may apply to phenolic compounds, but not to those toxic substances contributing to the measured toxicity. The reasons for this are not clear, and the reasons that I have suggested must be tested in further experiments.

The second objective was to determine how the growth and chemical variables change, and whether the patterns of correlations between the variables change, under conditions of nutrient stress relative to those provided to the plants in chapter II. My data showed a positive

correlation between relative growth rate and total phenolics for the plants grown with non-limiting nutrients. On the other hand, this trade-off disappeared for the plants grown under nutrient stress. In neither experiment did I observe a negative correlation between RGR and phenolic concentration. The plants in the first experiment had both higher growth and lower total phenolic concentrations, so there would be a negative correlation when comparing across experiments. These results are consistent with the previously cited literature that affirm a negative correlation between RGR and phenolics, but this negative correlation is due to each variable responding differently to a nutrient stress, not due to a physiological trade-off between growth and defense. Here I argue that those studies that did report such a correlation failed to measure whole-plant growth rate.

The initial claim for this trade-off, and much of the empirical evidence for it, come from the work of Coley and her coworkers (Coley, 1983, 1987, 1988; Coley *et al.*, 1985; Jing and Coley, 1990; Sagers and Coley, 1995). Coley (1983) claims to have demonstrated an inverse relationship between intrinsic growth rate of 42 canopy and 4 subcanopy tree species in a lowland tropical rain forest and defense in the form of chemical attributes (phenolics and tannins) and physical attributes (toughness, hairs, fibers), and the author reaffirms this idea in Coley (1987) when she is justifying her argument for the "selection for plant defense". Since these studies have been so influential to subsequent interpretations of the trade-off between growth and defense, they will be criticized here. Coley (1988) considered growth of 41 tree species as the annual increase in height of the tree sapling and as the annual increase in the total leaf area of the sapling for plants grown in the field and therefore in variables from uncontrolled environments. The measures of "growth" are absolute measures and, since growth in a compound process, this value will be strongly affected by the initial size of the plant. As well, her measures of growth were very crude and did not include the whole plant. There are some other confusing aspects of these data. For instance, in Coley (1988), data are presented to contrast light-gap versus shade-tolerant species, but a comparison of these data and those of Coley (1983) show that they are the same data with the species simply classed

differently. Thus, these two papers do not represent two different sets of empirical data. Furthermore, Coley (1988) actually reported a non-significant correlation between her measure of growth and phenolic content of the leaves. The significant negative correlations were between "growth" and leaf toughness and fiber content. Thus the trade-off was between "growth" and physical attributes, not chemical defenses. For all of these reasons, the data, which have so strongly influenced our notions of the trade-off between growth and chemical defense, are not very convincing. Sagers and Coley (1995) also found a negative correlation between total tannin and average relative growth rate between the planting and harvest date but the plants came from cuttings to which had been applied both fungicide and a rooting hormone, and they waited 8 weeks before transplanting to an outside garden with uncontrolled variations in light and nutrient levels. There were therefore several factors influencing the results of this experiment which make it difficult to interpret.

Deslow *et al.* (1990) found no evidence of a trade-off between growth and foliar phenolic concentration in seven shrub species from a rain forest of Costa Rica. The authors studied rooted cuttings of seven shrub species. This experiment involved both a field and a greenhouse experiment. In the field experiment the plants were planted into two replicate plots per site (4 sites- recent natural gaps with adjacent forest understory), each site had 3 treatments (clearing center, gap edge, forest understory) and each treatment had two levels of nutrient availability (control, added complete fertilizer). The soils were derived from volcanic parent material that was high in available nitrogen and low phosphorous and may be low in other nutrients as well. Also the authors reported that the existing litter and vegetation were left intact and because the existing vegetation continued to grow throughout the experiment, light available to the cuttings declined in the period between planting and harvest; wavelength composition may have changed also, according to the authors. The authors recorded data on survival, total stem length (sum of all branches), and number of leaves produced monthly on all plants. Carbon fixation at light saturation was measured on selected individuals in the field

after 6 months. All plants were harvested at the end of six months. They found an increase in both growth and phenolics at high light levels.

They also conducted an experiment for three species in a shade-house. They compared the growth rates under less variable conditions than those found in the gap environment. The relative growth rate based on total dry mass exclusive of the original cutting was calculated by treatment only in the shade-house for each species as the slope of natural logarithm of total dry mass plotted against time (in months) elapsed since establishment in the treatment light levels. This is therefore a relative growth rate, which corrected for differences in initial size. As in Rousi *et al.* (1996), the authors found little support for the hypothesis predicting a trade-off between growth and defenses when using this improved experimental design. McCanny *et al.* (1990) found no significant relationship between toxicity of chemical defenses and RGR in 30 species of wetland herbs. In that study chemical defense was measured as the percent reduction in the growth of a generalist herbivore when fed a corn agar diet to which known amounts of the chemical extracts of the plants had been added. Relative growth rate was measured on a whole plant basis from plants grown in the greenhouse. Although many other studies (for example: Bryant *et al.*, 1987; Rousi *et al.*, 1996; Wilkens *et al.*, 1996) claim to have tested the hypothesized trade-off, none of these studies actually performed a statistical test of the relationship. The published evidence in favor of the presumed trade-off is therefore of poor quality and this is one of the reasons why the present study was conducted.

Although there was a trade-off between total phenolics and leaf nitrogen content for both experiments, the data showed a trade-off between toxicity and leaf nitrogen content only for the nutrient stress experiment. This negative correlation cannot be interpreted as support for the carbon/nutrient hypothesis, for the reasons given above.

A potential criticism of the results presented in these two chapters is that only two levels of nutrient concentrations were used and light levels were not systematically manipulated. Of course, increasing the number of experimental treatments will result in decreasing the number of species that can be studied for logistical reasons but provides more detailed information on how these patterns change with changing resource supplies. In the next chapter I wish to test if the patterns detected up until now are maintained under different combinations of nutrient and light supplies.

CHAPTER IV

DIFFERENTIAL RESPONSES OF GROWTH AND CHEMICAL DEFENSES OF SIX SPECIES OF ASTERACEAE IN RELATION TO RESOURCE AVAILABILITY

4.1 INTRODUCTION

Studies of the resource availability hypothesis have tended to contrast the defense capacities of plant species growing in two different resource states (McKey *et al.,* 1978; Bryant and Kuropat, 1980; Coley, 1983; Newberry and de Foresta, 1985; Baldwin and Schultz, 1988). However, in most natural communities, individuals within a population of plants may often experience many different levels of resource availability (Grime, 1979; Keddy, 1989). Differences in resource availability have been shown to generate variation in defensive chemistry (Waterman *et al.,* 1984; Larsson *et al.*, 1986; Bryant *et al.,* 1987 a b; Shure and Wilson, 1993). Such variation in defensive chemistry, even on a small spatial scale, may influence host selection and subsequent success of insect herbivores (Zangerl and Berenbaum, 1993). Therefore, it is important to understand how a range of resource availabilities influences phenotypic variation in plant allocation to defensive chemistry. Few studies have examined how a range (i.e., more than two levels) of a resource affects allocation to defensive chemistry and growth-related characteristics (Mihaliak and Lincoln, 1985; Waring *et al.,* 1985; Shure and Wilson, 1993). Furthermore, few studies have examined how two resources, simultaneously manipulated, influence the allocation by plants to secondary chemicals (Larsson *et al.,* 1986; Bryant *et al.,* 1987 a b; Dudt and Shure, 1994). How might resource availability, constrain secondary metabolism and, thereby, plant defensive responses?

The goal of this chapter is to investigate if there is any correlation between RGR and secondary metabolism under different combinations of light intensity conditions and different levels of nutrient conditions for 6 species of Asteraceae.

4.2 MATERIALS & METHODS

4.2.1 The species

I worked with 6 different species (*Achillea millefolium*, *Arctium minus*, *Chrysanthemum leucanthemum*, *Cichorium intybus*, *Matricaria matricarioides* and *Rudbeckia hirta*) from 4 tribes. These 6 species were chosen based on the results presented in chapter II. I chose species that had high, intermediate and low values of RGR and of LC_{50}. Of the 6 species, there are 1 biennial, 2 annual and 3 perennial growth forms. As I wrote in chapter II these species display a wide variability in growth rate as well as physical and chemical defenses. In this project I concentrated on chemical defenses.

4.2.2 Experimental design

Seed collection and storage, as well as germination conditions, were as described in chapter II. The experiment was conducted from October 1995 until June 1996 under controlled conditions in a Conviron (PGW36) growth chamber at McGill University, Montreal, Quebec. This experiment was synchronized based on previous data (Appendix 1) on the time of the germination for these species.

Plants were supplied with photosynthetic photon flux density (PPFD) of 500, 250 and 125 μ mol/m^2/s (according to the light treatment) (fluorescent tubes (Sylvania cool white VHO, 240 W) and incandescent bulbs (Phillips 60 W lamps)) for 16 hours a day. This provided daily integrated photon flux of 28.8, 14.4, 7.2 moles/m^2 respectively. The temperature was

maintained at 25 °C day and 20 °C night and the relative humidity was 80%. Each light intensity represented a separate growth chamber.

The hydroponic system was the same as that described in chapter II. The experiment was in the form of randomized blocks. Each hydroponic container formed one block. The 140 individuals were randomly assigned positions within each container. The experimental design originally consisted of all possible combinations of three levels of light intensity (500, 250 and 125 $\mu mol/m^2/s$) and five levels of nutrient concentration (full-strength, 1/5, 1/10, 1/50, 1/100 dilution of the full-strength modified Hoagland solution). However, because the plants had grown very poorly in 1/100 dilution of the modified Hoagland solution even under the highest light intensity (500 $\mu mol/m^2/s$), I decided not to use this dilution for the two other light intensities. Instead I doubled the number of containers for the 1/50 dilution. This procedure assured that I had enough biomass for the bioassay (1 g fresh weight) and to estimate growth rates.

Three plants per species per container per treatment were randomly chosen for each harvest period giving total of 15 plants per species per treatment per harvest; exceptions were *Chrysanthemum leucanthemum* and *Rudbeckia hirta*. For these two species, 25 plants were harvested per treatment for the two first harvest dates and 30 plants were harvested per treatment for the two later harvest dates. The number of plants increased for these two species because of HPLC analysis (see chapter V) which required 10 g fresh weight.

Harvest dates were generally at 21, 28, 35, and 42 days after transplanting into the hydroponic system. However, at the lowest nutrient levels at a light intensity of 500 μ $mol/m^2/s$, I had to delay the beginning of harvests in order to insure that enough biomass was available. Therefore, at the 1/50 dilution *Achillea millefolium, Chrysanthemum leucanthemum, Matricaria matricarioides* and *Rudbeckia hirta* were harvested at 28, 35, 42,

and 49 days. For the 1/100 dilution *Arctium minus* and *Cichorium intybus* were harvested at 28, 35, 42, and 49 days and *Achillea millefolium, Chrysanthemum leucanthemum, Matricaria matricarioides* and *Rudbeckia hirta* were harvested at 35, 42, 49, and 56 days.

At each harvest, plants were separated into leaves, stem, bud flowers or flowers and roots. Roots were separated at the base of each plant at ground level and washed free of rock wool with tap water. All plant parts were blotted dry with paper towels and fresh weights were measured. Leaf blades and flowers were placed in a plant press and roots and stems were placed in paper bags. These were allowed to dry at 80°C in a forced air drying oven to a constant dry weight for a minimum period of 48 hours.

All other aspects of this experiment (measurements of plants, growth analyses and chemical analysis) were the same as those described in chapter II. One exception was in the nitrogen analyses where only the leaves samples were analyzed.

4.2.3 Statistical analyses

All data were analyzed using the Spearman correlation and/or the general linear model (GLM) procedure in the SAS statistical package (SAS, Inc. 1990). The trends in the relationships between the parameters were plotted using Sigma Plot (Jandel Scientific, 1994).

4.3 RESULTS

4.3.1 General observations

The nutrient solution was monitord daily for changes in pH and nitrate concentrations. The pH levels fluctuated daily from 5.48 to 6.01 (full-strength solution), from 5.40 to 6.0 (1/5 dilution of full-strength solution), from 5.43 to 5.87 (1/10 dilution of full-strength solution) and from 5.34 to 6.05 (1/50 dilution of full-strength solution) during the experimental period. Since these pH values were within the acceptable range, they were not adjusted. The concentration of nitrate in the solution ranged from 7.4 to 9.3 millimoles (full-strength solution), from 1.5 to 1.7 millimoles (1/5 dilution of full-strength solution), from 0.7 to 0.8 millimoles (1/10 dilution of full-strength solution) and from 0.16 to 0.15 millimoles (1/50 dilution of full-strength solution). A record of the daily changes in NO_3 and pH of the solution are given in the Appendices 9, 10 and 11. Samples of the hydroponic solution were taken for each container weekly. I measured the toxicity of these samples using the brine shrimp bioassay. The values of the measurable toxicity for the hydroponic samples were never different from the controls. This means that there were no detectable secondary compounds diluted in the hydroponic solution.

4.3.2 Variation in the growth parameters

The full data set of the 6 species investigated in this study are given in Appendices 12 and 13. In order to maintain a balanced experimental design, I separated the data of this experiment into two groups for statistical analysis in the analyses of variance. The first group contains 9 factorial combinations of light intensity (500, 250 and 125 $\mu mol/m^2/s$ PAR) and nutrient concentrations (full-strength, 1/5 and 1/10 dilution of the full-strength modified Hoagland

solution). The second group contains 8 factorial combinations of light intensity (250 and 125 μmol/m^2/s PAR) and nutrient concentrations (full-strength, 1/5, 1/10 and 1/50 dilution of the full-strength modified Hoagland solution). I will call the first group the "3L-3N" ("three light - three nutrient levels") treatment and the second group the "2L-4N" treatment ("two light - four nutrient levels"). I decided to drop the data involving the 1/50 and 1/100 dilutions of the 500 μmol/m^2/s PAR light intensity because of the harvesting delay for some species due to poor growth.

Differences in the mean of relative growth rates (RGR), root:shoot ratios, specific leaf area (SLA), and chemical characteristics [% nitrogen in leaves, mean total soluble phenolics (% total soluble phenolics GAE, g/g), and mean of measurable toxicity ($1/LC_{50}$; μg/ml) in the brine shrimp test] among treatments are summarized in Tables 11 and 12.

For the first group (3L-3N treatment) the mean relative growth rates (RGR) varied 4.2-fold between the slowest (*Arctium minus*, RGR= 0.06 g g^{-1} day^{-1}, grown under light intensity 250 μmol/m^2/s PAR and 1/10 dilution of the full-strength modified Hoagland solution) and the fastest growing species (*Rudbeckia hirta*, RGR= 0.250 g g^{-1} day^{-1}, grown under light intensity 250 μmol/m^2/s PAR and full-strength modified Hoagland solution). The same two species defined the slowest (*Arctium minus* RGR= 0.031 g g^{-1} day^{-1} grown under light intensity 250 μ mol/m^2/s PAR and 1/50 dilution of the full-strength modified Hoagland solution) and the fastest growing species (*Rudbeckia hirta*, RGR= 0.250 g g^{-1} day^{-1} grown under light intensity 250 μmol/m^2/s PAR and full-strength modified Hoagland solution) for the second group (2L-4N).

The specific leaf area (SLA) varied 4.0-fold between 144.677 to 580.611 cm^2 g^{-1} for *Arctium minus* (500 μmol/m^2/s PAR and 1/5 dilution of the full-strength modified Hoagland solution) and *Rudbeckia hirta*, (125 μmol/m^2/s PAR and full-strength modified Hoagland solution)

respectively, for the first treatment group. The second group shows similar values for the SLA (*Arctium minus,* 156.576 (250 μmol/m^2/s PAR and 1/50 dilution of the full-strength modified Hoagland solution) and *Rudbeckia hirta*, 580.611 cm^2 g^{-1} (125 μmol/m^2/s PAR and full-strength modified Hoagland solution).

The means of the root:shoot ratios for the first group (3L-3N) varied 8.2-fold between 0.123 to 1.005 g/g for *Matricaria matricarioides* (125 μmol/m^2/s PAR and 1/5 dilution of the full-strength modified Hoagland solution) and *Cichorium intybus* (500 μmol/m^2/s PAR and 1/10 dilution of the full-strength modified Hoagland solution), respectively. While for the second group (2L-4N) the means of the root:shoot ratios varied 10.6-fold between 0.123 to 1.298 g/g for *Matricaria matricarioides* (125 μmol/m^2/s PAR and 1/5 dilution of the full-strength modified Hoagland solution) and *Arctium minus* (250 μmol/m^2/s PAR and 1/50 dilution of the full-strength modified Hoagland solution).

The means of leaf nitrogen content for the first group (3L-3N) varied 2.9-fold between 1.799 % to 5.138 % for *Chrysanthemum leucanthemum* (500 μmol/m^2/s PAR and 1/10 dilution of the full-strength modified Hoagland solution) and *Arctium minus* (500 μmol/m^2/s PAR and full-strength modified Hoagland solution), respectively. For the second group (2L-4N) the means of the leaf nitrogen content varied 2.7-fold between 1.762 % to 4.734 % for *Arctium minus* (250 μmol/m^2/s PAR and 1/50 dilution of the full-strength modified Hoagland solution) and *Matricaria matricarioides* (250 μmol/m^2/s PAR and full-strength modified Hoagland solution).

The total phenolics for the first group varied 4.8-fold between 0.333 to 1.596 % GAE for *Chrysanthemum leucanthemum* (125 μmol/m^2/s PAR and 1/10 dilution of the full-strength modified Hoagland solution) and *Rudbeckia hirta* (500 μmol/m^2/s PAR and 1/10 dilution of the full-strength modified Hoagland solution), respectively. While for the second group (2L-

4N) the means varied 3.5-fold between 0.333 to 1.173 % GAE for *Chrysanthemum leucanthemum* (125 μmol/m^2/s PAR and 1/10 dilution of the full-strength modified Hoagland solution) and *Rudbeckia hirta* (250 μmol/m^2/s PAR and 1/50 dilution of the full-strength modified Hoagland solution), respectively.

The measurable toxicity in the brine shrimp test (1/LC_{50}; μg/ml) for the first group varied 27.5-fold between 0.01 to 0.275 μg/ml for *Arctium minus* (500 μmol/m^2/s PAR and 1/5 dilution of the full-strength modified Hoagland solution; and, 250 μmol/m^2/s PAR and 1/10 dilution of the full-strength modified Hoagland solution) and *Chrysanthemum leucanthemum* (125 μmol/m^2/s PAR and 1/5 dilution of the full-strength modified Hoagland solution), respectively. While for the second group (2L-4N) the means varied 44.6 fold between 0.01 for *Arctium minus* (250 μmol/m^2/s PAR and 1/10 dilution of the full-strength modified Hoagland solution) and *Matricaria matricarioides* (125 μmol/m^2/s PAR and 1/50 dilution of the full-strength modified Hoagland solution) to 0.446 μg/ml for *Chrysanthemum leucanthemum* (125 μmol/m^2/s PAR and 1/50 dilution of the full-strength modified Hoagland solution), respectively.

4.3.3 Effects of experimental manipulations on growth parameters and chemical parameters.

a- Growth parameters:

Relative Growth Rate (RGR)

Tables 11 and 12 show the mean of relative growth rate for the three different levels of light intensity over the entire harvest period. For the 3L-3N group the overall means were 0.086, 0.118 and 0.142 g/g/day for 500, 250 and 125 $\mu mol/m^2/s$ PAR, respectively. For the second group (2L-4N), the overall mean RGR values were 0.111 and 0.142 for 250 and 125 μ $mol/m^2/s$ PAR, respectively. These counterintuitive results will be further explored later.

For the 3L-3N group ANOVA an average RGR between days 21 and 42 shows significant differences between species means ($p= 0.0001$) and between the means of the 3 light levels ($p= 0.0001$). Nutrients had no significant effect over the range full-strength to 1/10 dilution of full-strength solution, and there are no interactions. An ANOVA on the dry weights, rather than on the average RGR, also detected an effect of species and of light intensity with no interactions. Furthermore, the ranking of dry weights (Tukey's Studentized range) showed a decrease in mean dry weight in the lowest light relative to the other two, for which there was no significant difference. Thus, mean dry weights for the 3 light levels in decreasing intensity were 0.205, 0.203 and 0.060 g. For the 2L-4N group ANOVA an average RGR between days 21 and 42 showed significant differences between species ($p= 0.0001$), light (0.0001) and nutrients ($p= 0.02$) and no significant interactions. This permitted to detect an effect of nutrients. The ANOVA on dry weights showed the same effects but (consistent with the first

analysis above) Tukey's Studentized range showed a decrease only in the lowest (1/50 dilution of the full-strength solution) nutrient level. Again, the lowest light level produced a decreased dry weight of the plants.

A very different picture emerges when we look at variation in the RGR values between each harvest rather than using only the average RGR values over the full harvest period. Now, the only significant effect (in either the 3L-3N or 2L-4N groups) is light; there are no significant differences in mean RGR between species or between nutrient levels. Furthermore, the highest RGR values occur at the lowest light levels and RGR decreases with increasing light intensity. This could be explained by the average RGR values increasing before harvesting began (i.e. 3-21 days) and then decreasing as plants increased in size. If so, then this could be detected using an analysis of covariance with dry weight used as a covariate.

Figure 19 shows that over the harvest period from 21 to 42 days, there was a general decrease in RGR as plants got bigger. The analysis of covariance with dry weight at the end of each harvest period as the covariate for the 3L-3N group shows that, after standardizing to common size, there are significant differences between species ($p= 0.0008$), i.e. the average RGR differed between species when compared at a common plant weight, but no significant differences in RGR between either the three light levels (500, 250 and 125 $\mu mol/m^2/s$ PAR) or the three nutrient levels (full-strength, 1/5 and 1/10 dilution of the full-strength modified Hoagland solution). Note that the probability levels (0.069 and 0.067 for light and nutrient respectively) are near the level of significance. A similar analysis on the 2L-4N group shows no significant differences in mean RGR between species ($p= 0.07$), between the two light levels 250 and 125 $\mu mol/m^2/s$ PAR ($p= 0.62$) or between the four nutrient levels ($p= 0.09$), but with a hint of an interaction between light levels and nutrient levels ($p= 0.05$). Thus, except for the differences between species in the 3L-3N group, the experimental treatments do not appear to have affected relative growth rates once we compare plants that are at a

common size. So, although plants had, on average, higher RGR values at lower light levels, RGR decreased with increasing plant size and this effect of light was removed once plants were compared at a common plant size.

It is logically impossible for a plant to maintain a lower RGR over the entire growth period but to have a lower final biomass than one that maintains a higher RGR over the entire growth period if both begin at the same initial size. Therefore, the only explanation for the fact that plants at a lower light level have a higher average RGR over the growth period 21-42 days yet a lower final biomass is that RGR was changing over the growth period in a compensatory fashion. This is what happened in this experiment. The average RGR before the harvests began (i.e. between 0-21 days) were 0.29, 0.28 and 0.21 g/g/day at light intensities of 500, 250 and 125 $\mu mol/m^2/s$. Note that the highest growth rates before the harvests began were at the highest light level - exactly the opposite of what happened after day 21. Thus, plants at the highest light levels, having the highest initial RGR values, were larger by day 21. Because RGR decreased with increasing plant size, these plants therefore had their RGR values reduced more rapidly during the harvest period, thus producing an average RGR after day 21 that was lower than those at lower light levels.

What could cause this decrease in RGR with increasing size? The data from Hunt (1982) and Hunt and Lloyd (1987), and re-analyzed in Shipley and Hunt (1996), in which daily changes in RGR from 0 to 60 days of *Holcus lanatus* L. (a grass) grown in hydroponic culture was measured, show that RGR increased from 0.1 to 0.3 from day 0 to day 20 and then decreased back to 0.1 by day 30. Since these plants were grown singly, this result is not due to correlation between plants. These changes in RGR are consistent with my results: average RGR values of 0.29 g/g/day before the harvests began, and RGR values of around 0.1 during the harvest period. If these changes in RGR are size-dependent, i.e. RGR increases up to some critical plant size and then begins decreasing with increasing plant size - then this

decreasing trend in RGR would occur earlier at the highest light intensities in which the plants increased in size more rapidly. Of course it could also be an indication of competition: the plants were largest at the highest light intensities and may have begun to compete more rapidly. The patterns in SLA argue against this explanation. SLA is a very plastic character that increases under light stress and this variable clearly showed such changes in the different light treatments. If the plants at the highest light intensities were competing for light, then the smaller species should have increased SLA as they were shaded, yet neither *Chrysanthemum leucanthemum* nor *Rudbeckia hirta* (the smallest species) showed any indication of this.

Specific Leaf Area (SLA)

The specific leaf area was measured independently for each harvest period. I ran separate ANOVAS for the first group (3L-3N group) and the second group (2L-4N group). ANOVA for the first group showed that SLA values differed between the 6 species ($p < 0.0001$) and between the three light levels ($p < 0.0001$), but not between the three levels of nutrients, nor were there any interactions among the treatments (Tables 11). The mean values of SLA were 210.655, 247.749 and 413.533 g/cm^2 for 500, 250 and 125 μmol/m^2/s PAR, respectively.

For the second group (2L-4N group) SLA values differed between the 6 species ($p < 0.0001$), between the two light levels ($p < 0.0001$) and between the four nutrient levels ($p = 0.0002$) but there were no significant interactions among the treatments (Table 12). The mean values of SLA were 234.969 and 400.005 g/cm^2 for 250 and 125 μmol/m^2/s PAR, respectively. Therefore the mean value of SLA behaved as expected for both groups (3L-3N and 2L-4N), i.e. increasing when submitted to light stress.

Root:Shoot Ratios

For the first group (3L-3N group) root:shoot ratios differed between the 6 species ($p < 0.0001$), between the three light levels ($p < 0.0001$) and between the three nutrient levels ($p< 0.0001$). There were interactions between light and species ($p= 0.02$), nutrients and species as well as between light and nutrients ($p= 0.002$) based on a 3-way ANOVA. The mean values of the root:shoot ratios for the first group were 0.500, 0.450 and 0.263 g/g for 500, 250 and 125 $\mu mol/m^2/s$ PAR, respectively (Table 11).

For the second group (2L-4N group) root:shoot ratios differed between the 6 species ($p< 0.0001$), between the two light levels ($p< 0.0001$) and between the four nutrient levels ($p< 0.0001$). The only significant interactions were between light and nutrients ($p< 0.0001$). The means values of the root:shoot ratios were 0.615 and 0.329 g/g for 250 and 125 $\mu mol/m^2/s$ PAR, respectively (Table 12).

b- Phytochemical parameter:

Total phenolics:

Arctium minus had the highest production of total phenolics when the data were pooled together (Table 11 and 12). It is conceivable that the amount of total phenolics may be affected by the amount of nutrients or by the light intensity. I therefore pooled the data by nutrient and by light intensity for each group (3L-3N and 2L-4N). The mean value for total phenolics values for the first group (3L-3N) increased as light intensity increased and decreased when nutrient concentrations increased (Table 11). For the 3L-3N group, an

ANOVA showed significant differences between species means ($p < 0.0001$), between the means of the 3 light levels ($p < 0.0001$) and between the means of the three nutrient levels ($p < 0.0001$). There were interactions between light and species ($p < 0.0001$) and between light and nutrients ($p < 0.0001$).

The mean value for total phenolics values for the second group (2L-4N) showed the same trends, increasing as light intensity increased and decreasing when nutrient concentrations increased (Table 12). Total phenolics values differed between the 6 species ($p < 0.0001$), between the two light levels ($p < 0.0001$) and between the four nutrient levels ($p < 0.0001$). The only interactions were between light and species ($p < 0.0001$).

Toxicity:

For the 3L-3N group the ANOVA shows significant differences between species means ($p < 0.0001$), and between the means of the 3 light levels ($p < 0.0001$). Nutrients had no significant effect over the range of nutrient concentrations from full-strength to a 1/10 dilution of the full-strength solution (Table 11). The only interaction was between light and species ($p < 0.0001$).

For the second group (2L-4N) the only significant factor in the ANOVA was between the species means ($p = 0.004$).

Leaf nitrogen content:

ANOVA showed similar results for both groups (3L-3N and 2L-4N, see Tables 11 and 12). Mean leaf nitrogen values were significantly different between species means ($p< 0.0001$ and $p= 0.0004$ for the two groups), between the means of the light levels ($p= 0.02$), and between nutrients ($p< 0.0001$). There are no interactions between the variables.

4.3.4 Comparisons between measured variables.

Growth parameters:

When pooling data across all treatments the Spearman correlation between the mean of relative growth rate (RGR; i.e. 21-42 days) and the mean of specific leaf area (SLA) was strong and positive ($r_s= 0.610$, $p= 0.0001$; Figure 20a). The correlation between the mean of RGR and the mean of root:shoot ratio was strong and negative ($r_s= -0.478$, $p= 0.0003$; Figure 21a) as was the correlation between SLA and root:shoot ratio ($r_s= -0.482$, $p= 0.0001$; Figure 22a), for the 3L-3N group.

The results for the second group were very similar to the first one. The Spearman correlation between the mean of RGR and the mean of SLA was strong and positive ($r_s= 0.606$, $p= 0.0001$, Figure 20b). The correlation between the mean of RGR and the mean of root:shoot ratio was strong and negative ($r_s= -0.420$, $p= 0.0003$; Figure 21b) as was the correlation between SLA and root:shoot ratio ($r_s= -0.512$, $p= 0.0001$; Figure 22b).

Phytochemical parameters:

For the 3L-3N group, when pooling data across the different environmental treatments, there was a negative weak significant correlation between total phenolics and measurable toxicity in the brine shrimp test (r_s= -0.186, p= 0.007). Therefore those plants producing more phenolics were less toxic. There was a strong negative significant correlation between leaf nitrogen content and total phenolics (r_s= -0.413, p= 0.0001), but a weak positive significant correlation between leaf nitrogen and measurable toxicity in the brine shrimp test (r_s= 0.161, p= 0.03).

For the 2L-4N group, the variables showed the same trends as in the first group. The correlation between total phenolics and measurable toxicity in the brine shrimp test (r_s= -0.258, p= 0.0005) was negative and significant, as was the correlation between leaf nitrogen content and total phenolics (r_s= -0.374, p= 0.0001). There was a weak positive significant correlation between leaf nitrogen and measurable toxicity in the brine shrimp test (r_s= 0.195, p= 0.01).

Growth parameters versus defense parameters:

For the 3L-3N group, there was a negative significant correlation between the mean of total phenolics and the mean of RGR (r_s= -0.317, p= 0.02; Figure 23a), and between total phenolics and SLA (r_s= -0.438, p= 0.0001; Figure 24a) but, a positive significant correlation between total phenolics and root:shoot ratio (r_s= 0.538, p= 0.0001). There was a positive but non significant correlation between the mean of measurable toxicity in the brine shrimp test and the mean of RGR (r_s= 0.260, p= 0.06). There was a positive significant correlation between measurable toxicity in the brine shrimp test and SLA (r_s= 0.18, p= 0.009) but there

was a negative significant correlation between measurable toxicity in the brine shrimp test and root:shoot ratios (r_s= -0.213, p= 0.002). There was no significant correlations between the mean of leaf nitrogen content and the mean of RGR (r_s= 0.173, p= 0.2). Finally, there were positive and significant correlations between leaf nitrogen content and SLA (r_s= 0.327, p= 0.0001) but a negative significant correlation between leaf nitrogen content and root:shoot ratios (r_s= -0.525, p= 0.0001).

For the 2L-4N group, there was a negative significant correlation between the mean of total phenolics and the mean of RGR (r_s=-0.089, p= 0.0001; Figure 23b). As in the first group (3L-3N), there was a negative correlation between total phenolics and SLA (r_s= -0.301, p= 0.5; Figure 24b) but the Spearman correlation showed a positive significant correlation between total phenolics and root:shoot ratios (r_s= 0.546, p= 0.0001). For measurable toxicity in the brine shrimp test and RGR (r_s= 0.453, p= 0.01) the correlation was positive and significant, as was the correlation between measurable toxicity in the brine shrimp test and SLA (r_s= 0.215, p= 0.004) but the correlation was negative and significant for measurable toxicity in the brine shrimp test and root:shoot ratios (r_s= -0.381, p= 0.002). There was no significant correlation between the mean of leaf nitrogen content and the mean of RGR (r_s= 0.176, p= 0.02). Finally, leaf nitrogen content and SLA (r_s= 0.387, p= 0.0001) showed a weak positive significant correlation but there was a negative strong significant correlation between leaf nitrogen content and root:shoot ratios (r_s= -0.6, p= 0.0001).

Correlations may be due to common responses to changing environments or to "genetic" linkages between variables in a constant environment. In order to distinguish between these two possibilities, I fit generalized linear models using the GLM procedure of SAS (SAS Institute Inc., 1990) relating the total phenolics and measurable toxicity in the brine shrimp test, in which the experimental treatments and species were included as covariates in order to

control for their effects. These results were then compared to models in which these effects were not controlled.

4.3.4.1 Correlations without controlling for the different environments:

Relative growth rate:

Although the relationships between the variables have been described above based on non-parametric Spearman correlations, analyses of covariance requires linear models. Here, I first present the results of linear regressions and then contrast these with the ANCOVA results. There were significant linear relationships between relative growth rate (RGR) and SLA ($p< 0.0001$), RGR and root:shoot ratio ($p< 0.0001$), between RGR and total phenolics ($p< 0.0001$), between RGR and measurable toxicity in the brine shrimp test ($p= 0.02$), but there was no significant linear relationships between RGR and leaf nitrogen ($p= 0.09$), for the 3L-3N group.

For the second group (2L-4N), there were significant linear relationships between relative growth rate (RGR) and SLA ($p< 0.0001$), between RGR and root:shoot ratio ($p< 0.0001$) and between RGR and leaf nitrogen ($p= 0.01$). There were no significant linear relationships between RGR and total phenolics ($p= 0.09$) or between RGR and measurable toxicity in the brine shrimp test ($p= 0.2$).

Total phenolics:

There were significant negative linear relationships between total phenolics concentration ($p< 0.0001$) and two growth parameters (SLA, root:shoot ratio) as well as the two chemical parameters (measurable toxicity in the brine shrimp test and leaf nitrogen content) for 3L-3N group.

For the second group (2L-4N), there were significant negative linear relationships between total phenolics concentration and SLA ($p< 0.0001$), but there were significant positive linear relationships between total phenolics concentration and root:shoot ratio ($p< 0.0001$). There were significant negative linear relationships between total phenolics concentration and leaf nitrogen content ($p< 0.0001$), as well as between total phenolics concentration and measurable toxicity in the brine shrimp test ($p= 0.03$). But there was no significant linear relationships between total phenolics concentration and RGR ($p= 0.09$).

Toxicity:

There were significant positive linear relationships between measurable toxicity in the brine shrimp test and RGR ($p= 0.02$) and SLA ($p= 0.03$), but there were significant negative linear relationships between measurable toxicity in the brine shrimp test and root:shoot ratio ($p= 0.03$) and total phenolics ($p< 0.0001$), but no linear relationships between measurable toxicity in the brine shrimp test and leaf nitrogen content ($p= 0.1$) for 3L-3N group.

For the second group (2L-4N), there were significant negative linear relationships between measurable toxicity in the brine shrimp test and total phenolics concentration ($p= 0.03$). There

were no linear relationships between measurable toxicity in the brine shrimp test and either RGR ($p= 0.2$), SLA ($p= 0.3$), root:shoot ratio ($p= 0.08$), leaf nitrogen content ($p= 0.1$).

4.3.4.2 Correlations after controlling for the different environments:

The regression analyses presented above involved data pooled over all experimental treatments. The significant relationships that were found could be due either to common responses of the dependent and independent variables to the changing light and nutrient conditions, to different average values between species or could be due to relationships between the variables independent of the environmental conditions or species. I therefore repeated the analyses but included species, light and nutrient treatments as covariates in order to differentiate between these two possibilities. After controlling for the different experimental conditions and species there were no linear relationships between RGR and any other variables. The same result was found with measurable toxicity in the brine shrimp test. In other words, the initial significant relationships that were detected do not exit within the same species at constant environmental conditions. The only significant relationship involving total phenolics concentrations was with the root:shoot ratio in the 2L-4N group ($p= 0.01$).

Table 11. Means of growth, dry matter partitioning, and chemical characteristics in six species of Asteraceae grown under 500, 250 and 125 μmol/m^2/s PAR with three different nutrient supply (full-strength, 1/5 and 1/10 dilution of full-strength Hoagland solution). Means by species (I); by light treatment (II); by nutrient treatment (III). Means followed by the same letters are not significantly different (HSD, 0.05 level).

I- Species	Mean					
	RGR (g/g/day)	Root/Shoot (g/g)	SLA (g/cm^2)	Nitrogen (% dw)	Total phenol (% dw -GAE)	Toxicity (μg/ml)
Achillea millefolium	0.123^{b}	0.358^{b}	242.6^{c}	3.29^{b}	0.72^{b}	0.071^{a}
Arctium minus	0.107^{de}	0.509^{a}	202.8^{c}	3.30^{b}	0.85^{a}	0.019^{b}
Chrysanthemum leucanthemum	0.110^{cd}	0.330^{b}	298.3^{b}	3.94^{a}	0.55^{c}	0.083^{a}
Cichorium intybus	0.116^{bc}	0.550^{a}	327.5^{ab}	3.66^{ab}	0.73^{ab}	0.039^{b}
Matricaria matricarioides	0.098^{e}	0.319^{b}	309.6^{b}	3.90^{a}	0.54^{c}	0.025^{b}
Rudbeckia hirta	0.137^{a}	0.350^{b}	372.0^{a}	2.59^{c}	0.77^{ab}	0.024^{b}

Pooled samples, n = 36

II- Level of light ($\mu mol/m^2/s$ PAR)	Mean					
	RGR (g/g/day)	Root/Shoot (g/g)	SLA (g/cm^2)	Nitrogen (% dw)	Total phenol (% dw -GAE)	Toxicity ($\mu g/ml$)
500	0.086^a	0.500^a	210.7^c	3.29^b	0.89^a	0.036^b
250	0.118^b	0.450^b	247.7^b	3.44^{ab}	0.65^b	0.031^b
125	0.142^c	0.263^c	413.5^a	3.71^b	0.56^c	0.066^a

Pooled samples, n = 72

III- Level of nutrients	Mean					
	RGR (g/g/day)	Root/Shoot (g/g)	SLA (g/cm^2)	Nitrogen (% dw)	Total phenol (% dw -GAE)	Toxicity ($\mu g/ml$)
full-strength	0.121^a	0.273^a	301.2^a	4.10^a	0.60^c	0.046^a
1/5 dilute	0.121^a	0.372^b	298.2^a	3.54^b	0.68^b	0.048^a
1/10 dilute	0.103^b	0.561^c	275.0^a	2.87^c	0.77^a	0.038^a

Pooled samples, n =72

Table 12. Means of growth, dry matter partitioning, and chemical characteristics in six species of Asteraceae grown under 250 and 125 μmol/m^2/s PAR with four different nutrient supply (full-strength, 1/5, 1/10 and 1/50 dilution of full-strength Hoagland solution). Means by species (I); by light treatment (II); by nutrient treatment (III). Means followed by the same letters are not significantly different (HSD, 0.05 level)

I- Species	Mean					
	RGR (g/g/day)	Root/Shoot (g/g)	SLA (g/cm^2)	Nitrogen (% dw)	Total phenol (% dw -GAE)	Toxicity (μg/ml)
Achillea millefolium	0.136^{b}	0.421^{b}	273.0^{dc}	3.15^{bc}	0.67^{a}	0.072^{ab}
Arctium minus	0.108^{d}	0.637^{a}	228.0^{d}	3.14^{bc}	0.76^{a}	0.017^{b}
Chrysanthemum leucanthemum	0.126^{c}	0.396^{b}	319.3^{bc}	3.68^{ab}	0.52^{b}	0.143^{a}
Cichorium intybus	0.127^{c}	0.606^{a}	368.3^{ab}	3.44^{ab}	0.69^{a}	0.032^{b}
Matricaria matricarioides	0.110^{d}	0.387^{b}	324.7^{bc}	3.84^{a}	0.54^{b}	0.019^{b}
Rudbeckia hirta	0.152^{a}	0.385^{b}	391.6^{a}	2.66^{c}	0.73^{a}	0.027^{b}

Pooled samples, n = 32

II- Level of light ($\mu mol/m^2/s$ PAR)	Mean					
	RGR (g/g/day)	Root/Shoot (g/g)	SLA (g/cm^2)	Nitrogen (% dw)	Total phenol (% dw -GAE)	Toxicity (µg/ml)
250	0.111^b	0.615^a	235.0^b	3.19^b	0.70^a	0.029^b
125	0.142^a	0.329^b	400.0^a	3.56^a	0.60^b	0.076^a

Pooled samples, n = 96

III- Level of nutrients	Mean					
	RGR (g/g/day)	Root/Shoot (g/g)	SLA (g/cm^2)	Nitrogen (% dw)	Total phenol (% dw -GAE)	Toxicity (µg/ml)
full-strength	0.139^a	0.254^c	338.9^a	3.95^a	0.58^b	0.047^a
1/5 dilute	0.135^a	0.326^c	337.5^a	3.76^a	0.58^b	0.055^a
1/10 dilute	0.116^b	0.489^b	315.5^{ab}	3.08^b	0.65^b	0.042^a
1/50 dilute	0.116^b	0.820^a	278.0^b	2.61^b	0.80^a	0.068^a

Pooled samples, n = 48

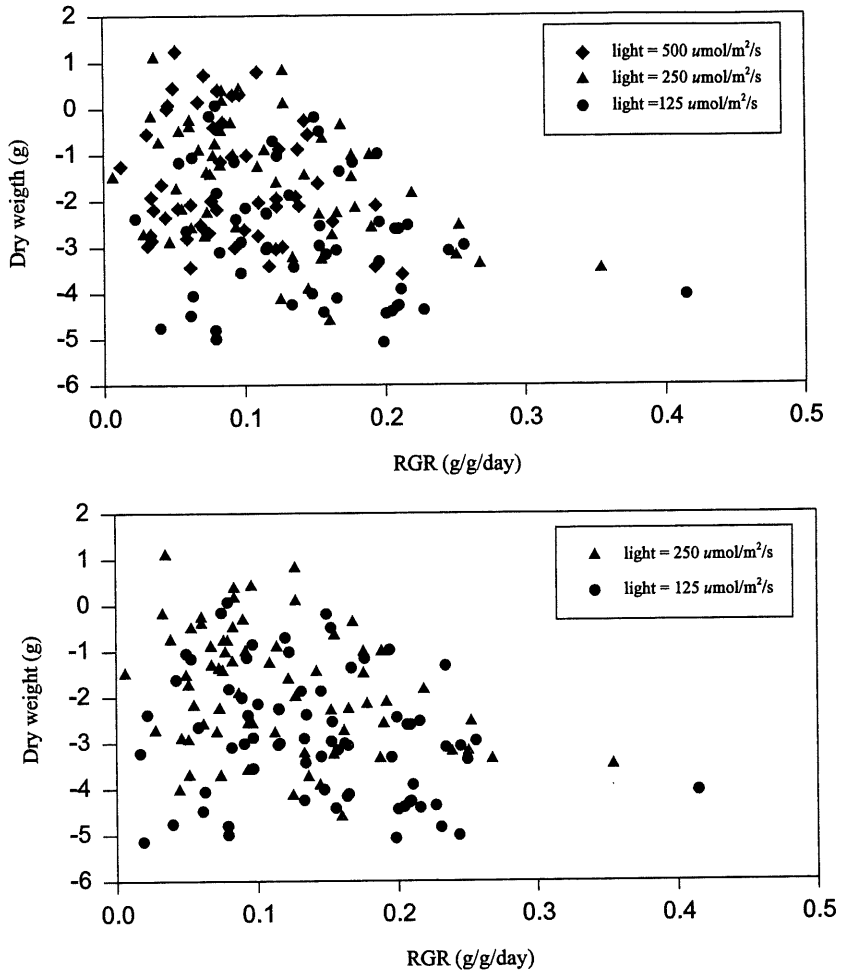


Figure 19. Relationship between means of RGR (g/g/day) and means dry weight (g) for 6 species of Asteraceae, grown under controlled conditions of temperature (25 °C), RH (80%), and photoperiod (16 h/day). a- Plants grown under high (500 μmol/m^2/s PAR), moderate (250 μmol/m^2/s PAR) and low light (125 μmol/m^2/s PAR) with three different nutrient supply (full-strength Hoagland solution; 1/5 dilute and 1/10 dilute). b- Plants grown under moderate (250 μmol/m^2/s PAR) and low light (125 μ mol/m^2/s PAR) with four different nutrient supply (full-strength Hoagland solution; 1/5 dilute; 1/10 dilute and 1/50 dilute). The negative correlation shown in this figure is less obvious because all species and treatments are plotted toghether.

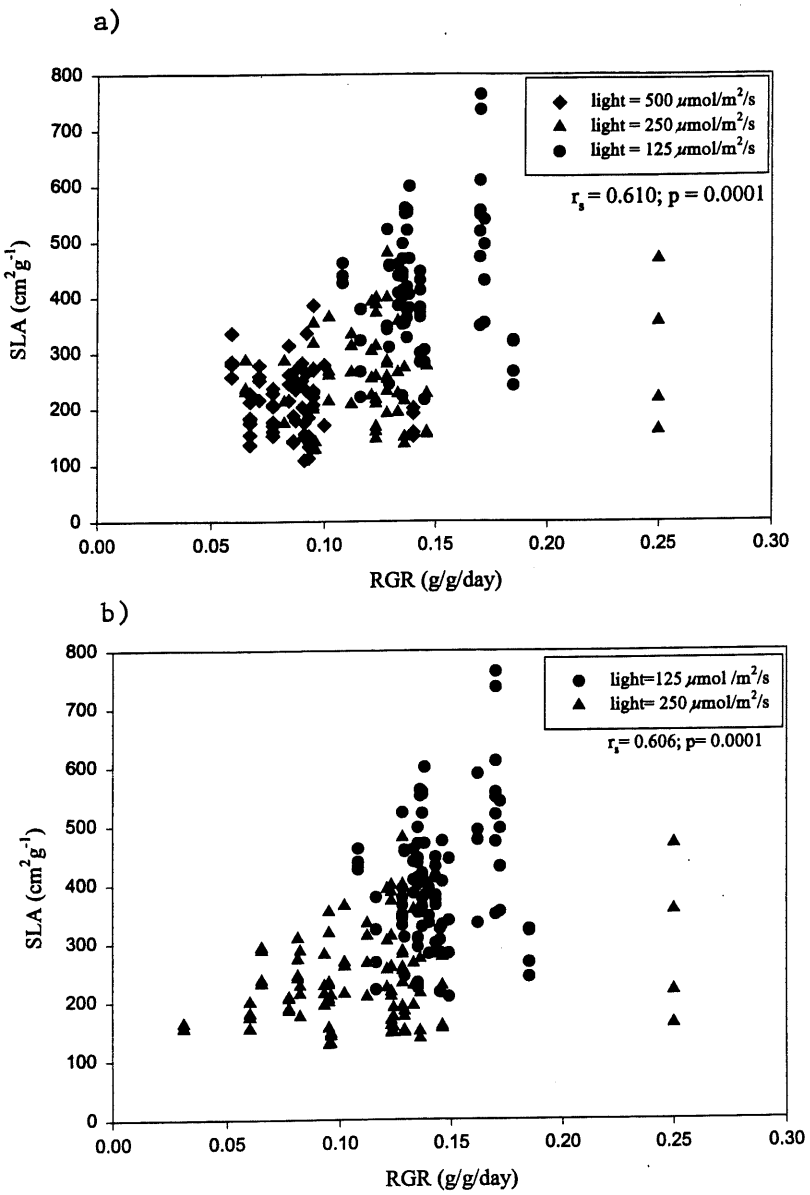


Figure 20. Relationship between means of RGR (g/g/day) and means of SLA (cm^2g^{-1}) for 6 species of Asteraceae, grown under controlled conditions of temperature (25 °C), RH (80%), and photoperiod (16 h/day). a- Plants grown under high (500 µmol/m^2/s PAR), moderate (250 µmol/m^2/s PAR) and low light (125 µmol/m^2/s PAR) with three different nutrient supply (full-strength Hoagland solution; 1/5 dilute and 1/10 dilute). b- Plants grown under moderate (250 µmol/m^2/s PAR) and low light (125 µ mol/m^2/s PAR) with four different nutrient supply (full-strength Hoagland solution; 1/5 dilute; 1/10 dilute and 1/50 dilute).

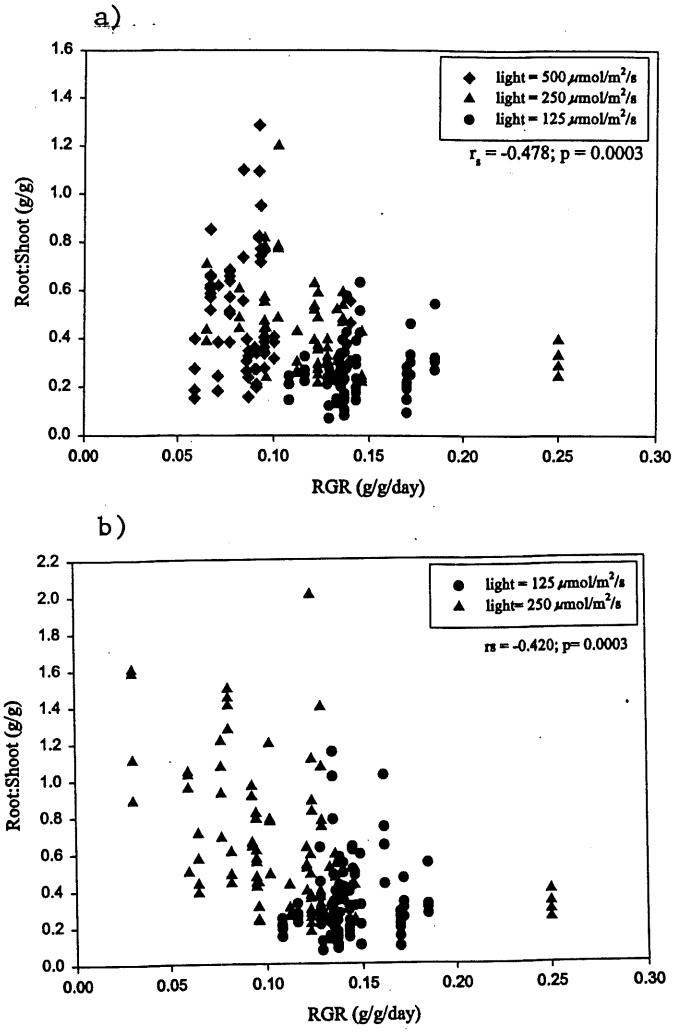


Figure 21. Relationship between means of RGR (g/g/day) and means of root:shoot ratio (g/g) for 6 species of Asteraceae, grown under controlled conditions of temperature (25 ° C), RH (80%), and photoperiod (16 h/day). a- Plants grown under high (500 µ mol/m^2/s PAR), moderate (250 µmol/m^2/s PAR) and low light (125 µmol/m^2/s PAR) with three different nutrient supply (full-strength Hoagland solution; 1/5 dilute and 1/10 dilute). b- Plants grown under moderate (250 µmol/m^2/s PAR) and low light (125 µmol/m^2/s PAR) with four different nutrient supply (full-strength Hoagland solution; 1/5 dilute: 1/10 dilute and 1/50 dilute).

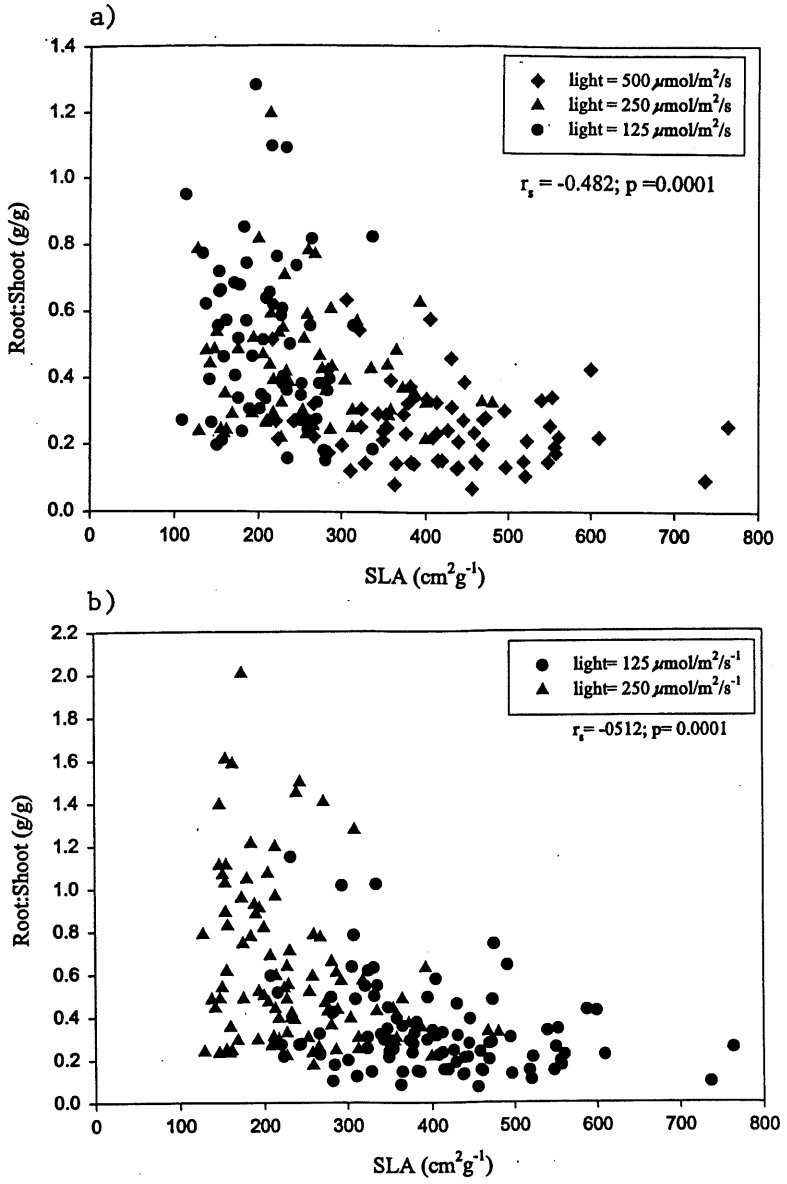


Figure 22. Relationship between means of SLA (cm^2g^{-1}) and root:shoot ratio (g/g) for 6 species of Asteraceae, grown under controlled conditions of temperature (25 °C), RH (80%), and photoperiod (16 h/day). a- Plants grown under high (500 $\mu mol/m^2/s$ PAR), moderate (250 $\mu mol/m^2/s$ PAR) and low light (125 $\mu mol/m^2/s$ PAR) with three different nutrient supply (full-strength Hoagland solution; 1/5 dilute and 1/10 dilute). b- Plants grown under moderate (250 $\mu mol/m^2/s$ PAR) and low light (125 μ $mol/m^2/s$ PAR) with four different nutrient supply (full-strength Hoagland solution; 1/5 dilute; 1/10 dilute and 1/50 dilute).

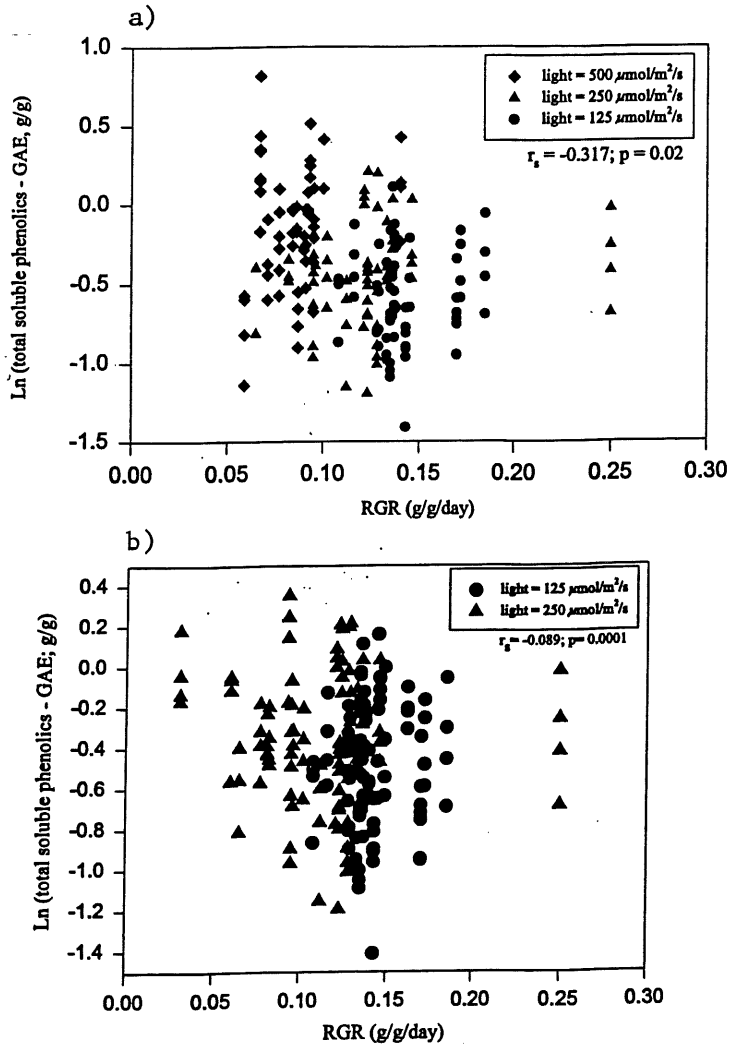


Figure 23. Relationship between means of RGR (g/g/day) and means of Ln (total soluble phenolics - GAE; g/g) for 6 species of Asteraceae, grown under controlled conditions of temperature (25 °C), RH (80%), and photoperiod (16 h/day). a- Plants grown under high (500 µmol/m^2/s PAR), moderate (250 µmol/m^2/s PAR) and low light (125 µmol/m^2/s PAR) with three different nutrient supply (full-strength Hoagland solution; 1/5 dilute 1/10 dilute). b- Plants grown under moderate (250 µ mol/m^2/s PAR) and low light (125 µmol/m^2/s PAR) with four different nutrient supply (full-strength Hoagland solution; 1/5 dilute; 1/10 dilute and 1/50 dilute).

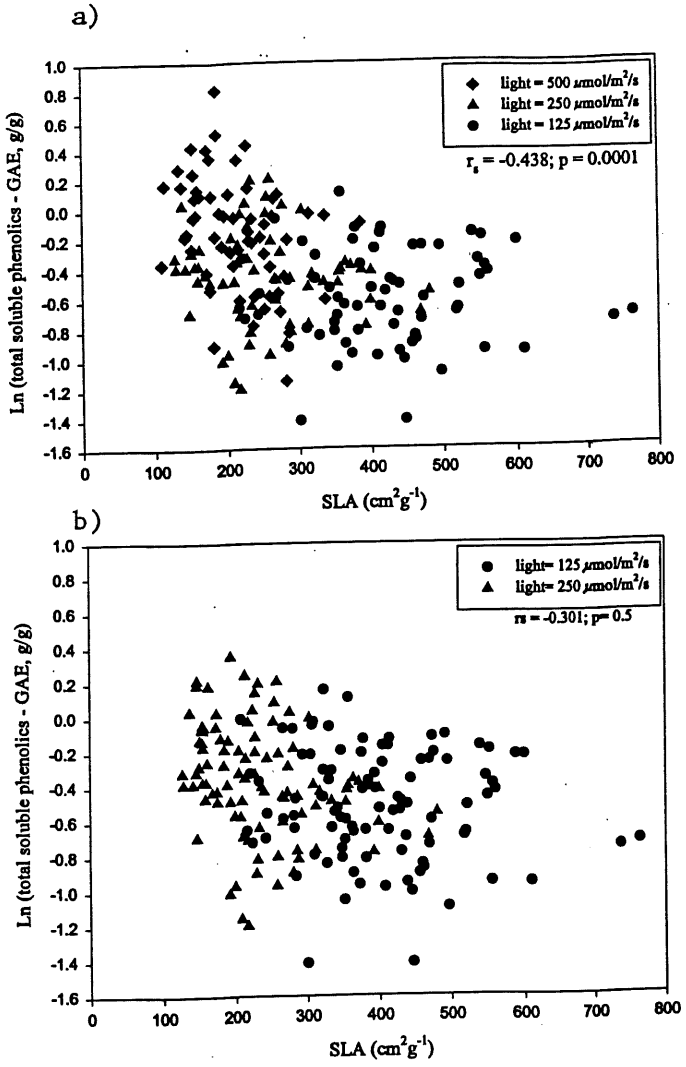


Figure 24. Relationship between means of SLA (cm^2g^{-1}) and means of Ln (total soluble phenolics - GAE; g/g) for 6 species of Asteraceae, grown under controlled conditions of temperature (25 °C), RH (80%), and photoperiod (16 h/day). a- Plants grown under high (500 µmol/m^2/s PAR), moderate (250 µmol/m^2/s PAR) and low light (125 µmol/m^2/s PAR) with three different nutrient supply (full-strength Hoagland solution; 1/5 dilute and 1/10 dilute). b- Plants grown under moderate (250 µmol/m^2/s PAR) and low light (125 µmol/m^2/s PAR) with four different nutrient supply (full-strength Hoagland solution; 1/5 dilute; 1/10 dilute and 1/50 dilute).

4.4 DISCUSSION

This chapter complements previous chapters by demonstrating how a range of resource availabilities influences the growth and chemical parameters of six species selected to span the range of relative growth rate and toxicity measured in the previous experiments. In other words, fast-growing plants were compared to slow-growing plants, plants with the highest total phenolics were compared to plants with the lowest total phenolics, as well as toxic plants were compared to non-toxic plants.

As the previously chapter demonstrated, studies of the resource availability hypotheses have tended to contrast the defense capacities of the plant species growing in two different resource states (McKey *et al.* 1978; Bryant and Kuropat 1980; Coley 1983; Newberry and de Foresta 1985; Baldwin and Schultz 1988), but there exists no unified interpretation of the results even though nutrient supply rates may be used to vary relative growth rates of young plants over ranges as wide as 0.02 to 0.60 day $^{-1}$ (see Ingestad 1982 for a review; Ericson *et al.*, 1982). According to Ågren (1985), the nutrients, notably nitrogen, in the plant exert a strict control over growth. However, in most natural communities, individuals within a population of plants may often experience a wide range of different levels of resource availability (Grime 1979, Keddy 1989). Differences in resource availability have been shown to generate variation in defensive chemistry within a single species (Waterman *et al.* 1984; Larsson *et al.* 1986; Bryant *et al.* 1987b; Shure and Wilson 1993). Therefore, it is important to understand how a range of resource availabilities influences phenotypic variation in plant allocation to defensive chemistry.

In recent years, much attention has been focused on the mechanisms by which the environment may alter the plant's production of chemical defenses, and thereby alter the susceptibility to herbivores (Mattson 1980; Bryant *et al.* 1983; Mooney *et al.* 1983; Tuomi *et*

al., 1984). Carbon/nutrient balance is viewed as a key to understanding why plant susceptibility changes under different growing conditions. We might expect that carbon-based defensive chemicals (e.g. phenols, terpenes, acetylenes) should be scarce in plants subjected to reduced carbon uptake or very high respiration, where a low carbon/nutrient ratio would result. On the other hand, plants provided with adequate light, but subjected to suboptimal nutrient availability, should exhibit a high carbon/nutrient ratio and resistance to herbivory (Bryant *et al.*, 1983).

Plants growing under nitrogen-limiting conditions generally have a slower growth rate than those growing under nitrogen-rich conditions. Carbon supply does not limit plant growth under low nitrate conditions and subsequently, increased quantities of carbon-based defenses should be selected for as nitrate availability decreases (Janzen 1974; McKey *et al.*, 1978; Bryant *et al.*, 1983; Coley *et al.*, 1985; Mihaliak and Lincoln, 1985).

A negative correlation between two traits can be generated in two general ways. One possibility is that there is no genetic link between the two traits, but each responds in an opposite way to some common environmental change. The other possibility is that the negative correlation is generated by the physiology or morphology of the plant even when the environment is constant. This second possibility is a "genetic" correlation and provides an operational definition of a "trade-off". The existence of a trade-off between growth and defense has generated some controversy. Even if some studies have found a negative correlation between RGR and the attack by herbivores (Coley, 1983; Sheldon, 1987), others (Meijden *et al.* 1988; McCanny *et al.*, 1990) did not find any correlation, and still others (Denslow *et al.*, 1987, 1990; Briggs and Schultz, 1990) show a positive correlation between the two variables.

4.4.1 Is there any trade-off between measured variables?

Growth parameters:

The Spearman correlation between the mean of relative growth rate (RGR; i.e. 21-42 days) and the mean of specific leaf area (SLA) was strong and positive (r_s= 0.610; r_s= 0.606, p= 0.0001, for the 3L-3N and 2L-4N group, respectively). Poorter and Remkes (1990) reported a strong positive correlation between RGR and SLA under constant environmental conditions of high nutrient supply but low light intensity (225 μmol/m^2/s). McKenna (1995) did not find such a correlation when light intensities were doubled. Shipley (1995) provided evidence that maximizing relative growth rate involves maximizing specific leaf area, which in turn involves maximizing leaf area with the least amount of biomass. Reich *et al.* (1992) in their review of the literature found a strong positive relationship between these two variables. In chapters II and III of this thesis the Spearman correlation coefficient between the mean relative growth rates (RGR) from day 14 to day 35 and mean SLA was weak, positive but non-significant (r_s= 0.14, p= 0.45) for the non-limiting experiment (chapter II) as well as for the nutrient stress experiment (chapter III). Note, however, that these experiments were conducted under the high light intensities that McKenna (1995) found to reduce the relationship between SLA and RGR. Correlations may be due to common responses to changing environments or to "genetic" linkages between variables in a constant environment. In order to distinguish between these two possibilities, I fit generalized linear models relating RGR and SLA, in which the experimental treatments and species were both included as covariates in order to control for their effects. These results are then compared to models in which these effects are not controlled. There were significant linear and positive relationships between relative growth rate (RGR) and SLA (p< 0.0001), for the 3L-3N group and the 2L-4N group. However, after controlling for the different experimental conditions (light and nutrient treatments), and species there were no linear relationships between RGR and SLA. In

other words, the initial significant relationships that were detected do not exist within the same species at constant environmental conditions.

The correlation between the mean of RGR and the mean of root:shoot ratio was strong and negative (r_s= -0.478; r_s= -0.420, p= 0.0003, for the 3L-3N and 2L-4N group, respectively). Although the data from chapters II and III showed no significant correlation between mean RGR and average root:shoot ratio, the data showed a decrease of 25 % for mean RGR while root:shoot ratio increased 320 % when the nutrient availabilities decreased 10-fold. One possibility is that there is no genetic link between the two traits, but each responds in an opposite way to some common environmental change (light intensity or nutrients availability). It is well known that plants are capable of adjusting the relative sizes and distributions of organ systems (shoot canopies, root systems) in response to changes in the external supply of resources (Johnson, 1985; Robinson, 1986; Johnson and Thornley, 1987; Van der Werf *et al.*, 1993) and that these adjustments may ultimately affect plant growth rate (Poorter, 1989). Gedroc *et al.* (1996) provided evidence that plants (*Abutilon theophrasti* and *Chenopodium album*) under low nutrient availability had the highest root:shoot ratios. As I discussed above correlations may be due to common responses to changing environments or to "genetic" linkages between variables in a constant environment. So, I followed the same procedure described above, I fit generalized linear models. There were significant linear relationships between RGR and the root:shoot ratio ($p< 0.0001$), for the 3L-3N group and the 2L-4N group. However, after controlling for the different experimental conditions (light and nutrient treatments), and species there were no linear relationships between RGR and root:shoot ratios. So, the initial significant relationships that were detected do not exist within the same species at constant environmental conditions.

Phytochemical parameters:

There was a strong negative significant correlation between leaf nitrogen content and total phenolics (r_s= -0.413; r_s= -0.374, p= 0.0001, for the 3L-3N and the 2L-4N group, respectively). These results are supported by the results of the previous chapters (non-limiting and nutrient stress experiments) that showed a negative relation between leaf nitrogen and soluble phenolics. The mean tissue nitrogen content was negatively correlated with the mean tissue phenolic content (r_s= -0.42, p= 0.02) but this trend was diluted when looking only at leaf tissues (r_s= -0.31, p= 0.09) or only at root tissues (r_s= 0.18, p= 0.32) for the plants grown under non-limiting nutrient conditions. For the nutrient stress experiment, the mean of leaf nitrogen content was negatively correlated with the mean of the natural logarithm of total soluble phenolics (r_s= -0.475; p= 0.04). When I fit generalized linear models relating for the total phenolics and leaf nitrogen content for the results of this chapter, in which the experimental treatments and species were both included as covariates in order to control for their effects, the data still showed a significant linear relationship between total phenolics concentration (p< 0.0001) and leaf nitrogen content for 3L-3N group and the second group (2L-4N). However, the initial significant relationships that were detected disappeared after controlling for the different experimental conditions and species. This again demonstrates that this negative correlation does not exist within a given species grown under constant environmental conditions.

Several studies demonstrated that nitrogen is negatively correlated with foliage phenol concentrations (Haukioja *et al.*, 1985; Dustin and Cooper-Driver, 1992; Kainulainen *et al.*, 1996). Coley (1983), studying the herbivory and defensive characteristics of young and mature leaves of 46 tree species in a lowland tropical forest rain forest, demonstrated that gap-colonizer (carbon available) species had lower concentrations of phenolics and higher levels of nitrogen, faster growth rates than do shade-tolerant species. Bryant *et al.* (1987)

demonstrated that when the plants are fertilized they increased the growth rate, increased the leaf nitrogen content and reduced the concentration of papyriferic acid (phenolic) and condensed tannin in Alaska paper birch (*Betula papyrifera* ssp. *humilis*).

There was a weak positive significant correlation between leaf nitrogen and measurable toxicity in the brine shrimp test (r_s= 0.161, p= 0.03) for the 3L-3N group, and (r_s= 0.195, p= 0.01) for the 2L-4N group. There was no evidence for such a positive correlation when the plants were grown with non-limiting nutrients (chapter II), since the correlation was not significant. On the other hand, the mean of leaf nitrogen content was negatively correlated with the measurable toxicity ($1/LC_{50}$; μg/ml) in brine shrimp test (r_s= -0.525; p= 0.02) when the plants were grown under nutrient stress (chapter III). Clearly, these different results are contradictory. I fit generalized linear models relating the leaf nitrogen content and measurable toxicity in the brine shrimp test for the data in this chapter, in which the experimental treatments and species were both included as covariates in order to control for their effects. There were no linear relationships between these two variables before controlling as well as after controlling for the different experimental conditions (light and nutrient treatments), and species. Similarly, there was no significant relation between the mean of leaf nitrogen and the measurable toxicity ($1/LC_{50}$; μg/ml) in brine shrimp test, for the non-limiting nutrient experiment. However, the mean of leaf nitrogen content was negatively correlated with the measurable toxicity ($1/LC_{50}$; μg/ml) in brine shrimp test (r_s= -0.525; p= 0.02) for the nutrient stress experiment. How can one explain these results? Here, I will use the explanation given before by Larsson *et al.* (1986), that nutrient stress generally reduces growth more than it reduces photosynthesis per se (e.g. McKey, 1979; also cf. Waring *et al.*, 1985), and thus, it has been argued that the expected surplus of carbon can lead to an accumulation of carbon-based secondary substances (as the case of Asteraceae compounds) under such circumstances (Bryant *et al.*, 1983). Mihaliak and Lincoln (1985) studied growth patterns and carbon allocation to volatile leaf terpene under nitrogen-limiting conditions in *Heterotheca subaxillaris*, camphorweed, (Asteraceae). In their experiment the rosettes were grown under

four levels of nitrate, and the authors observed individual leaf volatile mono- and sesquiterpene content and leaf nitrogen content on individual leaves. The results demonstrated that rosettes with the highest nitrate availability had 2.2-fold greater leaf nitrogen levels compared to plants with the lowest availability. The authors' data also showed that leaf mono- sesquiterpene content was greatest in the young leaves of individuals growing at the lowest nitrate availability. The authors observed that the average leaf terpene content increased from 3.1 to 5.1 mg/g as external nitrate supply declined from 15.0 to 0.5 mM (the highest and the lowest nitrate supply). Thus, the concentration of terpenes was highest in the leaves of plants grown with 0.5 mM nitrate and was reduced in plants grown at higher nitrate availability. Yet, the difference in leaf mono- and sesquiterpene concentration between young and mature leaves of individual camphorweed plants was greatest among plants with low nitrate availability. The authors provided evidence that terpenoid content was greatest in young leaves of 0.5 mM nitrate plants but at the highest nitrate availability there was less of a decrease in total volatiles as leaves aged. So, I concluded that the nitrate supply influenced more the terpenoid concentration than did the age of leaves. In Mihaliak's and Lincoln's (1985) study, high allocation to leaf volatiles was associated with low plant productivity and, because of the low leaf nitrogen content, low leaf photosynthetic rates. Furthermore, in my opinion this study has three weak points: First, only two plants were sampled from each of the nutrient treatments per harvest period; second, they studied only one species; third, and probably the most critical point, the plants were grown with 292 μmol $m^{-2}s^{-1}$ of photosynthetically active light, which is far below the light saturation point of species. So, according to my data I believe it is possible that the plants grown under non-limiting nutrients accumulated the nitrogen beyond what was needed for growth. In contrast, the plants grown with nutrient-stress (low nitrogen available) produced a surplus of carbon, once the growth was reduced, the plants accumulated the carbon as carbon-based secondary compounds. Consequently, nutrient availability can affect the level of carbon-based secondary substances by controlling the amount of excess carbon. According to Bryant *et al.* (1983) a reduction in nutrient concentration reduces photosynthetic rate directly by reducing RuBP carboxylase,

chlorophyll, and phospholipid contents. As a result of nutrient stress carbon, which cannot be invested in growth, is diverted to secondary metabolite production (Chew and Rodman, 1979). Mattson (1990) predicts that secondary metabolite production is inversely related to plant nutrients in species and in environmental conditions where growth is limited by nutrients rather than by carbohydrate reserves. Under conditions of nutrient limitation carbon is relatively cheap (Bryant *et al.*, 1983), and the nutrients in leaves are difficult to replace. So, how one can explain the observation that the mean of leaf nitrogen content was negatively correlated with the measurable toxicity, in chapter II?

First, it is important to remember that under nutrient stress all species had both less toxic tissues (except, *Artemisia vulgaris, Lapsana communis and Tanacetum vulgare)* and less leaf nitrogen, but those species whose toxicity was less reduced had their nitrogen concentrations more reduced. It is possible that not all species were equally limited in their nitrogen demands in the nutrient-stress experiment. Those species least strongly limited had their leaf nitrogen levels least depressed and therefore their photosynthetic rates were not as strongly depressed. This allowed these species to still produce some carbon-based toxic compounds. Since different species produce different secondary compounds, this negative correlation that I found in the chapter III could be just because some secondary compounds responded to the nutrient treatment in differents ways.

There was a negative weak significant correlation between total phenolics and measurable toxicity in the brine shrimp test (r_s= -0.186, p= 0.007) for the 3L-3N group and (r_s= -0.258, p= 0.0005) for the 2L-4N group. This negative correlation between toxicity (based on carbon containing compounds, since the Asteraceae do not generally possess nitrogen-based toxins) and total phenolics (other carbon-based compounds) could be just because some secondary compounds responded to the nutrient treatment in differents ways, as I explained previously. In order to distinguish between common response to changing environments or to "genetic"

linkages between variables in a constant environment, I fit generalized linear models relating for the total phenolics and measurable toxicity in the brine shrimp test, in which the experimental treatments and species were both included as covariates in order to control for their effects. There were significant linear relationships between total phenolics concentration and measurable toxicity in the brine shrimp test ($p< 0.0001$) for 3L-3N group, and ($p= 0.03$) for the 2L-4N group. Furthermore, the initial significant relationships that were detected do not exist between the two variables within the same species at constant environmental conditions.

Crankshaw and Langenheim (1981) studied leaf sesquiterpene resins and phenolics compounds through leaf development in young greenhouse grown plants of 10 species of the tropical legume *Hymenaea*. All species of *Hymenaea* contain essentially the same sesquiterpene hydrocarbons, but quantitative compositional differences occur between species. The consistency of these patterns of composition across species is such that they may be grouped into a limited number of distinct compositional types, based upon the resin components, which comprise more than 10 % of the total. According to Crankshaw and Langenheim (1981), the most common pattern is type II, which occurs in all species examined by the authors. The type II consists of intermediate amounts of caryophyllene and α- and β-selinene which together comprise 60-65% of the total resin. Type I and III are dominated by α- and β-selinene and caryophyllene respectively. Type I has over 65% but less than 80% selinenes with low levels of caryophyllene, while type III has similarly high caryophyllene and low selinene. Type IV is characterized by high selinene (40%), moderately high δ-cardinene (<25%) and α-copaene (>15%) accompanying low caryophyllene (<10%). According to the results of Crankshaw and Langenheim (1981), although both relative tannin astringency (expressed as the percentage of the hemoglobin precipitated/mg dry weight of leaf) and resin yields (mg resin/g dry weight) are high in early stages of development, the relative astringency is highest in the bud while the terpene yield is lowest. Furthermore the terpene yield increased and by the second leaf stage had the highest value, by contrast the

relative tannin astringency was reduced to intermediate levels. The authors also found that developmental changes in yield in type II were highly significant ($p= 0.009$), whereas they are not significantly different in the other three types. Likewise notable is that type IV leaves on average had twice as much resin as the other types at most stages of development (Crankshaw and Langenheim, 1981). This study supports the idea that the initial significant relationships that were detected between total phenolics and measurable toxicity in my experiment could be a consequence of differential responses of compounds to environmental changes.

According to the optimal defense theory, plants allocate defenses in order to maximize their inclusive fitness by balancing the cost of defense against possible gain. Factors affecting the costs and benefits to the plant include the risk of herbivory, the value of the tissue and the overall energy budget of the plant (Rhoades, 1979). Although these considerations should also justify the high cost of the quantitative defense in terms of the overall budget of the plant, additional considerations should be made regarding these assumed high costs. First, the high cost of quantitative vs. qualitative defense compounds (sensu Feeny, 1976) has been questioned (Swain, 1979; Gershenzon, 1994). Even though quantitative compounds are usually present in high concentrations, while qualitative compounds (toxins) are usually present in low concentrations, relatively rapid turnover has been observed in many toxins including sesquiterpene lactones and acetylenes, but not in phenolics (a quantitative compound). Since the resources allocated to such toxins can be recovered by the plant, the cost would be lower that the cost associated with phenolics. This suggests that predictions based on the assumption that quantitative defenses are produced at low metabolic cost are likely to be erroneous (Gershenzon, 1994).

Growth parameters versus chemical parameters:

There was a negative significant correlation between the mean of total phenolics and the mean of RGR (r_s= -0.317, p= 0.02) for the 3L-3N group and (r_s=-0.089, p= 0.0001) for the 2L-4N group when comparing across environments. If this negative correlation is due to a necessary physiological conflict between allocation of resources to growth versus defense, then this correlation would support the predicted trade-off between growth and defense. However, it is also possible that the negative correlation is simply due to both variables being affected by the changing experimental conditions in opposite ways. Ross and Berisford (1990) and Sunnerheim-Sjöberg and Hämäläinen (1992) have also observed that concentrations of phenolic compounds are inversely related to tree growth. Bryant *et al.* (1987) found the same trend in Alaska paper birch. Since both of these studies were based on plants growing in the variable conditions of the field, we cannot tell whether their negative correlations were due to necessary physiological tradeoffs, as required for the growth defense hypothesis. I therefore fit generalized linear models, in which the experimental treatments and species were both included as covariates in order to control for their effects. There were significant linear relationships between mean of total phenolics and mean of RGR (p< 0.0001), for the 3L-3N group, but no significant relationship (p= 0.09) for the second group (2L-4N) before controlling for species and experimental treatments. After controlling for the different experimental conditions (light and nutrient treatments), and species there were no linear relationships between mean of RGR and mean of total phenolics for the 3L-3N group nor for the second group (2L-4N).

Although a negative correlation was found before controlling for the different experimental conditions (light and nutrient treatments) and species the negative correlation disappeared after controlling for different environments and species effects. This means that the initial

negative correlation was simply due to both RGR and phenolic concentrations being affected in opposite ways by the environmental stresses rather than being due to a necessary physiological trade-off. Furthermore, the data of the chapter II, which involved a constant environment, showed a positive non-parametric correlation between the average total phenolic content per species and its average RGR (r_s= 0.40, p= 0.03) as well as with leaf phenolic content (r_s= 0.47, p= 0.007) but not with root phenolic content (r_s= 0.20, p= 0.28) for the plants grown under non-limiting nutrient conditions. However, I did not find any relation between these two variables when the plants were grown under nutrient stress (chapter III). In other words, the positive non-parametric correlation between the average total phenolic content per species and its average RGR found under non-limiting nutrient experiment disappeared when the plants were grown under nutrient stress experiment. All of these results argue against a necessary physiological trade-off between growth and phenolic production. Instead, it seems that the observed negative correlations between these two variables that have been reported from field experiments are due to the fact that nutrient stresses independently reduce RGR and also increase phenolic production. In other words, the "trade-off" that has been reported in the literature is due to a phenotypic correlation rather than a genetic correlation.

There was a negative significant correlation between total phenolics and SLA (r_s= -0.438, p= 0.0001) for the 3L-3N group but not for the 2L-4N group (r_s= -0.301, p= 0.5). The generalized linear model showed a significant linear relationship between total phenolics concentration and SLA (p< 0.0001) for both the 3L-3N and the 2L-4N groups before controlling for species and experimental treatments. On the other hand, there were no linear relationships between those variables within the same species at constant environmental conditions.

A possible explanation for these results comes from Crankshaw and Langenheim (1981), who observed in ten species of *Hymenaea* that leaves expand rapidly, essentially reaching their maximum area by the third leaf stage of the plant. However, by the third leaf total phenolic compounds and condensed tannin decreased to low levels. This is due to the initially high concentrations being diluted as the leaf cells expand; it is therefore possible that a nutrient stress simply slows down the rate of leaf development and expansion. If this were true, then leaves compared at the same age (but not at the same developmental stage) would have more phenolics when grown with a nutrient stress.

There was a positive significant correlation between measurable toxicity in the brine shrimp test and SLA (r_s= 0.18, p= 0.009) for the 3L-3N group, and (r_s= 0.215, p= 0.004) for the 2L-4N group. Also, there were significant linear relationships between measurable toxicity in the brine shrimp test and SLA (p= 0.03), for 3L-3N group, but no significant relationship (p= 0.3), for the 2L-4N group before controlling for species and experimental treatments. However, the initial significant relationships that were detected do not exit within the same species at constant environmental conditions. The results of the previous chapters showed no significant correlation for the species grown in the non-limiting nutrient treatment (chapter II), nor for the species grown in the nutrient stress treatment (chapter III). In Crankshaw and Langenheim (1981), only one (Type III caryophyllene) of the sesquiterpenes studied increased when leaf area increased.

There was a positive but non significant correlation between the mean of measurable toxicity in the brine shrimp test and the mean of RGR (r_s= 0.260, p= 0.06) for the 3L-3N group. There was a positive significant correlation between these two variables (r_s= 0.453, p= 0.01) for the 2L-4N group. Note that this positive correlation is the opposite of what the C/N hypothesis predicts. Those correlations may be due to common responses to changing environments or to "genetic" linkages between variables in a constant environment. There were significant linear

relationships between RGR and measurable toxicity in the brine shrimp test (p= 0.02), for the 3L-3N group, but non significant relationships (p= 0.2), for the 2L-4N group. Furthermore, after controlling for the different experimental conditions (light and nutrient treatments), and species there were no linear relationships between the mean of measurable toxicity in the brine shrimp test and mean of RGR.

Similar results were found in the previous chapters. There was no significant relationship between mean RGR of species and the mean measurable toxicity of their tissues for either the non-limiting nutrient experiment or the nutrient stress experiment.

There was a negative significant correlation between measurable toxicity in the brine shrimp test and root:shoot ratios (r_s= -0.213; r_s= -0.381 p= 0.002, for the 3L-3N and the 2L-4N group, respectively). There were significant linear relationships between measurable toxicity in the brine shrimp test and root:shoot ratios (p= 0.03) for 3L-3N group but no significant relationships (p= 0.08), for the 2L-4N group before controlling for species and experimental treatments. But, the initial significant relationships that were detected do not exist after controlling for the different experimental conditions (light and nutrient treatments), and species. The results of the previous chapters showed no significant correlation for the species grown neither under a constant but non-limiting nutrient treatment (chapter II), nor for the species grown under a constant but nutrient stress treatment (chapter III).

There was no significant correlations between the mean of leaf nitrogen content and the mean of RGR (r_s= 0.173, p= 0.2) for the 3L-3N group. There was a weak positive significant correlation between these two variables (r_s= 0.176, p= 0.02) for the 2L-4N group. These same results were found when I fit linear models to the data but without controlling for differences between species or experimental treatments. After including the covariates, the relationship between RGR and leaf nitrogen was not significant for the group 3L-3N, but still significant

(p= 0.01) for the 2L-4N group. The results of the previous chapters showed no significant correlation for the species grown under non-limiting nutrient treatment (chapter II), nor for the species grown under nutrient stress treatment (chapter III). Freijsen and Otten (1987) demonstrated in their study with *Plantago lanceolata* and *P. major* ssp *major* a linear regression of relative growth rate on nitrogen concentration in shoot fresh weight.

There was a positive significant correlation between total phenolics and root:shoot ratio (r_s= 0.538; r_s= 0.546, p= 0.0001) for the 3L-3N and the 2L-4N group, respectively. There were also significant linear relationships between total phenolics concentration and root:shoot ratio (p< 0.0001) for 3L-3N group and the 2L-4N group. The only significant relationship involving total phenolics concentrations after controlling for the experimental treatments and species was with the root:shoot ratio in the 2L-4N group (p= 0.01). The results of the previous chapters showed no significant correlation for the species grown under non-limiting nutrient treatment (chapter II), nor for the species grown under nutrient stress treatment (chapter III) for the two variables.

Finally, I would like to emphasize that most of the information on plant/herbivore interactions come from studies on the effectiveness of specific defenses from the viewpoint of the herbivore rather than the plant. These include surveys with generalists and investigations of more tightly coevolved systems between host and herbivore (Jones, 1962, 1972; Ehrlich and Raven, 1964; Gilbert, 1971, 1975; Gibert and Raven, 1975; Jermy, 1976; Lawton, 1976; Roeske *et al.*, 1976; Edmunds and Alastad, 1978).

Another approach has been to document broad-scale associations of plant life history, successional status, habitat preference, or leaf age with either herbivory or plant defense. Since these community level studies have examined patterns of herbivory and defense separately, their relationships can only be inferred (but see Rhoades 1977 a, b; McKey *et al.*,

1978; Milton 1979; Oates *et al.*, 1980). The general trend, however, is for higher concentrations and more effective characteristics (e.g. as phenolics and tannins) as well as lower grazing susceptibility in late successional or woody species, mature leaves (but see Crankshaw and Langenheim, 1981) and plants of nutrient-poor areas (Feeny, 1970, 1975, 1976; Dement and Mooney, 1974; Janzen, 1974; McKey, 1974, 1979; Cates and Orians, 1975; Johnson, 1975; Rhoades and Cates, 1976; Cates and Rhoades, 1977; McKey *et al.*, 1978; Milton, 1979; Bryant and Kuropat, 1980; Coley, 1980; Gartlan *et al.*, 1980; Oates *et al.*, 1980). Coley (1983) tried to do an extensive study testing the theories of apparency and the evolution of plant defenses by simultaneously evaluating an array of plants characters and ecological factors and this study has had a large impact on current views concerning plant defense. In my opinion Coley's experimental approach contains some flaws. First, the author ran the experiments under field conditions, and therefore without any control over varying environmental conditions. Secondly, she measured the rates of herbivory under natural conditions and rates of herbivory would be affected not only by plant defenses but also by the nutritional quality of the leaves. both of which could be affected in different ways by soil fertility. The author did not know the age of the plants yet it is clear that various defensive compounds change over time. The individual saplings were chosen according the height (1-2 m tall). The plants were studied in 49 gaps scattered over the island (Barro Colorado Island, Panama), and therefore with different degrees of soil fertility. According to Grime (1979) and Keddy (1989), in most natural communities, individuals within a population of plants may often experience a wide range of different levels of resource availability. Overall, Coley (1983) measured the grazing rates on young and mature leaves, but the author did not include control plants. In my opinion this experiment had several uncontrolled variables (light intensity, nutrient availability, plant age, life history, herbivory) which makes it very difficult to conclude that there is a necessary physiological trade-off between growth and defense. Finally, her data show that the primary determinants of leaf defense against the herbivores were morphological, not chemical. I decided to compare Coley's (1983) conclusions with

mine because this work used the largest number of species to date in order to test the plant-defense theories.

My study included a number of different species that differ both in their growth potentials and in their production of secondary metabolites, as did Coley (1983). This is important because the ecological questions refer to general responses, not responses limited to any particular species. Second, the study species should share a common known phylogenetic history in contrast to Coley (1983). This is important because the types of secondary compounds produced by a species are strongly constrained by its evolutionary history. Third, the variation in resource availability should be imposed through a controlled randomized experiment in order to separate genetic and environmental correlations. Coley (1983) did not do this. Fourth, the range of resource availabilities should be sufficient to detect any non-linear responses by either growth or nutrient availabilities.

In the present study I first described the interspecific relationship between RGR and plant chemical defenses under conditions of high levels of resource availability in 31 species of Asteraceae, under controlled conditions. Second, I investigated if there is any correlation between relative growth rate (RGR - fast and slow growing plants) and secondary metabolism (soluble phenolics and toxicity) in 20 species, under controlled conditions of high light intensity but suboptimal levels of mineral nutrients. Third, I determined how the growth and chemical variables changed, and whether the patterns of correlations between the variables changed, under such conditions relative to those provided previously to the plants. Finally, in this chapter I determined how a range of resources availabilities influenced growth and chemical parameters for six species selected by different characteristics according to the data obtained in the previous chapters. The last objective is to investigate if there is any difference concerning the amount of secondary metabolism produced by resource availability in

Chrysanthemum leucanthemum and *Rudbeckia hirta.* The following chapter will describe the results of this investigation.

The idea that a plant must accept tradeoffs because it must allocate limited resources among growth, reproduction, and defense has been central to ecological and evolutionary theories, but the existence of a trade-off between growth and defense has generated some controversy. The data and analyses in this chapter suggest that there is no necessary trade-off between growth rate and chemical defense when species are grown under the same environmental conditions. The "trade-off" that has been reported from field experiments seems to arise because researchers have failed to control for different soil fertilities, and differing soil fertilities affect phenolic production and growth in opposite ways. Until now my findings have been based on either an indirect bioassay of chemical defense using a measure of toxicity or on a general quantitative measure for total phenolics that does not discriminate between those phenolic compounds related to defense and those having other primary functions. In the next chapter I will concentrate on only two of the six species studied in this chapter and on only two levels of nutrient availability but will obtain quantitative measures of pure compounds by HPLC known to have a primary defensive function.

CHAPTER V

EFFECTS OF NUTRIENT AVAILABILITY ON THE PRODUCTION OF SECONDARY COMPOUNDS RELATED TO DEFENSE IN *Rudbeckia hirta* and *Chrysanthemum leucanthemum*, AS REVEALED BY HPLC

5.1 INTRODUCTION

The early plant herbals reveal that a surprisingly large number of plants of the Asteraceae were used for their curative properties (Heywood and Harborne, 1977). Undoubtedly the wide medicinal use of many composites inspired the early organic chemists at the turn of the century to explore plants in order to identify the active constituents. Several classes of plant compounds are characteristic of this family, notably the terpenoid based sesquiterpene lactones, the fatty acid derived polyacetylenes and the polysaccharide fructans. Many of the substances elaborated by the family are toxic or show other significant physiological activity. Chemical factors are, moreover, important in Asteraceae weeds in providing protection from over-grazing. The presence of sesquiterpene lactones in Asteraceae is often associated with a bitter taste, and it is likely that this repellent taste response acts as a signal to protect the plants from being heavily grazed. Another type of secondary compound produced by the Asteraceae is the polyacetylenes. The polyacetylenes are reactive substances that have been found in roots flowers and/or leaves of the great majority of the Asteraceae that have been surveyed (Heywood and Harborne, 1977). They possess both light activated (phototoxic activity) and dark toxicity. It is important to note that all of these secondary compounds are carbon-based; nitrogen-based compounds are rare in the family.

Comparable loss of leaf nitrogen to herbivores by nitrate-limited or nitrate-rich plants presumably has a greater impact on the growth of nitrogen-limited plants. Carbon supply does not limit plant growth under low nitrate conditions and subsequently the carbon/nutrient hypothesis predicts that increased quantities of carbon-based defenses should be selected for as nitrate availability decreases (Janzen 1974; McKey *et al.*, 1978; Bryant *et al.,* 1983; Coley *et al.,* 1985; Mihaliak and Lincoln, 1985).

The objective of this chapter was to investigate if there is any variation in the expression of secondary metabolism produced by resource availability in *Chrysanthemum leucanthemum* and *Rudbeckia hirta.*

5.2 MATERIALS & METHODS

5.2.1 Experimental design

This part of the project used two different species (*Chrysanthemum leucanthemum* and *Rudbeckia hirta*). Seed collection and storage, germination conditions, growth of the seedlings, hydroponic system as well as plant harvests were as described in chapter IV. One exception was the harvest period for *Rudbeckia hirta*. Some plants had their harvest period delayed until flowering time (around 80 days after transplanting into the hydroponic system). The flowers used in this chapter came from plants grown under 500 $\mu mol/m^2/s$ and two different nutrient availabilities (full-strength and 1/5 dilution of the full-strength modified Hoagland solution). At least three flowers were harvested from a single plant at 0, 1, 2, 3, 4, 5, 10 and 15 days after flowering.

5.2.2 Phytochemical analysis

Plant extraction:

Ten grams of fresh tissues (bulked by species for each harvest period) were placed in 95% ethanol after weighing. This resulted in a general extraction of secondary compounds. Leaves (*Chrysanthemum leucanthemum*) or flowers (*Rudbeckia hirta*) were homogenized in a blender in 50-100 ml of ethanol. The extract was filtered through Whatman N°1 paper using a Buchner funnel and aspiration. The volume of the extract was reduced to 10 ml on a flash evaporator. The residue was brought back into a standardized ethanol extract with a ratio of

20 ml ethanol (95 %) per 10 g (fresh weight) of tissue. The solutions were then filtered first through cotton wool, and then through a 0.2 μm membrane filter.

The samples were analyzed for parthenolide, artecanin, reynosin (sesquiterpenes lactones), pentaynene (polyacetylene) and flavonoids using HPLC. These compounds were chosen on the basis of previous studies of this family and on the availability of standards. The HPLC system was a Beckman System Gold, with a module 126 Solvent delivery system, a module 168 photodiode array detection system, and an autosampler. The column was a Beckman RP-C18, 5 μm, Ultrasphere ODS, 250 x 4.6 mm, fitted with a Beckman 5 μm Ultrasphere ODS, 45 x 4.6 mm Precolumn. For the parthenolide, artecanin, reynosin and flavonoids the mobile phase consisted of water (55 %) and acetonitrile (45 %). The flow rate was 1.75 ml/min and measurements were taken at 210 nm for parthenolide, artecanin, reynosin and flavonoids (Awang *et al.*, 1991). For pentaynene, the mobile phase consisted of water (30 %) and acetonitrile (70 %) and flow rate of 1 ml/min. In each case, the injection volume was 20 μl.

5.2.3 Statistical analysis

The data were analyzed using the Spearman correlation and/or the general linear model (GLM) procedure in the SAS statistical package (SAS, Inc. 1990). The trends in the relationships between the parameters were plotted using Sigma Plot (Jandel Scientific, 1994).

The statistical analysis of pentaynene data from *Rudbeckia hirta* (flowers) were pooled by flower age and nutrient availabilities (full-strength and 1/5 dilution of the full-strength modified Hoagland solution).

5.3 RESULTS

The samples of *Chrysanthemum leucanthemum* (leaves) and *Rudbeckia hirta* (flowers), grown under controlled conditions free of herbivores, presented no detectable amount of flavonoids nor any sesquiterpene lactones (parthenolide, artecanin, reynosin or other related STL) as analyzed by HPLC.

The HPLC analysis did however show a compound eluting at 23 min for *Rudbeckia hirta* with UV absorption peaks at 265, 287, 329, 353 and 379 nm (Figure 25). Bohlmann *et al.* (1973) reported distinct absorption maxima at 265, 285, 327, 349, 378 and 410 nm for the pentaynene (polyacetylene, Figure 26). The same author reported the presence of pentaynene in *Rudbeckia hirta* and its identity was confirmed by comparison with an authentic standard. The amount of pentaynene of *Rudbeckia hirta* (flowers) ranged from 227.2 ± 152.2 μg pentaynene/g fresh weight (young flowers) to 13.6 ± 4.8 μg pentaynene/g fresh weight (old flowers) of flowers for plants grown in the full-strength solution and from 365.5 ± 163.6 μg pentaynene/g fresh weight (young flowers) to 105.4 ± 98.2 μg pentaynene/g fresh weight (old flowers) for plants grown under 1/5 dilution of the full-strength solution (Figure 27). It is interesting to note that the flowers showed a different morphology in the two different nutrient treatments. The petal shape of the ray flowers from plants grown under full-strength solution were less expanded than the ones from plants grown under 1/5 dilute of full-strength solution. As well, the center of the capitulum was also different in the two nutrient treatments. The center of the capitulum from plants grown under full-strength solution were larger (probably with more seeds) than the ones from plants grown under 1/5 dilute of full-strength solution.

There were eight young (0-5 days) flowers available for the full strength nutrient solution and seven for the 1/5 solution. Four old (10-15 days) flowers were available for the full strength

solution and six for the 1/5 solution. This unbalanced design required the use of Type III sums of squares analyses. ANOVA of the log-transformed data showed that there were significantly different amounts of pentaynene in the flowers of *Rudbeckia hirta* between the two nutrient levels (p= 0.003) and between flowers of different ages (p= 0.0001); there were no significant interactions.

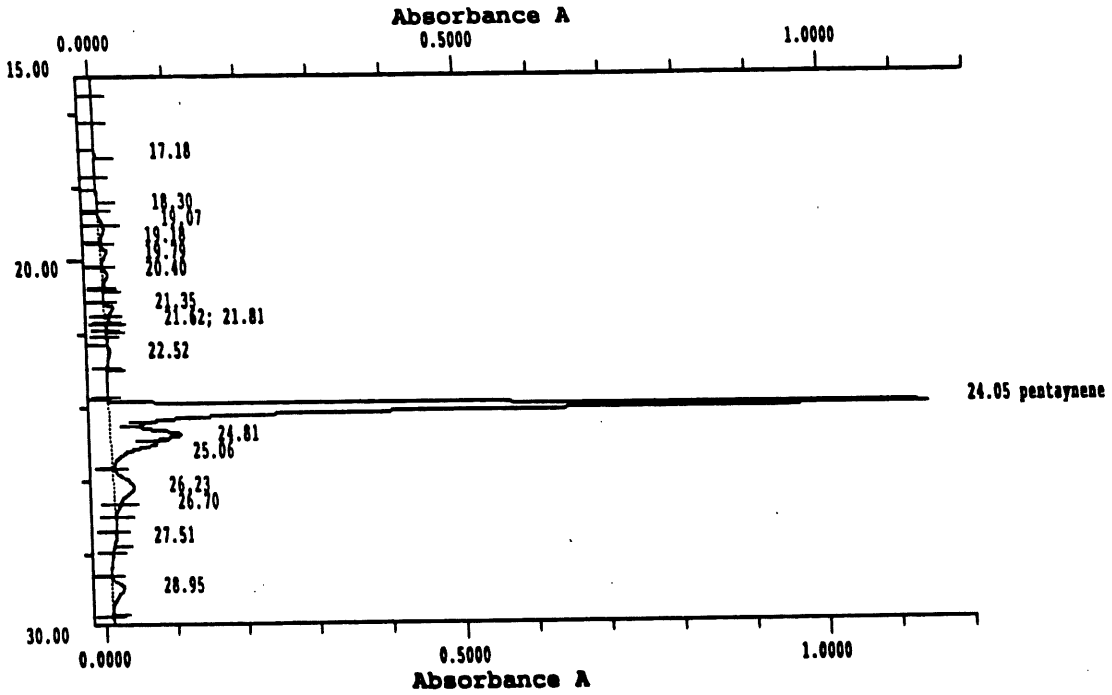


Figure 25. Chromatograms of *Rudbeckia hirta* flowers after extraction with ETOH . Peak identified as pentaynene (polyacetylene).

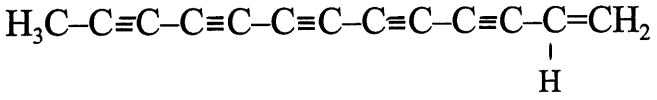


Figure 26. Polyacetylene derivative (pentaynene) occurring in *Rudbeckia hirta* (Asteraceae).

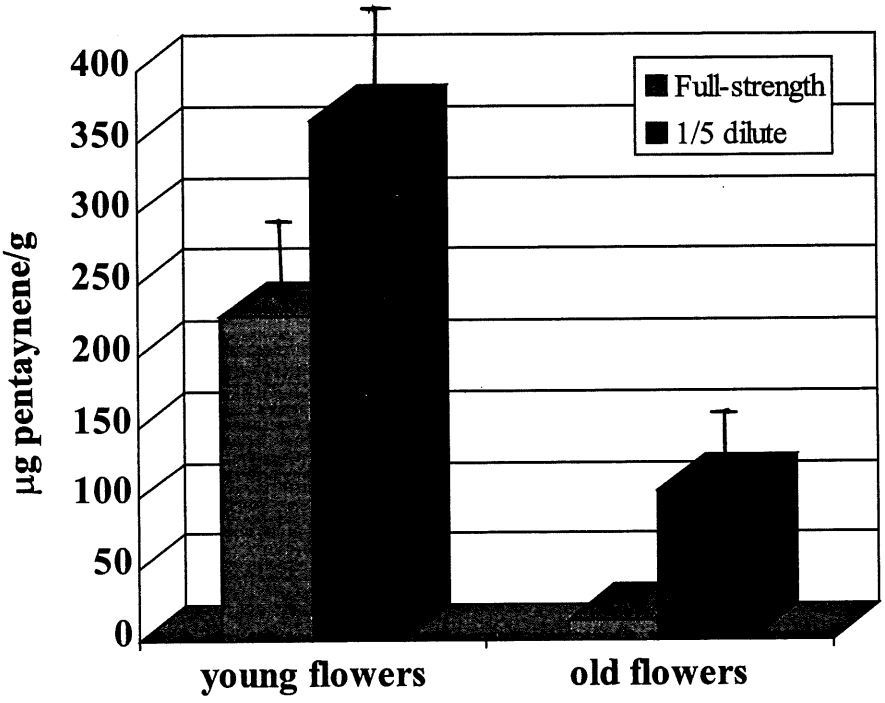


Figure 27. Effect of nutrient availability (full-strenght and 1/5 dilution of Hoagland solution) and flower age on pentaynene concentration. Bars represent standard errors.

5.4 DISCUSSION

The various hypotheses studied in this thesis are related to the production of defense-related secondary compounds to whole plant growth rate and the relative supply rates of light and mineral nutrients in a general (i.e. multi-species) context. The ideal experiment to test these hypotheses would be to identify each of the secondary compounds in a large number of species, and then directly measure their production and plant growth rate over a range of light levels and nutrient concentrations. No published study has succeeded in carrying out such an experiment. Most studies use only a single, or at most a few, species. Most studies use only a single, or at most a few, resource supply rates. No studies have actually measured the production of all or several secondary compounds; most use an approximate measure such as the total phenol assay or else measure directly only one or a few compounds.

Time and space constraints and the fact that few species have ever been exhaustively screened for many types of secondary compounds explain why these weaknesses exist. In this thesis I have tried to reduce these weaknesses though a hierarchical approach in which first a large number of species were tested at each of two levels of nutrients (chapters II and III) but using indirect measures of secondary compound production (the toxicity assay and the total phenolics assay). In chapter IV, I reduced the number of species but increased the number of levels of light and mineral nutrient concentrations. Finally in this chapter I reduced even further the number of species but obtained direct measures of a small number of secondary compounds.

In this study only the polyacetylene pentaynene occurred in sufficient quantity to be detected by HPLC in the flowers of *Rudbeckia hirta.* According to Bohlmann (1988), pentaynene and its derivatives are present in nearly all tribes of Asteraceae and can therefore be taken as representative of the Asteraceae. However, there are a few exceptions. These compounds are

absent in the tribes Anthemideae (*Chrysanthemum leucanthemum*), Astereae and Lactuceae and they are rare in Senecioneae (Figure 28). Guillet *et al.* (in press) studying the polyacetylene derivatives occurring in *Rudbeckia hirta* provided evidence of the insecticidal properties against mosquito larvae. They found that the polyacetylenes present in inflorescences and roots of *Rudbeckia hirta* possess both light and dark toxicity. Previously, Camm *et al.* (1975) reported the presence of polyacetylenes exhibiting phototoxic properties in the stem, root and flowers for this species. This study was confirmed later by Guillet *et al.* (1995) that investigated the phototoxic properties of inflorescences of this species.

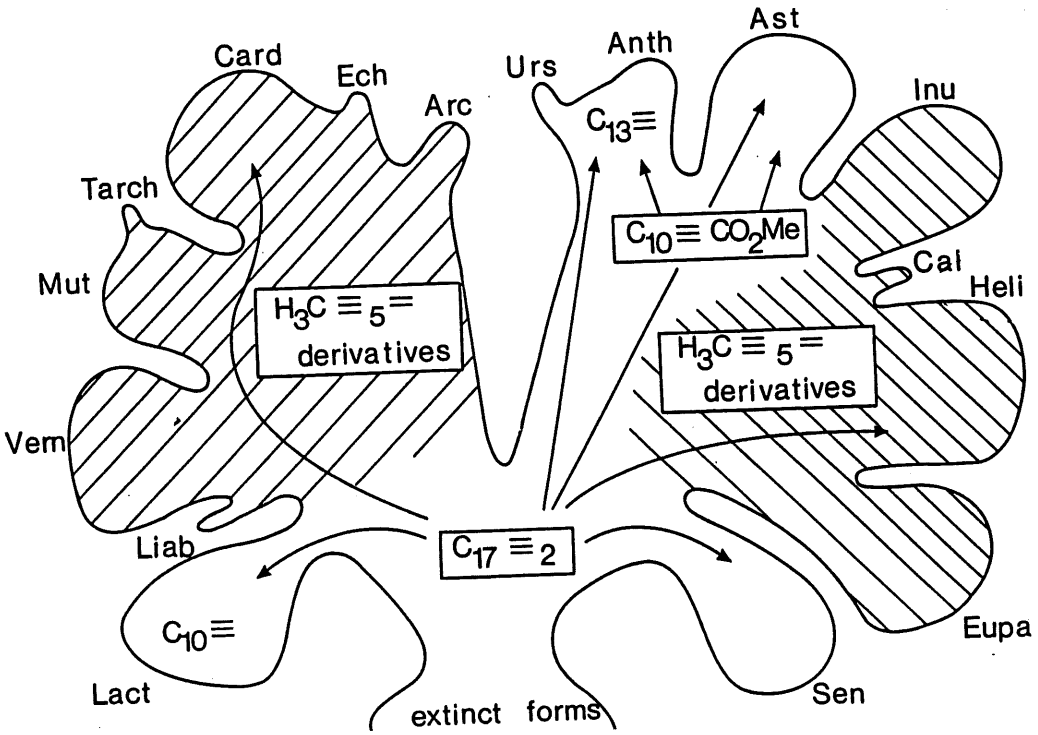


Figure 28. The distribution of acetylenes within the whole family of the Asteraceae (copy from Bohlmann, 1988).

The effect of a nutrient reduction was to increase the production of the carbon-based pentaynene in the flowers of *Rudbeckia hirta*, in accordance with the prediction of the carbon/nutrient hypothesis (Bryant *et al.*, 1983). These results for the flowers of plants aged 80 days were the opposite of the toxicity measures of the leaves of younger plants of this species (Chapters II, III and IV). Zangerl and Berenbaum (1987) studied the influence of environmental factors (soil nutrients, photosynthetically active radiation, and ultraviolet radiation) on the production of furanocoumarins in the wild parsnip (*Pastinaca sativa*). These authors found that light and nutrient availability jointly affected the concentration of the six furanocoumarins present in the study species. In particular they found that reduced nutrient levels increased the concentration of the furanocoumarins, as also found in my experiment. They also found that both nutrients and light were limiting factors in furanocoumarin production insofar as low availability of either resources limited the effect of variation in the other resource on production of these furanocoumarins. Light and nutrient availability independently influenced relative amounts of the furanocoumarins.

My results are also supported by Crankshaw and Langenheim (1981) who demonstrated that terpene yield (mg resin/g dry wt leaf) was highest early in leaf development in all resin compositional types (see chapter III – page 154). Mihaliak and Lincoln (1985) also obtained results that are similar to my findings. The authors studied *Heterotheca subaxillaris* (Asteraceae) to test the prediction that carbon allocation to defensive terpene production would be greater at low nitrogen availability than at high availability. The plants were grown from seedlings through the rosette stage in an environmental growth chamber. The experimental design consisted of four different levels of external nitrate supply (0.5, 1.5, 5.0 and 15.0 mM) with 292 μmol m^{-2} s^{-1} of photosynthetically active light. Volatile leaf mono- and sesquiterpene content was determined by gas chromatography at 0-2, 2-4, 4-6 and 6-8 weeks. Mihaliak and Lincoln (1985) obtained results similar to mine. They found that the average leaf terpene content increased from 3.1 to 5.1 mg/g as nitrate supply declined from

15.0 to 0.5 mM. Also, they found that terpenoid content was greatest in young leaves of 0.5 mM plants.

Increased leaf mono- and sesquiterpene content, furanocoumarin or polyacetylene content with decreased nitrate availability is consistent with the hypothesis that increased allocation to carbon-based defense chemicals would be favored in nitrogen-poor environments. Carbon not allocated to growth could be utilized for secondary chemical production (Chew and Rodman 1979). Alternatively, increased terpene or polyacetylene production could be due to relative increase in available carbon resources under low nitrate conditions. Allocation to defense (polyacetylene) is highest among young flowers of low nutrient plants and declines with age. If flower "value" is measured by the relative contribution to plant productivity (reproduction) plus the cost of replacement (Mooney and Gulmon, 1982), then young flowers should be of greater value, particularly in low nitrate environments. Here I speculate that chemical defense will be allocated preferentially from the plant to the seeds.

The toxicity tests in general showed reduced toxicity at lower nutrient levels. In the other three chapters I measured toxicity by a bioassay test while in this chapter I used HPLC to analyze for a single toxin in the plants. Although the results seem to be contradictory I could explain this contradiction in two different ways. First, pentaynene is not usually present in vegetative tissues, which may be regulated in a different way from flowers (Bohlmann *et al.*, 1973). Even if present, it is possible that pentaynene and other more toxic compounds are regulated in opposite ways. It is important to remember that the bioassay used does not directly measure the total production of secondary compounds but rather the toxicity of these compounds taken together. On the other hand, HPLC is a highly sophisticated instrumental technique, with high-efficiency columns and sensitive detection methods, characterized by both high speed and high performance. Furthermore the HPLC measures the exact amount of a specific compound.

CHAPTER VI

GENERAL DISCUSSION

This thesis tried to critically evaluate certain points concerning theories of plant chemical defense. My goal was to investigate if there were tradeoffs between growth parameters and chemical defenses, focusing on just the plants. I did this by exploring a wide set of species and resource availabilities, in systematic and standardized conditions, from an ecological viewpoint. This thesis contributed to a better understanding of the controversy involving tradeoffs between growth and defense in different resource environments.

The main hypothesis tested in this thesis is that there is a necessary trade-off between the potential growth rate of a plant and the amount of defensive secondary compounds that it produces; i.e. an increased production of such compounds causes a decrease in growth rate. This prediction is found in the following theories: the optimal defense hypothesis (McKey, 1974; Rhoades, 1979), the resource availability theory (Coley *et al.*, 1985), the carbon/nutrient balance hypothesis (Bryant *et al.*, 1983) and the growth-differentiation balance hypothesis (Herms and Mattson, 1992).

6.1 What would be an ideal experiment to test these hypotheses?

An "ideal experiment" to test this hypothesis, would be modifications of those described in chapters IV and V. In other words three different combinations of light intensity (500, 250 and 125 $\mu mol\ m^{-2}\ s^{-1}$) with four different levels of nutrients (full-strength, 1/5, 1/10 and 1/50 dilution of full-strength Hoagland solution), but still using a larger number of species.

I suggest twenty-five species for the following reasons: 1) I would still have a sufficiently large number of species to have general results, and 2) I could therefore increase the spacing between plants inside of each container by decreasing the number of plants from 144 per container to 100 per container. Also, I would include an early harvest period (7 days post-germination) to avoid the problem I had in the experiment of chapter IV (see explanation page 124) when the plants grew fast at the beginning of the experiment and slower after the second week. To make this study possible, twelve different growth chambers should be used, each one with a different combination of treatments, as described above. For this "ideal experiment", fifteen plants would be harvested after each seven days, starting with one week after germination. All plants would be analyzed for total phenolics, tannins, general toxicity and polyacetylenes. Since I could use the same extract of plants for the bioassays and for the HPLC, at least secondary compounds present for the majority of species would be tested. It should have at least one species producing a nitrogen-based defensive compound, such as *Senecio* ssp or *Tussilago farfara* to confirm or deny the trade-off between the RGR and nitrogen-based secondary compounds. I should do the analysis of total phenolics and toxicity by each tissue type, plant, species and harvest day. In fact, the best way to test the theories would be to identify and analyze all different secondary compounds by HPLC.

One cannot do this ideal experiment because of the demands on money, time and labor. Another reason is that analyses by HPLC would need a great number of different standards, or techniques to purify and identify the compounds. Here I advocate for the need to have a multidisciplinary research group involving experts from the different fields.

Since this "ideal experiment" is not possible for a Ph.D. program for the reasons described above, I have attempted to overcome these problems in a number of different ways. First of all, I tried to solve the problem of how to measure the production of secondary compounds

by using three different methods with different advantages and disadvantages, namely: total phenolics, toxicity and HPLC.

The advantages of measuring total phenolics are (1) this measure is most commonly used and so my values can be compared to those in the existing literature and (2) they give at least an index of the quantitative amount of phenolics. On the other hand, the disadvantage is that this variable measures all phenolic compounds and many of these have nothing to do with plant defense.

The advantage of measurable toxicity in the brine shrimp bioassay is that it is a direct measure of the compounds that present any biological activity in the form of toxicity. The disadvantage is that it does not measure directly the amount of such compounds.

Finally, the advantage of HPLC is that it is a direct measure of the amount of a given secondary compound although the ecological relevance of the compound must still be determined by a toxicity bioassay. Furthermore it has the disadvantage that we lack knowledge of the identity of many such compounds in wild plants and the cost and time required to purify and identify all of these potential compounds related to plant defense means that it is impossible to study more than a few species at a time.

Until the present day, there is no single measure, which is both quantitatively accurate, biologically relevant and practical, and so it is best in practice to use a combination of different chemical analyses. In this work I chose the ones described above because I believe the three should give a more accurate description of the secondary compounds present in the Asteraceae.

Second, it is necessary to measure growth and allocation to secondary compounds of the whole plant in order to study tradeoffs. The use of seedlings in controlled conditions allows me to do this. The disadvantage is that such results may not be applicable to adult plants, especially woody species.

6.2 Plant-herbivore defense theories in relation to the findings of this thesis.

After describing how an "ideal experiment" should be conducted in order to test the main hypotheses posed in this thesis and how I conducted my tests in practice with their limitations, I would like to compare the results found in this work with the main defense theories.

6.2.1. Optimal Defense Hypothesis (OD)

I cannot compare the results found in this thesis with all of the predictions of the OD hypothesis, since I did not consider the effects of the herbivory on the plants. The OD hypothesis argues that allocation to defense by any given plant can only be understood in terms of the herbivore pressure experienced by that plant over evolutionary time (McKey, 1974; Rhoades, 1979). However, this hypothesis does predict that there is a negative relationship between growth and defense since it claims that defenses are always costly. That is, any carbon allocated to defense is removed from a pool of carbon that the plant could partition for growth, and that there are no internal physiological constraints on how a plant may allocate fixed carbon (Rhoades, 1979). In this case my findings did not support this theory since I never found any negative trade-off over the experiments developed in this thesis.

6.2.2. Resource Availability Theory

Coley *et al.* (1985) proposed this theory, as an alternative to the apparency theory. This "apparency theory" suggests that some species are poorly defended because they are sufficiently rare (in either time or space) that they escape discovery by herbivores. Thus the apparency theory predicts that only species that are easily found by herbivores need to invest in defenses. The theory implies that species should have similar rates of damage in the field, with some species (unapparent) minimizing damage by escaping and others (apparent) by chemical defenses. Coley *et al.* (1985) proposed that plant species differ in their defenses because they differ in their intrinsic rate of growth. They assume that in a world without herbivores, the maximum potential growth rates would be determined by the resource availability in the environment (modified slightly by allocation patterns of individual species). Inherent growth rates of plants may influence the type of defense as well as the amount. According to them, intrinsically slow growth rates are thought to favor selection for high amounts of defense, because the opportunity costs of defense are relatively low, and the potential impact of herbivory is extremely high. My findings did not support this prediction. I never observed negative correlations between toxicity and growth that could not be explained by each variable responding in different ways to the same change in the environment. And once, in chapter II, I even found a positive correlation, rather than a negative one, between RGR and total phenolics. I did not find any evidence that would make me believe that the inherent growth rates of plants may influence the type of defense as well as the amount. As we can see in Table 7 of chapter II, the amount of total phenolics or toxicity varied with each harvest period, but without any trend in relation to growth rate.

The cost of defense by immobile compounds (tannins) is logically independent of leaf lifetime and would be most cost-effective in long-lived leaves. Coley *et al.* (1985) predicts that species adapted to low-resource habitats will have intrinsically slow growth rates, and

therefore high amounts of defense. In the nutrient stress experiment, in chapter III, my data showed that plants grown under nutrient limitation decreased the RGR and increased the total phenolic compounds. Also in chapter V, the HPLC analyses show an increase in the amounts of the polyacetylene, pentaynene, as nutrient availability decreased.

6.2.3 The Carbon/Nutrient Balance Hypothesis (CNB)

In their carbon/nutrient hypotheses, Bryant *et al.* (1983) suggest that resources present in excess of growth demands are put into defense. For example, in sunny conditions but with limiting nutrients, carbon will be relatively in excess and carbon-based defenses such as tannins and terpenoids would increase. Conversely, in shaded conditions, carbon-based defenses would decrease. Analogous patterns are predicted for nitrogen-based defense and nitrogen availability. The CNB hypothesis predicts that concentrations of carbon-based secondary metabolites (e.g. terpenes, phenolics, and other compounds that have only C, H and O as part of their structure) will be positively correlated with the carbon/nutrient (C/N) ratio of the plant (Bryant *et al.* 1983). In chapter III, the results for total phenolics support this prediction. In other words, the plants grown under high light conditions with nutrient stress increased the amount of total phenolics as compared to the experiment under non-limiting nutrient conditions. The results in Chapter V, also give support to this premise, since the amount of pentaynene present in the flowers of *Rudbeckia hirta* increased as the nutrient availability decreased 5-fold. However, I did not find the same trend for toxicity, remembering that in general the Asteraceae produce carbon-based secondary compounds. One explanation I gave previously was that different carbon-based secondary compounds are affected in different ways, which would be contrary to the C/N hypothesis.

The above prediction deals with how a particular species should change its allocation to defensive compounds in relation to changing external supplies of carbon and nitrogen.

However, the C/N hypothesis makes a further prediction. It also predicts, along with the other theories, that those species that allocate more of their resources to defense must reduce their growth rates as well. This second prediction was not verified in my experiments.

The carbon-nutrient balance hypothesis makes explicit predictions about the relationship between the C/N ratio of the plant and allocation to defensive chemistry but these predictions have not always been satisfied in the literature (Baldwin *et al.* 1993; Ohnmeiss and Baldwin, 1994) nor in my experiments. I believe that more research needs to be done exploring all these possibilities in controlled conditions. There is also a need to understand better how the secondary compounds act in whole plant systems. Furthermore this theory predicts a negative trade-off between defense and growth.

6.2.4 Growth-differentiation balance (GDB)

The GDB hypothesis provides a framework for predicting how plants will balance allocation between differentiation-related processes over a range of resource environments. Loomis (1932, 1953) defined "growth" as the process of cell division and cell elongation that results in an irreversible increase in size and "differentiation" as the process that leads to and enhances morphological and metabolic features of cells or tissues.

In all experiments, an incremental increase in plant mass occurred as resource availability increased. With that relevant increase in plant mass, there was an associated notable increase in allocation to total phenolics, which are carbon-based secondary metabolites (chapter II). There was a negative significant correlation between the mean of total phenolics and the mean of RGR (r_s= -0.317, p= 0.02) for the 3L-3N group and (r_s=-0.089, p= 0.0001) for the 2L-4N group when comparing across environments (chapter IV). If this negative correlation

is due to a necessary physiological conflict between allocation of resources to growth versus defense, then this correlation would support the predicted trade-off between growth and defense. However, it is also possible that the negative correlation is simply due to both variables being affected by the changing experimental conditions in opposite ways. After controlling for the different experimental conditions (light and nutrient treatments), and species the linear relationships between the mean of RGR and the mean of total phenolics disappeared. The results also showed that there was no significant relationship between the mean RGR of species and the mean measurable toxicity of their tissues for either the non-limiting nutrient experiment (chapter II) or the nutrient stress experiment (chapter III) or the range resources availabilities (Chapter IV).

The GBD hypothesis predicts that plants that are limited in resources will exhibit reduced growth and reduced allocation to secondary chemicals (Herms and Mattson, 1992). In chapter III, in which the plants were nitrogen limited but with high light intensity, the results showed that the mean RGR (0.12 $gg^{-1}day^{-1}$) was reduced by 25 % relative to the first experiment with non-limiting nutrient (chapter II). While the mean total phenolics of the experiment with non-limiting nutrients (0.781 % GAE) was increased 25% relative to a mean value of 1.046 % GAE in the experiment with nutrient stress (chapter III).

In chapter IV the trend of the average relative growth rates were difficult to interpret because they were changing rapidly in the different treatments, but the ranking of dry weights (Tukey's Studentized range) showed a decrease in mean dry weight in the lowest light relative to the other two, for which there was no significant difference. Thus, mean dry weights for the 3 light levels in decreasing intensity were 0.205, 0.203 and 0.060 g. These changes in growth showed the same trends as for total phenolics, decreasing also from 0.89, 0.65 to 0.56 % GAE (3L-3N group) and 0.70 to 0.60 % GAE (2L-4N group) as light intensity decreased. As predicted by the GDB hypothesis, those plants had reduced their RGR and also

had lower amounts of total phenolics. On the other hand, the mean values of total phenolics for the plants grown in the three different nutrient treatments (full-strength, 1/5 dilute and 1/10 dilute) increased as nutrient availability decreased and increased when light intensity increased. Again, this was not true for measurable toxicity in the brine shrimp test based on the 3L-3N group since toxicity increased when light intensity decreased and reduced when nutrient availability decreased. For the 2L-4N group there was no significant difference in measurable toxicity between the different nutrient treatments, and toxicity increased when light intensity decreased. One explanation could be that different secondary compounds (e.g. phenols, terpenes, polyacetylenes) respond to light availability or nutrient availability in different ways.

The GDB hypothesis predicts that if intermediate levels of resources limit growth more than photosynthesis, then plants will allocate the accumulated carbohydrates in excess of growth requirements and, thus will have higher concentrations of carbon-based secondary compounds. However, because resource availability will limit their ability to grow, such plants will have a reduced ability to accumulate plant mass (Herms and Mattson, 1992). My findings did not support this prediction. In chapter IV, the intermediate nutrient treatment (1/10 dilute) had the lower mean of RGR and final plant weight, but not necessarily the lower mean of total phenolics or measurable toxicity in brine shrimp test.

The GDB hypothesis asserts that when grown under high-resource conditions, neither growth nor photosynthesis of plants will be as limited (Herms and Mattson, 1992). Therefore, these plants are free to allocate a greater proportion of their photosynthate to growth-related characters. In both experiments (chapters II and IV), plants grown under the highest resource conditions (high light and full-strength solution) had higher plant mass than the other treatments (Tables 7, 11 and 12). In chapter II, the high-resource plants had concentrations of total phenolics that were less than in the nutrient stress experiment (chapter III). In chapter

IV, for the 3L-3N group the high-resource (full-strength solution) plants had phenolic concentrations lower than in the other two nutrient treatments (1/5 and 1/10 dilute). The same trend was observed for the group 2L-4N. This pattern is consistent with the predictions of the GDB hypothesis.

The "trade-off" that has been reported from field experiments, and which is an important component of the different plant defense theories, seems to arise because researchers have failed to control for different soil fertilities, and differing soil fertilities affect phenolic production and growth in opposite ways. The data and analyses in this thesis suggest that there is no necessary trade-off between growth rate and chemical defense when species are grown under the same environmental conditions. For the chapters II, III, and IV my findings have been based on either an indirect bioassay of chemical defense using a measure of toxicity or on a general quantitative measure for total phenolics that does not discriminate between those phenolic compounds related to defense and those having other primary functions. In chapter V involving only two of the set of species studied in the previous chapters and only two levels of nutrient availability with high light intensity, I obtained quantitative measures of pure compounds by HPLC known to have a primary defensive function. The effect of a nutrient reduction was to increase the production of the carbon-based pentaynene in the flowers of *Rudbeckia hirta*, in accordance with the carbon/nutrient hypothesis (chapter V). These results for the flowers of plants aged 80 days were the opposite of the toxicity measures of the leaves for younger plants (chapters II, III and IV).

At the end of this work I would like to outline some weak points of this study and be critical toward my own work. One weak point of this work is that the analysis of total phenolics was based on tissues pooled by plants by species and by harvest day. It would have been better to do these analyses separately for each individual plant. I did this to save time and money. The same criticism applies to the bioassay that was used to detect toxicity. In fact, the best way to

test the theories would be by analyzing all different secondary compounds implicated in plant defense by HPLC. Clearly, this is not possible at our present state of knowledge for these species since the Asteraceae is well known to have a large number of polyacetelynes, sesquiterpene lactones, and other secondary compounds for which standards are lacking and for which we do not even know their ecological functions.

CHAPTER VII

SUMMARY AND GENERAL CONCLUSIONS

In this study I first described the interspecific relationship between RGR and plant chemical defenses under conditions of high levels of resource availability in 31 species of Asteraceae, under controlled conditions (chapter II). Second, I investigated if there is any correlation between relative growth rate (RGR - fast and slow growing plants) and secondary metabolism (soluble phenolics and toxicity) in 20 species, under controlled conditions of high light intensity but suboptimal levels of mineral nutrients (chapter III). Third, I determined how the growth and chemical variables changed, and whether the patterns of correlations between the variables changed, under such conditions relative to those provided previously to the plants (chapter III). Finally, I determined how a range of resource availabilities influenced growth and chemical parameters of six species selected by different characteristics according to the data obtained in the previously chapters (chapter IV). The last objective was to investigate if there is any difference concerning the amount of secondary metabolism produced by resource availability in *Chrysanthemum leucanthemum* and *Rudbeckia hirta* (chapter V).

Four hypothesis were tested: 1) that there was a negative correlation between RGR of slow and fast-growing plants and their secondary compounds under controlled and enriched environmental conditions; 2) that there was a negative correlation between mobile defense (toxicity) and immobile defense (phenol) under suboptimal environmental condition; 3) that the study plants grown under light-stressed conditions but optimal nutrient conditions produce less carbon-based secondary compounds than plants grown under nutrient-stressed conditions but optimal light conditions, and 4) that plants under optimal environmental

conditions have a high RGR but produce less secondary compounds than plants grown under stressful environmental conditions.

Here are my conclusions based on how the data behaved in relation to each of my hypotheses.

1. There is no trade-off between growth and chemical defense for the 31 species of Asteraceae grown under controlled conditions.

2. There is a partial support for the idea that the C/N ratio predicts the amount of carbon-based secondary compounds produced because of phenolics and one polyacetylene (pentaynene). However, the toxicity test contradicts this prediction and therefore puts into doubt the ecological consequences of this theory. So, this idea seems to be correct for phenolics and for the pentaynene, but this does not seem to translate into a greater chemical defense.

3. This thesis provides evidence that the resource availabilities affect the growth and the chemical parameters in different ways (chapters II, III and IV). First, the relative growth rate and the specific leaf area are reduced under nutrient stress. In contrast, the root:shoot ratio increased under such conditions. As expected, leaf nitrogen content was reduced under nitrogen stress. The complication occurs in the parameters related to chemical defense: while total phenolics content increased, toxicity decreased. I have suggested that the carbon/nutrient hypothesis may apply to phenolic compounds, but not to those toxic substances contributing to the measured toxicity. The reasons for this are not clear, and the reasons that I have suggested must be tested in further experiments. Testing these ideas using

species which produce nitrogen-based compounds (e.g. *Senecio* ssp. and *Tussilago farfara*), would confirm the importance of this approach.

4. The second objective was to determine how the growth and chemical variables change, and whether the patterns of correlations between the variables change, under conditions of nutrient stress (chapter III) relative to those provided to the plants in chapter II. My data showed a positive correlation between relative growth rate and total phenolics for the plants grown with non-limiting nutrients (chapter II). On the other hand, this trade-off disappeared for the plants grown under nutrient stress (chapter III). I found no trade-off between growth and chemical defense when comparing species within a given experiment (chapter IV). In neither experiments did I observe a negative correlation between RGR and phenolic concentration. These results are contrary the previously cited literature that affirm a trade-off and therefore a negative correlation between RGR and phenolics. Here I argue that those studies that did report such a correlation failed to measure whole-plant growth rate and/or failed to provide a constant external environment for plant growth. I suggest that phenolics analyzed by HPLC should be done before denying the trade-off between the RGR and phenolics.

5. There was no significant relationship between mean RGR of species and the mean measurable toxicity of their tissues for either the non-limiting nutrient experiment or the nutrient stress experiment, nor the range of resource availabilities experiment. Again, it would be useful to use morphological criteria related to plant defense and HPLC for the different chemical compounds, such as terpenes and polyacetylenes, and analyzed for many species and different resources availabilities before completely rejecting the prediction of a trade-off between growth and production of secondary compounds.

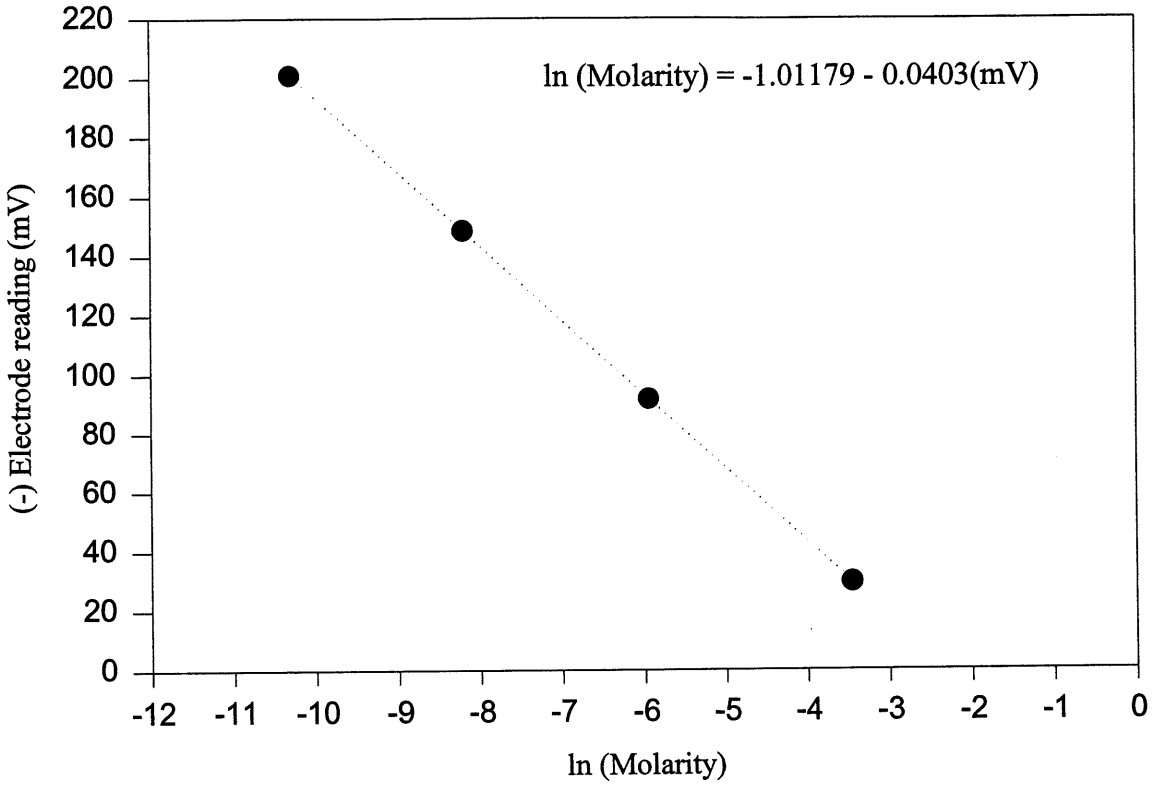
In summary, this thesis has examined the allocation of resources of plants grown under controlled conditions and has tested the trade-off between growth and chemical defenses. The

experiments used thirty-one species in the first experiment (chapter II), twenty species in the second one (chapter III), six species in the third one (chapter IV), and finally two species in chapter V. The examination has been comprehensive and has applied principles of physiological ecology and chemical ecology. Evidence from the several complimentary approaches taken in this thesis denies the existence of a necessary physiological negative trade-off between growth and chemical defense. This thesis contributed to a better understanding of the controversy involving tradeoffs between growth and defense in different resource environments. I did not expect to solve all outstanding problems related to the plant defenses theories. I believe much more needs to done until we can have all answers that might be used to elaborate a complete theory.

Appendix 1. List of species germination rates used in chapter II.

Tribe		Genus	Species	germination time (days)
Anthemideae		*Achillea*	*millefolium*	2-5
		Artemisia	*vulgaris*	2-7
		Chrysanthemum	*leucanthemum*	5-10
		Matricaria	*matricarioides*	2-5
		Tanacetum	*vulgare*	2-5
Astereae		*Erigeron*	*canadensis*	5-8
		Solidago	*canadensis*	5-11
		S.	*graminifolia*	>15
Cichorieae		*Cichorium*	*intybus*	2-3
		Hieracium	*aurantiacum*	5-9
		H.	*venosum*	7-9
		H.	*vulgatum*	>15
		Lactuca	*biennis*	>15
		L.	*canadensis*	2-5
		L.	*muralis*	12-15
		Lapsana	*communis*	2-5
		Leontodon	*autumnalis*	7-10
		Sonchus	*asper*	2-5
		Taraxacum	*officinale*	2-5
		Tragopogon	*pratensis*	2-5
Cynareae	Carduinae	*Arctium*	*lappa*	2-7
		A.	*minus*	2-5
		Cirsium	*arvense*	5-7
	Centaureinae	*Centaurea*	*nigra*	6-10
Eupatorieae	Eupatoriinae	*Eupatorium*	*maculatum*	>15
		E.	*rugosum*	7-10
Heliantheae	Coreopsidinare	*Bidens*	*cernua*	7-10
		B.	*frondosa*	8-12
	Helianthinae	*Rudbeckia*	*hirta*	2-5
	Galinsoginae	*Galinsoga*	*ciliata*	7-11
Senecioneae		*Senecio*	*vulgaris*	7-10

Appendix 2. Nitrogen standard curve.



Nitrogen standard curve. Electrode reading (mV) vs. ln (molarity) nitrate standard solutions. Four standards were prepared whose nitrate concentration ranged from 0.1 M to 0.1 mM.

Millivolts	Molarity	ln(Molarity)
-29.5	0.1	2.30259
-91.7	0.01	4.60517
-148.3	0.001	6.90776
-200.8	0.0001	9.21034

Appendix 3. Daily measurements of pH, conductivity (ms) and nitrate during the growth period from February-March (chapter II). Full-strength solution.

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
6-Feb	1	5.78	1.92	93.5	-4.7860	0.0083
	2	5.69	1.93	92.5	-4.7457	0.0087
	3	5.68	1.88	93.5	-4.7860	0.0083
	4	5.71	1.76	93.3	-4.7779	0.0084
	5	5.65	1.92	92.8	-4.7577	0.0086
	6	5.6	1.91	93.1	-4.7698	0.0085
	7	5.8	1.86	93	-4.7658	0.0085
	8	5.62	1.9	92.5	-4.7457	0.0087
	9	5.58	1.95	93.1	-4.7698	0.0085
	10	5.55	1.9	92.4	-4.7416	0.0087
	11	5.64	1.89	92.5	-4.7457	0.0087
	12	5.6	1.8	92.3	-4.7376	0.0088
	13	5.5	1.81	92.9	-4.7618	0.0086
	14	5.7	1.92	92.1	-4.7295	0.0088
	15	5.63	1.75	93.2	-4.7739	0.0084
7-Feb	1	5.77	1.93	93	-4.7658	0.0085
	2	5.7	1.93	92.8	-4.7577	0.0086
	3	5.67	1.89	93.5	-4.7860	0.0083
	4	5.7	1.8	93.8	-4.7980	0.0082
	5	5.66	1.93	92.6	-4.7497	0.0087
	6	5.62	1.92	93.3	-4.7779	0.0084
	7	5.78	1.86	93.2	-4.7739	0.0084
	8	5.66	1.89	93.1	-4.7698	0.0085
	9	5.62	1.95	93.7	-4.7940	0.0083
	10	5.61	1.9	92.1	-4.7295	0.0088
	11	5.64	1.88	92.4	-4.7416	0.0087
	12	5.61	1.82	91.1	-4.6892	0.0092
	13	5.54	1.8	90.9	-4.6812	0.0093
	14	5.69	1.91	94.5	-4.8263	0.0080
	15	5.64	1.82	92.6	-4.7497	0.0087
8-Feb	1	5.75	1.92	96.3	-4.8988	0.0075
	2	5.71	1.92	93.1	-4.7698	0.0085
	3	5.72	1.91	94.3	-4.8182	0.0081
	4	5.71	1.81	92.7	-4.7537	0.0086
	5	5.7	1.91	93.1	-4.7698	0.0085

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	6	5.68	1.89	92.8	-4.7577	0.0086
	7	5.7	1.88	92.9	-4.7618	0.0086
	8	5.6	1.88	93.6	-4.7900	0.0083
	9	5.6	1.9	93.5	-4.7860	0.0083
	10	5.61	1.88	92.2	-4.7336	0.0088
	11	5.62	1.88	92.6	-4.7497	0.0087
	12	5.59	1.82	91.1	-4.6892	0.0092
	13	5.53	1.82	91.8	-4.7174	0.0089
	14	5.65	1.89	91.2	-4.6933	0.0092
	15	5.63	1.8	91.5	-4.7054	0.0090
9-Feb	1	5.63	1.92	96	-4.8867	0.0075
	2	5.69	1.93	95.5	-4.8666	0.0077
	3	5.68	1.88	95.6	-4.8706	0.0077
	4	5.71	1.76	94.9	-4.8424	0.0079
	5	5.65	1.92	94.7	-4.8343	0.0080
	6	5.6	1.91	95.2	-4.8545	0.0078
	7	5.61	1.86	95.8	-4.8786	0.0076
	8	5.62	1.9	94.8	-4.8383	0.0079
	9	5.58	1.95	95.2	-4.8545	0.0078
	10	5.6	1.9	95.6	-4.8706	0.0077
	11	5.59	1.89	95.1	-4.8504	0.0078
	12	5.6	1.8	95.6	-4.8706	0.0077
	13	5.5	1.81	95.4	-4.8625	0.0077
	14	5.61	1.92	94.8	-4.8383	0.0079
	15	5.61	1.75	95.1	-4.8504	0.0078
11-Feb	1	5.72	1.92	94.5	-4.8263	0.0080
	2	5.6	1.93	92.5	-4.7457	0.0087
	3	5.65	1.88	93.5	-4.7860	0.0083
	4	5.63	1.76	93.3	-4.7779	0.0084
	5	5.65	1.92	92.8	-4.7577	0.0086
	6	5.6	1.91	93.1	-4.7698	0.0085
	7	5.61	1.86	93	-4.7658	0.0085
	8	5.62	1.9	92.5	-4.7457	0.0087
	9	5.58	1.95	93.1	-4.7698	0.0085
	10	5.61	1.9	94.8	-4.8383	0.0079
	11	5.64	1.89	92.5	-4.7457	0.0087
	12	5.6	1.8	93.9	-4.8021	0.0082
	13	5.61	1.81	93.8	-4.7980	0.0082
	14	5.65	1.92	93.5	-4.7860	0.0083

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	15	5.63	1.75	93.7	-4.7940	0.0083
12-Feb	1	5.61	1.92	96	-4.8867	0.0075
	2	5.62	1.93	95.5	-4.8666	0.0077
	3	5.68	1.88	95.1	-4.8504	0.0078
	4	5.62	1.76	92.1	-4.7295	0.0088
	5	5.65	1.92	92.8	-4.7577	0.0086
	6	5.6	1.91	93.1	-4.7698	0.0085
	7	5.6	1.86	93	-4.7658	0.0085
	8	5.62	1.9	92.5	-4.7457	0.0087
	9	5.58	1.95	93.1	-4.7698	0.0085
	10	5.55	1.9	94.5	-4.8263	0.0080
	11	5.64	1.89	92.5	-4.7457	0.0087
	12	5.6	1.8	93.6	-4.7900	0.0083
	13	5.5	1.81	93.8	-4.7980	0.0082
	14	5.65	1.92	93.7	-4.7940	0.0083
	15	5.63	1.75	94.2	-4.8142	0.0081
13-Feb	1	5.6	1.92	96	-4.8867	0.0075
	2	5.62	1.93	95.5	-4.8666	0.0077
	3	5.68	1.88	94.6	-4.8303	0.0080
	4	5.59	1.76	93.3	-4.7779	0.0084
	5	5.63	1.92	93.8	-4.7980	0.0082
	6	5.6	1.91	93.6	-4.7900	0.0083
	7	5.58	1.86	93	-4.7658	0.0085
	8	5.55	1.9	94.3	-4.8182	0.0081
	9	5.58	1.95	93.1	-4.7698	0.0085
	10	5.55	1.9	94.2	-4.8142	0.0081
	11	5.6	1.89	94.2	-4.8142	0.0081
	12	5.59	1.8	94.3	-4.8182	0.0081
	13	5.54	1.81	94.7	-4.8343	0.0080
	14	5.63	1.92	94.5	-4.8263	0.0080
	15	5.61	1.75	93.9	-4.8021	0.0082
14-Feb	1	5.62	1.95	93.2	-4.7739	0.0084
	2	5.6	1.93	93.6	-4.7900	0.0083
	3	5.55	1.92	93.1	-4.7698	0.0085
	4	5.52	1.95	92.8	-4.7577	0.0086
	5	5.58	1.89	92.5	-4.7457	0.0087
	6	5.56	1.94	92.8	-4.7577	0.0086
	7	5.55	1.92	93.4	-4.7819	0.0084
	8	5.54	1.93	92.8	-4.7577	0.0086

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	9	5.53	1.9	94.5	-4.8263	0.0080
	10	5.51	1.92	93.8	-4.7980	0.0082
	11	5.57	1.93	92.8	-4.7577	0.0086
	12	5.59	1.91	92.4	-4.7416	0.0087
	13	5.52	1.89	93.2	-4.7739	0.0084
	14	5.5	1.96	93.7	-4.7940	0.0083
	15	5.6	1.94	94.6	-4.8303	0.0080
15-Feb	1	5.63	1.92	95.4	-4.8625	0.0077
	2	5.45	1.93	92.5	-4.7457	0.0087
	3	5.32	1.88	93.5	-4.7860	0.0083
	4	5.45	1.76	93.3	-4.7779	0.0084
	5	5.18	1.92	92.5	-4.7457	0.0087
	6	5.6	1.91	93.4	-4.7819	0.0084
	7	5.8	1.86	93	-4.7658	0.0085
	8	5.62	1.9	94.1	-4.8101	0.0081
	9	5.1	1.95	94.3	-4.8182	0.0081
	10	5.55	1.9	93.8	-4.7980	0.0082
	11	5.42	1.89	94.6	-4.8303	0.0080
	12	5.46	1.8	92.7	-4.7537	0.0086
	13	5.4	1.81	93.3	-4.7779	0.0084
	14	5.38	1.92	92.8	-4.7577	0.0086
	15	5.63	1.75	94.1	-4.8101	0.0081
16-Feb	1	5.29	2.06	95.8	-4.8786	0.0076
	2	5.14	1.86	95.5	-4.8666	0.0077
	3	5.15	1.8	95.1	-4.8504	0.0078
	4	5.5	1.64	95.4	-4.8625	0.0077
	5	5.12	1.81	95.7	-4.8746	0.0076
	6	5.49	1.82	95.8	-4.8786	0.0076
	7	5.2	1.75	95	-4.8464	0.0079
	8	5.59	1.75	96.1	-4.8907	0.0075
	9	5.21	1.81	96.7	-4.9149	0.0073
	10	5.31	1.69	96.3	-4.8988	0.0075
	11	5.26	1.74	95.6	-4.8706	0.0077
	12	5.16	1.82	95.7	-4.8746	0.0076
	13	5.06	1.84	96.3	-4.8988	0.0075
	14	5.24	1.74	96.7	-4.9149	0.0073
	15	5.28	1.68	94.6	-4.8303	0.0080
18-Feb	1	5.71	1.9	99.9	-5.0439	0.0064

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	2	5.75	1.9	98.9	-5.0036	0.0067
	3	5.63	1.82	100	-5.0479	0.0064
	4	5.65	1.82	101.8	-5.1204	0.0060
	5	5.75	1.82	101.7	-5.1164	0.0060
	6	5.76	1.88	99.9	-5.0439	0.0064
	7	5.74	1.83	102.1	-5.1325	0.0059
	8	5.71	1.83	101.6	-5.1124	0.0060
	9	5.72	1.81	101.8	-5.1204	0.0060
	10	5.69	1.8	102.1	-5.1325	0.0059
	11	5.7	1.85	102.5	-5.1487	0.0058
	12	5.71	1.86	101.5	-5.1084	0.0060
	13	5.64	1.84	101.1	-5.0922	0.0061
	14	5.63	1.85	101.1	-5.0922	0.0061
	15	5.65	1.8	101.3	-5.1003	0.0061
19-Feb	1	5.68	1.88	103.1	-5.1728	0.0057
	2	5.69	1.85	102.5	-5.1487	0.0058
	3	5.6	1.81	101.9	-5.1245	0.0059
	4	5.62	1.8	101.7	-5.1164	0.0060
	5	5.7	1.78	101.5	-5.1084	0.0060
	6	5.68	1.82	102	-5.1285	0.0059
	7	5.7	1.82	101.7	-5.1164	0.0060
	8	5.65	1.78	101.3	-5.1003	0.0061
	9	5.68	1.79	101.6	-5.1124	0.0060
	10	5.66	1.76	103	-5.1688	0.0057
	11	5.63	1.85	101.9	-5.1245	0.0059
	12	5.65	1.86	101.5	-5.1084	0.0060
	13	5.62	1.81	102.3	-5.1406	0.0059
	14	5.59	1.84	101.2	-5.0963	0.0061
	15	5.6	1.77	102.9	-5.1648	0.0057
20-Feb	1	5.65	1.96	99.9	-5.0439	0.0064
	2	5.68	1.91	99.5	-5.0278	0.0066
	3	5.58	1.85	99.6	-5.0318	0.0065
	4	5.6	1.85	99.8	-5.0398	0.0065
	5	5.55	1.8	98.9	-5.0036	0.0067
	6	5.64	1.96	99.6	-5.0318	0.0065
	7	5.67	1.89	99.9	-5.0439	0.0064
	8	5.61	1.81	99.8	-5.0398	0.0065
	9	5.65	1.81	99.5	-5.0278	0.0066
	10	5.62	1.81	99.7	-5.0358	0.0065

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	11	5.65	1.91	99.8	-5.0398	0.0065
	12	5.6	1.94	101	-5.0882	0.0062
	13	5.56	1.81	99.9	-5.0439	0.0064
	14	5.58	1.86	99.7	-5.0358	0.0065
	15	5.58	1.79	99.5	-5.0278	0.0066
21-Feb	1	5.6	1.98	95.2	-4.8545	0.0078
	2	5.63	2.01	93	-4.7658	0.0085
	3	5.34	1.96	90.5	-4.6651	0.0094
	4	5.33	1.96	88.9	-4.6006	0.0100
	5	5.5	1.92	89.7	-4.6328	0.0097
	6	5.66	1.97	93.6	-4.7900	0.0083
	7	5.6	1.95	94.3	-4.8182	0.0081
	8	5.34	1.92	90	-4.6449	0.0096
	9	5.42	1.92	89.2	-4.6127	0.0099
	10	5.28	1.9	90.8	-4.6771	0.0093
	11	5.63	1.97	91	-4.6852	0.0092
	12	5.55	1.98	91.6	-4.7094	0.0090
	13	5.45	1.94	89.3	-4.6167	0.0099
	14	5.48	1.97	90.3	-4.6570	0.0095
	15	5.48	1.89	90.5	-4.6651	0.0094
22-Feb	1	5.55	1.99	102.8	-5.1607	0.0057
	2	5.57	1.98	101.7	-5.1164	0.0060
	3	5.3	1.86	101.5	-5.1084	0.0060
	4	5.31	1.96	101	-5.0882	0.0062
	5	5.5	1.87	102.2	-5.1366	0.0059
	6	5.55	1.84	101	-5.0882	0.0062
	7	5.5	1.64	102.7	-5.1567	0.0058
	8	5.32	1.92	102.1	-5.1325	0.0059
	9	5.36	1.81	100	-5.0479	0.0064
	10	5.29	1.81	101	-5.0882	0.0062
	11	5.5	1.81	99.7	-5.0358	0.0065
	12	5.4	1.94	102.5	-5.1487	0.0058
	13	5.4	1.82	102	-5.1285	0.0059
	14	5.32	1.85	98.8	-4.9995	0.0067
	15	5.49	1.82	100.7	-5.0761	0.0062
23-Feb	1	5.38	1.94	107.1	-5.3340	0.0048
	2	5.45	1.84	105.1	-5.2534	0.0052
	3	5.51	1.84	105.1	-5.2534	0.0052
	4	5.3	1.76	100.5	-5.0681	0.0063

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	5	5.48	1.79	102	-5.1285	0.0059
	6	5.56	1.76	100	-5.0479	0.0064
	7	5.49	1.8	100.9	-5.0842	0.0062
	8	5.4	1.87	100.5	-5.0681	0.0063
	9	5.31	1.77	101	-5.0882	0.0062
	10	5.32	1.65	100.8	-5.0801	0.0062
	11	5.45	1.7	101.3	-5.1003	0.0061
	12	5.49	1.91	100.2	-5.0560	0.0064
	13	5.51	1.8	101.6	-5.1124	0.0060
	14	5.29	1.84	100.5	-5.0681	0.0063
	15	5.37	1.67	100.3	-5.0600	0.0063
25-Feb	1	5.71	1.91	100	-5.0479	0.0064
	2	5.76	1.9	101.3	-5.1003	0.0061
	3	5.58	1.82	102	-5.1285	0.0059
	4	5.64	1.82	101.3	-5.1003	0.0061
	5	5.77	1.82	101.1	-5.0922	0.0061
	6	5.72	1.88	103.2	-5.1769	0.0056
	7	5.77	1.83	101.1	-5.0922	0.0061
	8	5.67	1.83	102	-5.1285	0.0059
	9	5.65	1.81	102.3	-5.1406	0.0059
	10	5.67	1.8	101.1	-5.0922	0.0061
	11	5.71	1.85	102.7	-5.1567	0.0058
	12	5.68	1.86	101.9	-5.1245	0.0059
	13	5.61	1.84	102.8	-5.1607	0.0057
	14	5.57	1.85	101.2	-5.0963	0.0061
	15	5.63	1.8	101.9	-5.1245	0.0059
26-Feb	1	5.73	1.88	101.5	-5.1084	0.0060
	2	5.7	1.85	100.8	-5.0801	0.0062
	3	5.56	1.81	102.5	-5.1487	0.0058
	4	5.54	1.8	103.1	-5.1728	0.0057
	5	5.65	1.78	101.4	-5.1043	0.0061
	6	5.68	1.82	101.6	-5.1124	0.0060
	7	5.69	1.82	102.3	-5.1406	0.0059
	8	5.56	1.78	101.8	-5.1204	0.0060
	9	5.55	1.79	102.1	-5.1325	0.0059
	10	5.53	1.76	99.9	-5.0439	0.0064
	11	5.6	1.85	100.1	-5.0519	0.0064
	12	5.56	1.86	101.3	-5.1003	0.0061
	13	5.5	1.81	101.1	-5.0922	0.0061

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	14	5.5	1.84	101.6	-5.1124	0.0060
	15	5.53	1.77	100	-5.0479	0.0064
27-Feb	1	5.77	1.96	97.3	-4.9391	0.0072
	2	5.73	1.91	96.8	-4.9189	0.0073
	3	5.35	1.85	93	-4.7658	0.0085
	4	5.4	1.85	92.4	-4.7416	0.0087
	5	5.55	1.8	93.1	-4.7698	0.0085
	6	5.64	1.96	95.3	-4.8585	0.0078
	7	5.72	1.89	96.4	-4.9028	0.0074
	8	5.46	1.81	93.1	-4.7698	0.0085
	9	5.46	1.81	92.1	-4.7295	0.0088
	10	5.34	1.81	92.8	-4.7577	0.0086
	11	5.65	1.91	93.8	-4.7980	0.0082
	12	5.51	1.94	92.9	-4.7618	0.0086
	13	5.36	1.81	92.6	-4.7497	0.0087
	14	5.36	1.86	91.8	-4.7174	0.0089
	15	5.39	1.79	92.5	-4.7457	0.0087
28-Feb	1	5.92	1.98	95.2	-4.8545	0.0078
	2	5.94	2.01	93	-4.7658	0.0085
	3	5.34	1.96	92.5	-4.7457	0.0087
	4	5.33	1.96	90.9	-4.6812	0.0093
	5	5.5	1.92	90.7	-4.6731	0.0093
	6	5.92	1.97	93.6	-4.7900	0.0083
	7	6.07	1.95	94.3	-4.8182	0.0081
	8	5.34	1.92	90	-4.6449	0.0096
	9	5.42	1.92	91	-4.6852	0.0092
	10	5.28	1.9	90.8	-4.6771	0.0093
	11	5.82	1.97	91	-4.6852	0.0092
	12	5.76	1.98	91.6	-4.7094	0.0090
	13	5.29	1.94	90.6	-4.6691	0.0094
	14	5.3	1.97	90.3	-4.6570	0.0095
	15	5.32	1.89	90.5	-4.6651	0.0094
1-Mar	1	5.82	1.98	99	-5.0076	0.0067
	2	5.78	2.01	98	-4.9673	0.0070
	3	5.3	1.92	92.2	-4.7336	0.0088
	4	5.24	1.91	92.3	-4.7376	0.0088
	5	5.39	1.89	92.7	-4.7537	0.0086
	6	5.73	1.98	98.2	-4.9754	0.0069
	7	5.87	1.94	98.6	-4.9915	0.0068

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	8	5.28	1.88	92.8	-4.7577	0.0086
	9	5.3	1.89	91.8	-4.7174	0.0089
	10	5.15	1.89	93.5	-4.7860	0.0083
	11	5.64	1.99	95	-4.8464	0.0079
	12	5.65	1.98	95.3	-4.8585	0.0078
	13	5.18	1.91	92.2	-4.7336	0.0088
	14	5.2	1.94	92	-4.7255	0.0089
	15	5.17	1.88	92.4	-4.7416	0.0087
2-Mar	1	5.73	1.82	93.8	-4.7980	0.0082
	2	5.7	1.79	93.4	-4.7819	0.0084
	3	5.62	1.68	93.1	-4.7698	0.0085
	4	5.7	1.76	93.3	-4.7779	0.0084
	5	5.7	1.74	93.6	-4.7900	0.0083
	6	5.72	1.72	93.7	-4.7940	0.0083
	7	5.78	1.72	93.4	-4.7819	0.0084
	8	5.64	1.73	93	-4.7658	0.0085
	9	5.71	1.74	92	-4.7255	0.0089
	10	5.69	1.76	92.3	-4.7376	0.0088
	11	5.66	1.72	93.8	-4.7980	0.0082
	12	5.64	1.76	93.2	-4.7739	0.0084
	13	5.57	1.76	92.7	-4.7537	0.0086
	14	5.64	1.75	91.9	-4.7215	0.0089
	15	5.64	1.75	92.1	-4.7295	0.0088
4-Mar	1	5.77	1.91	94.3	-4.8182	0.0081
	2	5.72	1.78	93	-4.7658	0.0085
	3	5.44	1.68	93.1	-4.7698	0.0085
	4	5.58	1.77	93	-4.7658	0.0085
	5	5.55	1.74	92.8	-4.7577	0.0086
	6	5.62	1.73	92.4	-4.7416	0.0087
	7	5.79	1.73	92.5	-4.7457	0.0087
	8	5.53	1.75	92.6	-4.7497	0.0087
	9	5.66	1.75	93.1	-4.7698	0.0085
	10	5.54	1.77	92.8	-4.7577	0.0086
	11	5.57	1.73	93.4	-4.7819	0.0084
	12	5.59	1.75	92.1	-4.7295	0.0088
	13	5.45	1.76	94.5	-4.8263	0.0080
	14	5.5	1.76	93	-4.7658	0.0085
	15	5.44	1.74	92.6	-4.7497	0.0087
5-Mar	1	5.78	1.88	93.8	-4.7980	0.0082

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	2	5.64	1.83	93.6	-4.7900	0.0083
	3	5.35	1.72	92.8	-4.7577	0.0086
	4	5.51	1.8	93.1	-4.7698	0.0085
	5	5.44	1.77	91.8	-4.7174	0.0089
	6	5.57	1.75	91.8	-4.7174	0.0089
	7	5.79	1.76	92.9	-4.7618	0.0086
	8	5.5	1.77	92.2	-4.7336	0.0088
	9	5.62	1.78	92.5	-4.7457	0.0087
	10	5.46	1.79	92.6	-4.7497	0.0087
	11	5.53	1.77	92.4	-4.7416	0.0087
	12	5.54	1.79	92.7	-4.7537	0.0086
	13	5.47	1.8	92.2	-4.7336	0.0088
	14	5.43	1.79	92.1	-4.7295	0.0088
	15	5.55	1.77	92.3	-4.7376	0.0088
6-Mar	1	5.91	1.91	93.5	-4.7860	0.0083
	2	5.69	1.91	92.3	-4.7376	0.0088
	3	5.29	1.8	92.2	-4.7336	0.0088
	4	5.4	1.87	93.1	-4.7698	0.0085
	5	5.28	1.82	93.3	-4.7779	0.0084
	6	5.49	1.79	93.7	-4.7940	0.0083
	7	5.82	1.79	93.5	-4.7860	0.0083
	8	5.36	1.84	93.5	-4.7860	0.0083
	9	5.54	1.83	93.5	-4.7860	0.0083
	10	5.34	1.85	93.4	-4.7819	0.0084
	11	5.46	1.84	93.6	-4.7900	0.0083
	12	5.5	1.86	93.8	-4.7980	0.0082
	13	5.39	1.85	93.7	-4.7940	0.0083
	14	5.28	1.86	93.8	-4.7980	0.0082
	15	5.43	1.87	93.4	-4.7819	0.0084
7-Mar	1	5.8	1.91	93.4	-4.7819	0.0084
	2	5.7	1.92	92.2	-4.7336	0.0088
	3	5.45	1.85	94.9	-4.8424	0.0079
	4	5.4	1.87	94.2	-4.8142	0.0081
	5	5.26	1.85	94.5	-4.8263	0.0080
	6	5.35	1.88	93.7	-4.7940	0.0083
	7	5.81	1.83	93.9	-4.8021	0.0082
	8	5.25	1.92	94.5	-4.8263	0.0080
	9	5.6	1.87	94.3	-4.8182	0.0081
	10	5.4	1.85	94.7	-4.8343	0.0080

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	11	5.3	1.87	94.8	-4.8383	0.0079
	12	5.5	1.89	94.6	-4.8303	0.0080
	13	5.39	1.89	94.5	-4.8263	0.0080
	14	5.33	1.89	94.6	-4.8303	0.0080
	15	5.43	1.87	94.8	-4.8383	0.0079
8-Mar	1	5.78	1.92	94.3	-4.8182	0.0081
	2	5.65	1.95	94.7	-4.8343	0.0080
	3	5.32	1.88	94.6	-4.8303	0.0080
	4	5.38	1.93	93.9	-4.8021	0.0082
	5	5.18	1.92	95.1	-4.8504	0.0078
	6	5.24	1.91	94.8	-4.8383	0.0079
	7	5.8	1.86	95	-4.8464	0.0079
	8	5.1	1.95	95.2	-4.8545	0.0078
	9	5.55	1.9	95.6	-4.8706	0.0077
	10	5.42	1.89	94.8	-4.8383	0.0079
	11	5.25	1.92	94.6	-4.8303	0.0080
	12	5.51	1.91	94.8	-4.8383	0.0079
	13	5.38	1.91	94.6	-4.8303	0.0080
	14	5.38	1.92	94.5	-4.8263	0.0080
	15	5.46	1.92	94.8	-4.8383	0.0079
9-Mar	1	5.29	2.06	96.2	-4.8948	0.0075
	2	5.14	1.86	95.9	-4.8827	0.0076
	3	5.15	1.8	96.1	-4.8907	0.0075
	4	5.5	1.64	94.6	-4.8303	0.0080
	5	5.12	1.81	94.3	-4.8182	0.0081
	6	5.49	1.82	92.2	-4.7336	0.0088
	7	5.2	1.75	94	-4.8061	0.0082
	8	5.59	1.75	94.3	-4.8182	0.0081
	9	5.21	1.81	95	-4.8464	0.0079
	10	5.31	1.69	94.3	-4.8182	0.0081
	11	5.26	1.74	93.8	-4.7980	0.0082
	12	5.16	1.82	92.3	-4.7376	0.0088
	13	5.06	1.84	95.8	-4.8786	0.0076
	14	5.24	1.74	93.7	-4.7940	0.0083
	15	5.28	1.68	93.5	-4.7860	0.0083
11-Mar	1	5.76	1.91	94.3	-4.8182	0.0081
	2	5.7	1.78	93	-4.7658	0.0085
	3	5.46	1.68	93.1	-4.7698	0.0085
	4	5.59	1.77	91	-4.6852	0.0092

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	5	5.56	1.74	91.8	-4.7174	0.0089
	6	5.6	1.73	92.4	-4.7416	0.0087
	7	5.75	1.73	92.5	-4.7457	0.0087
	8	5.78	1.75	91.6	-4.7094	0.0090
	9	5.7	1.75	90.5	-4.6651	0.0094
	10	5.6	1.77	91.3	-4.6973	0.0091
	11	5.61	1.73	91.4	-4.7013	0.0091
	12	5.62	1.75	92.1	-4.7295	0.0088
	13	5.5	1.76	91.1	-4.6892	0.0092
	14	5.61	1.76	90	-4.6449	0.0096
	15	5.52	1.74	91.5	-4.7054	0.0090
12-Mar	1	5.75	1.88	93.8	-4.7980	0.0082
	2	5.62	1.83	93.6	-4.7900	0.0083
	3	5.4	1.72	92.8	-4.7577	0.0086
	4	5.5	1.8	91	-4.6852	0.0092
	5	5.46	1.77	91.8	-4.7174	0.0089
	6	5.53	1.75	91.8	-4.7174	0.0089
	7	5.71	1.76	92.9	-4.7618	0.0086
	8	5.61	1.77	92.2	-4.7336	0.0088
	9	5.59	1.78	90.1	-4.6489	0.0096
	10	5.46	1.79	91.6	-4.7094	0.0090
	11	5.49	1.77	91.4	-4.7013	0.0091
	12	5.52	1.79	92.7	-4.7537	0.0086
	13	5.49	1.8	90.2	-4.6530	0.0095
	14	5.46	1.79	90.1	-4.6489	0.0096
	15	5.53	1.77	91.7	-4.7134	0.0090
13-Mar	1	5.8	1.91	93.5	-4.7860	0.0083
	2	5.59	1.91	92.3	-4.7376	0.0088
	3	5.35	1.8	92.2	-4.7336	0.0088
	4	5.42	1.87	90.3	-4.6570	0.0095
	5	5.28	1.82	91.3	-4.6973	0.0091
	6	5.49	1.79	91.7	-4.7134	0.0090
	7	5.82	1.79	92.7	-4.7537	0.0086
	8	5.39	1.84	90	-4.6449	0.0096
	9	5.44	1.83	88.9	-4.6006	0.0100
	10	5.49	1.85	90.4	-4.6610	0.0095
	11	5.5	1.84	89.4	-4.6207	0.0098
	12	5.5	1.86	91.8	-4.7174	0.0089
	13	5.46	1.85	89	-4.6046	0.0100
	14	5.32	1.86	88.8	-4.5965	0.0101

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	15	5.43	1.87	89.9	-4.6409	0.0096
14-Mar	1	5.72	1.88	93.4	-4.7819	0.0084
	2	5.5	1.89	92.7	-4.7537	0.0086
	3	5.3	1.78	92.5	-4.7457	0.0087
	4	5.35	1.86	91	-4.6852	0.0092
	5	5.4	1.8	91.5	-4.7054	0.0090
	6	5.3	1.78	91.6	-4.7094	0.0090
	7	5.4	1.77	92.1	-4.7295	0.0088
	8	5.38	1.8	90.3	-4.6570	0.0095
	9	5.41	1.81	89	-4.6046	0.0100
	10	5.46	1.83	90.1	-4.6489	0.0096
	11	5.49	1.82	89.7	-4.6328	0.0097
	12	5.48	1.85	91.3	-4.6973	0.0091
	13	5.43	1.84	89.3	-4.6167	0.0099
	14	5.31	1.83	88.9	-4.6006	0.0100
	15	5.4	1.85	89.5	-4.6248	0.0098
15-Mar	1	5.63	1.87	93.6	-4.7900	0.0083
	2	5.45	1.93	92.5	-4.7457	0.0087
	3	5.19	1.87	93.3	-4.7779	0.0084
	4	5.45	1.76	93.3	-4.7779	0.0084
	5	5.15	1.82	93.6	-4.7900	0.0083
	6	5.6	1.91	90	-4.6449	0.0096
	7	5.41	1.88	91.3	-4.6973	0.0091
	8	5.62	1.9	90.5	-4.6651	0.0094
	9	5.66	1.8	90.4	-4.6610	0.0095
	10	5.73	1.76	91.8	-4.7174	0.0089
	11	5.74	1.73	90.6	-4.6691	0.0094
	12	5.46	1.8	90.8	-4.6771	0.0093
	13	5.4	1.81	90.8	-4.6771	0.0093
	14	5.59	1.81	90.1	-4.6489	0.0096
	15	5.63	1.75	91	-4.6852	0.0092
16-Mar	1	5.62	1.86	99.5	-5.0278	0.0066
	2	5.33	1.94	97.8	-4.9592	0.0070
	3	5.17	1.9	95.1	-4.8504	0.0078
	4	5.32	1.78	94.3	-4.8182	0.0081
	5	5.13	1.84	96.6	-4.9109	0.0074
	6	5.57	1.96	95.8	-4.8786	0.0076
	7	5.27	1.89	95.6	-4.8706	0.0077
	8	5.62	1.89	96.8	-4.9189	0.0073
	9	5.6	1.8	95.3	-4.8585	0.0078

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	10	5.72	1.74	95.2	-4.8545	0.0078
	11	5.69	1.71	96.8	-4.9189	0.0073
	12	5.34	1.79	97.2	-4.9351	0.0072
	13	5.3	1.84	97.6	-4.9512	0.0071
	14	5.55	1.82	96.4	-4.9028	0.0074
	15	5.6	1.76	96.5	-4.9069	0.0074
18-Mar	1	5.57	2.01	90	-4.6449	0.0096
	2	5.21	2.08	90.1	-4.6489	0.0096
	3	5.14	2.01	89.9	-4.6409	0.0096
	4	5.25	1.88	89.4	-4.6207	0.0098
	5	5.1	1.96	89.9	-4.6409	0.0096
	6	5.52	2.04	89.7	-4.6328	0.0097
	7	5.18	1.98	90.1	-4.6489	0.0096
	8	5.61	1.96	89.8	-4.6368	0.0097
	9	5.57	1.85	89.9	-4.6409	0.0096
	10	5.67	1.84	89.9	-4.6409	0.0096
	11	5.62	1.83	89.4	-4.6207	0.0098
	12	5.3	1.91	89.7	-4.6328	0.0097
	13	5.24	1.87	89.5	-4.6248	0.0098
	14	5.52	1.96	89.5	-4.6248	0.0098
	15	5.56	1.92	89.5	-4.6248	0.0098
19-Mar	1	5.6	1.96	90	-4.6449	0.0096
	2	5.3	1.99	90.7	-4.6731	0.0093
	3	5.22	1.98	91	-4.6852	0.0092
	4	5.26	1.91	91.1	-4.6892	0.0092
	5	5.16	1.95	91.4	-4.7013	0.0091
	6	5.6	1.99	91.2	-4.6933	0.0092
	7	5.3	1.98	90.8	-4.6771	0.0093
	8	5.63	1.96	90.9	-4.6812	0.0093
	9	5.61	1.9	91.2	-4.6933	0.0092
	10	5.65	1.89	90.6	-4.6691	0.0094
	11	5.68	1.89	90.1	-4.6489	0.0096
	12	5.3	1.92	91.2	-4.6933	0.0092
	13	5.31	1.89	91.3	-4.6973	0.0091
	14	5.49	1.92	90.8	-4.6771	0.0093
	15	5.36	1.92	90	-4.6449	0.0096
20-Mar	1	5.65	1.88	91	-4.6852	0.0092
	2	5.67	1.96	91.1	-4.6892	0.0092
	3	5.23	1.86	93.6	-4.7900	0.0083
	4	5.41	1.95	91.2	-4.6933	0.0092

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	5	5.32	1.8	93.9	-4.8021	0.0082
	6	5.35	1.91	91.7	-4.7134	0.0090
	7	5.46	1.89	91.6	-4.7094	0.0090
	8	5.6	1.83	90.8	-4.6771	0.0093
	9	5.8	1.79	92.3	-4.7376	0.0088
	10	5.7	1.76	91.7	-4.7134	0.0090
	11	5.36	1.99	92.1	-4.7295	0.0088
	12	5.55	1.9	95.2	-4.8545	0.0078
	13	5.42	1.96	90.6	-4.6691	0.0094
	14	5.63	1.83	91.5	-4.7054	0.0090
	15	5.52	1.95	90.5	-4.6651	0.0094
21-Mar	1	5.63	1.87	93.6	-4.7900	0.0083
	2	5.65	1.95	94	-4.8061	0.0082
	3	5.19	1.87	93.3	-4.7779	0.0084
	4	5.38	1.93	94.2	-4.8142	0.0081
	5	5.15	1.82	93.6	-4.7900	0.0083
	6	5.24	1.91	93.9	-4.8021	0.0082
	7	5.41	1.88	94.3	-4.8182	0.0081
	8	5.66	1.8	95.1	-4.8504	0.0078
	9	5.73	1.76	95.2	-4.8545	0.0078
	10	5.74	1.73	95.1	-4.8504	0.0078
	11	5.25	1.92	94.8	-4.8383	0.0079
	12	5.51	1.91	94.7	-4.8343	0.0080
	13	5.38	1.91	94.6	-4.8303	0.0080
	14	5.59	1.81	95.8	-4.8786	0.0076
	15	5.46	1.92	94.7	-4.8343	0.0080
22-Mar	1	5.45	1.74	94.5	-4.8263	0.0080
	2	5.16	1.84	94.5	-4.8263	0.0080
	3	5.15	1.84	95.3	-4.8585	0.0078
	4	5.58	1.65	95.4	-4.8625	0.0077
	5	5.13	1.79	95.6	-4.8706	0.0077
	6	5.56	1.76	95.8	-4.8786	0.0076
	7	5.14	1.8	95.7	-4.8746	0.0076
	8	5.75	1.75	96.1	-4.8907	0.0075
	9	5.31	1.77	96.3	-4.8988	0.0075
	10	5.44	1.65	96.1	-4.8907	0.0075
	11	5.34	1.7	96.4	-4.9028	0.0074
	12	5.22	1.78	96.5	-4.9069	0.0074
	13	5.11	1.8	96.4	-4.9028	0.0074
	14	5.35	1.72	96.7	-4.9149	0.0073

Date	Container	pH	Conductance (ms)	(-) Millivolts	ln (M)	NO_3^- (M)
	15	5.37	1.67	96.4	-4.9028	0.0074
23-Mar	1	5.38	1.94	97.1	-4.9310	0.0072
	2	5.15	1.99	97.8	-4.9592	0.0070
	3	5.17	1.98	97.6	-4.9512	0.0071
	4	5.57	1.76	96.8	-4.9189	0.0073
	5	5.11	1.96	98	-4.9673	0.0070
	6	5.53	1.87	98.5	-4.9875	0.0068
	7	5.21	1.84	97.6	-4.9512	0.0071
	8	5.67	1.87	97.2	-4.9351	0.0072
	9	5.26	1.92	98.4	-4.9834	0.0069
	10	5.36	1.81	99.1	-5.0116	0.0067
	11	5.29	1.81	99.3	-5.0197	0.0066
	12	5.2	1.91	98.5	-4.9875	0.0068
	13	5.12	1.94	98.6	-4.9915	0.0068
	14	5.29	1.84	98.4	-4.9834	0.0069
	15	5.32	1.85	98.1	-4.9713	0.0069
24-Mar	1	5.29	2.06	101	-5.0882	0.0062
	2	5.14	1.86	99.8	-5.0398	0.0065
	3	5.15	1.8	99.7	-5.0358	0.0065
	4	5.5	1.64	99.6	-5.0318	0.0065
	5	5.12	1.81	100.1	-5.0519	0.0064
	6	5.49	1.82	100.1	-5.0519	0.0064
	7	5.2	1.75	99.7	-5.0358	0.0065
	8	5.59	1.75	101	-5.0882	0.0062
	9	5.21	1.81	99.8	-5.0398	0.0065
	10	5.31	1.69	99.7	-5.0358	0.0065
	11	5.26	1.74	99.3	-5.0197	0.0066
	12	5.16	1.82	99.1	-5.0116	0.0067
	13	5.06	1.84	99.7	-5.0358	0.0065
	14	5.24	1.74	99.8	-5.0398	0.0065
	15	5.28	1.68	101	-5.0882	0.0062

Appendix 4. Primary data set of 31 species used in chapter II.

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
Achillea millefolium	14	0.167	3.77	166.079	5.112	0.023	0.004	0.027	0.000	0.000	0.000
	14	0.440	1.57	172.527	5.151	0.009	0.004	0.013	0.000	0.000	0.000
	14	0.349	1.02	237.209	5.469	0.004	0.002	0.006	0.000	0.000	0.000
	14	0.413	1.51	201.333	5.305	0.008	0.003	0.011	0.000	0.000	0.000
	14	2.667	0.46	383.333	5.949	0.001	0.003	0.004	0.000	0.000	0.000
	14	0.206	0.75	220.588	5.396	0.003	0.001	0.004	0.000	0.000	0.000
	14	0.197	1.31	198.485	5.291	0.007	0.001	0.008	0.000	0.000	0.000
	14	0.818	0.61	554.545	6.318	0.001	0.001	0.002	0.000	0.000	0.000
	14	0.316	1.52	192.405	5.260	0.008	0.003	0.010	0.000	0.000	0.000
	14	0.354	1.2	146.341	4.986	0.008	0.003	0.011	0.000	0.000	0.000
	14	0.500	0.75	625.000	6.438	0.001	0.001	0.002	0.000	0.000	0.000
	14	0.900	0.54	540.000	6.292	0.001	0.001	0.002	0.000	0.000	0.000
	14	0.098	1.96	321.311	5.772	0.006	0.001	0.007	0.000	0.000	0.000
	14	0.303	1.11	336.364	5.818	0.003	0.001	0.004	0.000	0.000	0.000
	14	0.174	1.23	267.391	5.589	0.005	0.001	0.005	0.000	0.000	0.000
Achillea millefolium	21	0.242	11.64	218.386	5.386	0.053	0.013	0.066	0.000	0.000	0.000
	21	0.249	13.57	241.459	5.487	0.056	0.014	0.070	0.000	0.000	0.000
	21	0.246	8.2	288.732	5.666	0.028	0.007	0.035	0.000	0.000	0.000
	21	0.186	13.44	197.067	5.284	0.068	0.013	0.081	0.000	0.000	0.000
	21	0.352	10.68	190.714	5.251	0.056	0.020	0.076	0.000	0.000	0.000
	21	0.342	13.08	161.282	5.083	0.081	0.028	0.109	0.000	0.000	0.000
	21	0.155	15.5	237.730	5.471	0.065	0.010	0.075	0.000	0.000	0.000
	21	0.197	11.99	167.225	5.119	0.072	0.014	0.086	0.000	0.000	0.000
	21	0.386	4.8	179.775	5.192	0.027	0.010	0.037	0.000	0.000	0.000
	21	0.312	4.65	166.667	5.116	0.028	0.009	0.037	0.000	0.000	0.000
	21	0.419	5.4	237.885	5.472	0.023	0.010	0.032	0.000	0.000	0.000
	21	0.249	5.5	163.205	5.095	0.034	0.008	0.042	0.000	0.000	0.000
	21	0.217	7.43	278.277	5.629	0.027	0.006	0.033	0.000	0.000	0.000
	21	0.348	10.97	195.544	5.276	0.056	0.020	0.076	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
Achillea	28	0.238	11.7	252.700	5.532	0.046	0.011	0.057	0.000	0.000	0.000
millefolium	28	1.660	10.6	400.000	5.991	0.027	0.044	0.071	0.000	0.000	0.000
	28	0.314	41.12	157.790	5.061	0.261	0.082	0.342	0.000	0.000	0.000
	28	0.400	10.53	177.872	5.181	0.059	0.024	0.083	0.000	0.000	0.000
	28	0.182	19.8	275.382	5.618	0.072	0.013	0.085	0.000	0.000	0.000
	28	0.186	14.5	464.744	6.141	0.031	0.006	0.037	0.000	0.000	0.000
	28	0.273	29.99	192.367	5.259	0.156	0.043	0.198	0.000	0.000	0.000
	28	0.259	30.16	209.590	5.345	0.144	0.037	0.181	0.000	0.000	0.000
	28	0.225	8.87	111.572	4.715	0.080	0.018	0.097	0.000	0.000	0.000
	28	0.393	6.91	205.655	5.326	0.034	0.013	0.047	0.000	0.000	0.000
	28	0.778	10.25	84.501	4.437	0.121	0.094	0.216	0.000	0.000	0.000
	28	1.323	24.46	404.967	6.004	0.060	0.080	0.140	0.000	0.000	0.000
	28	0.427	16.28	163.948	5.100	0.099	0.042	0.142	0.000	0.000	0.000
Achillea	35	0.386	110.54	174.601	5.163	0.633	0.244	0.877	0.000	0.000	0.000
millefolium	35	0.344	57.23	241.783	5.488	0.237	0.081	0.318	0.000	0.000	0.000
	35	0.140	36.53	321.284	5.772	0.114	0.016	0.130	0.000	0.000	0.000
	35	0.391	32.34	302.526	5.712	0.107	0.042	0.149	0.000	0.000	0.000
	35	0.467	42.9	389.646	5.965	0.110	0.051	0.162	0.000	0.000	0.000
	35	0.356	98.39	136.957	4.920	0.718	0.256	0.974	0.000	0.000	0.000
	35	0.489	20.8	334.405	5.812	0.062	0.030	0.093	0.000	0.000	0.000
	35	0.527	35.82	74.953	4.317	0.478	0.252	0.730	0.000	0.000	0.000
	35	0.687	18.76	301.124	5.708	0.062	0.043	0.105	0.000	0.000	0.000
	35	0.466	32.55	119.450	4.783	0.273	0.127	0.399	0.000	0.000	0.000
	35	0.330	21.25	140.635	4.946	0.151	0.050	0.201	0.000	0.000	0.000
	35	0.683	25.11	145.734	4.982	0.172	0.118	0.290	0.000	0.000	0.000
	35	1.073	28.78	215.904	5.375	0.133	0.143	0.276	0.000	0.000	0.000
	35	0.299	40.37	111.335	4.713	0.363	0.108	0.471	0.000	0.000	0.000
Arctium	14	0.229	33.29	265.048	5.580	0.126	0.029	0.154	0.000	0.000	0.000
lappa	14	0.295	28.95	225.678	5.419	0.128	0.038	0.166	0.000	0.000	0.000
	14	0.435	30.16	239.289	5.478	0.126	0.055	0.181	0.000	0.000	0.000
	14	0.179	20.02	231.579	5.445	0.086	0.016	0.102	0.000	0.000	0.000
	14	0.295	42.03	273.686	5.612	0.154	0.045	0.199	0.000	0.000	0.000
	14	0.287	31.77	185.226	5.222	0.172	0.049	0.221	0.000	0.000	0.000
	14	0.358	33.15	221.695	5.401	0.150	0.054	0.203	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	14	0.313	33.06	224.623	5.414	0.147	0.046	0.193	0.000	0.000	0.000
	14	0.231	26.57	307.203	5.728	0.086	0.020	0.106	0.000	0.000	0.000
	14	0.297	34.31	299.808	5.703	0.114	0.034	0.148	0.000	0.000	0.000
	14	0.203	33.19	235.976	5.464	0.141	0.029	0.169	0.000	0.000	0.000
	14	0.318	31.32	146.636	4.988	0.214	0.068	0.282	0.000	0.000	0.000
Arctium	21	0.155	55.59	310.385	5.738	0.179	0.028	0.207	0.000	0.000	0.000
lappa	21	0.213	104.55	208.267	5.339	0.502	0.107	0.609	0.000	0.000	0.000
	21	0.210	129.2	153.335	5.033	0.843	0.177	1.020	0.000	0.000	0.000
	21	0.154	49.91	194.733	5.272	0.256	0.039	0.296	0.000	0.000	0.000
	21	0.232	125.61	219.867	5.393	0.571	0.132	0.704	0.000	0.000	0.000
	21	0.214	100.79	183.689	5.213	0.549	0.118	0.666	0.000	0.000	0.000
	21	0.265	141.36	188.883	5.241	0.748	0.198	0.947	0.000	0.000	0.000
	21	0.278	133.36	190.978	5.252	0.698	0.194	0.893	0.000	0.000	0.000
	21	0.251	115.72	193.060	5.263	0.599	0.151	0.750	0.000	0.000	0.000
	21	0.190	87.98	233.183	5.452	0.377	0.072	0.449	0.000	0.000	0.000
	21	0.150	57.25	224.246	5.413	0.255	0.038	0.294	0.000	0.000	0.000
	21	0.111	103.7	189.303	5.243	0.548	0.061	0.609	0.000	0.000	0.000
Arctium	28	0.238	144.87	219.002	5.389	0.662	0.157	0.819	0.000	0.000	0.000
lappa	28	0.241	66.08	331.228	5.803	0.200	0.048	0.248	0.000	0.000	0.000
	28	0.231	134.22	223.887	5.411	0.600	0.138	0.738	0.000	0.000	0.000
	28	0.264	154.29	254.562	5.540	0.606	0.160	0.766	0.000	0.000	0.000
	28	0.251	196.12	212.458	5.359	0.923	0.232	1.155	0.000	0.000	0.000
	28	0.198	57.12	277.956	5.627	0.206	0.041	0.246	0.000	0.000	0.000
	28	0.266	94.88	401.354	5.995	0.236	0.063	0.299	0.000	0.000	0.000
	28	0.290	69.13	216.981	5.380	0.319	0.092	0.411	0.000	0.000	0.000
	28	0.456	29.75	634.328	6.453	0.047	0.021	0.068	0.000	0.000	0.000
	28	0.226	118.24	201.294	5.305	0.587	0.133	0.720	0.000	0.000	0.000
Arctium	35	0.714	294.56	159.480	5.072	1.847	0.649	2.496	0.000	0.000	0.000
lappa	35	0.209	321.46	170.319	5.138	1.887	0.394	2.282	0.000	0.000	0.000
	35	0.224	475.38	158.613	5.066	2.997	0.672	3.669	0.000	0.000	0.000
	35	0.214	386.33	148.138	4.998	2.608	0.558	3.166	0.000	0.000	0.000
	35	0.288	319.51	172.076	5.148	1.857	0.535	2.391	0.000	0.000	0.000
	35	0.514	207.2	107.553	4.678	1.927	0.991	2.917	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	35	0.506	307.65	124.419	4.824	2.473	1.252	3.724	0.000	0.000	0.000
	35	0.346	193.8	120.253	4.790	1.612	0.557	2.169	0.000	0.000	0.000
	35	0.475	118.07	105.354	4.657	1.121	0.532	1.653	0.000	0.000	0.000
	35	0.377	137.5	219.473	5.391	0.627	0.236	0.863	0.000	0.000	0.000
Arctium	14	0.432	16.16	245.967	5.505	0.066	0.028	0.094	0.000	0.000	0.000
minus	14	0.517	9.98	225.282	5.417	0.044	0.023	0.067	0.000	0.000	0.000
	14	0.331	14.82	226.953	5.425	0.065	0.022	0.087	0.000	0.000	0.000
	14	0.610	12.66	314.144	5.750	0.040	0.025	0.065	0.000	0.000	0.000
	14	0.339	23.21	204.134	5.319	0.114	0.039	0.152	0.000	0.000	0.000
	14	0.569	7.42	248.161	5.514	0.030	0.017	0.047	0.000	0.000	0.000
	14	0.390	5.13	298.256	5.698	0.017	0.007	0.024	0.000	0.000	0.000
	14	0.354	8.02	257.878	5.552	0.031	0.011	0.042	0.000	0.000	0.000
	14	0.343	4.5	195.652	5.276	0.023	0.008	0.031	0.000	0.000	0.000
	14	0.313	17.35	231.025	5.443	0.075	0.024	0.099	0.000	0.000	0.000
	14	0.273	3.89	121.944	4.804	0.032	0.009	0.041	0.000	0.000	0.000
	14	0.153	3.67	87.799	4.475	0.042	0.006	0.048	0.000	0.000	0.000
	14	0.332	15.89	286.306	5.657	0.056	0.018	0.074	0.000	0.000	0.000
Arctium	21	0.531	16.2	141.485	4.952	0.115	0.061	0.175	0.000	0.000	0.000
minus	21	0.632	19.63	116.223	4.756	0.169	0.107	0.276	0.000	0.000	0.000
	21	0.640	18.56	180.369	5.195	0.103	0.066	0.169	0.000	0.000	0.000
	21	0.371	15.28	145.663	4.981	0.105	0.039	0.144	0.000	0.000	0.000
	21	0.172	32.22	149.443	5.007	0.216	0.037	0.253	0.000	0.000	0.000
	21	0.772	15.64	149.094	5.005	0.105	0.081	0.186	0.000	0.000	0.000
	21	0.650	22.04	226.051	5.421	0.098	0.063	0.161	0.000	0.000	0.000
	21	0.307	9	111.386	4.713	0.081	0.025	0.106	0.000	0.000	0.000
	21	0.642	21.12	214.852	5.370	0.098	0.063	0.161	0.000	0.000	0.000
	21	0.725	28.63	204.793	5.322	0.140	0.101	0.241	0.000	0.000	0.000
	21	0.527	14.68	227.597	5.428	0.065	0.034	0.099	0.000	0.000	0.000
	21	2.496	34.69	202.984	5.313	0.171	0.427	0.597	0.000	0.000	0.000
Arctium	28	0.513	53.24	161.089	5.082	0.331	0.170	0.500	0.000	0.000	0.000
minus	28	0.640	50.38	146.241	4.985	0.345	0.220	0.565	0.000	0.000	0.000
	28	0.694	64.97	149.597	5.008	0.434	0.301	0.736	0.000	0.000	0.000
	28	0.522	49.34	168.052	5.124	0.294	0.153	0.447	0.000	0.000	0.000
	28	0.704	27.13	78.981	4.369	0.344	0.242	0.585	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	28	0.821	36.61	106.301	4.666	0.344	0.283	0.627	0.000	0.000	0.000
	28	0.824	54.66	139.119	4.935	0.393	0.324	0.717	0.000	0.000	0.000
	28	0.588	37.89	94.560	4.549	0.401	0.236	0.636	0.000	0.000	0.000
	28	0.561	26.4	129.348	4.863	0.204	0.115	0.319	0.000	0.000	0.000
	28	0.508	32.84	118.642	4.776	0.277	0.141	0.418	0.000	0.000	0.000
	28	0.309	25.49	125.074	4.829	0.204	0.063	0.267	0.000	0.000	0.000
	28	0.406	24.67	144.269	4.972	0.171	0.070	0.241	0.000	0.000	0.000
Arctium	35	0.606	303.98	133.835	4.897	2.271	1.376	3.647	0.000	0.000	0.000
minus	35	0.426	278.37	147.122	4.991	1.892	0.806	2.698	0.000	0.000	0.000
	35	0.570	177.29	141.289	4.951	1.255	0.715	1.970	0.000	0.000	0.000
	35	0.528	180.19	140.773	4.947	1.280	0.676	1.956	0.000	0.000	0.000
	35	0.516	149.03	140.224	4.943	1.063	0.548	1.611	0.000	0.000	0.000
	35	0.726	102.23	171.096	5.142	0.598	0.434	1.031	0.000	0.000	0.000
	35	1.020	91.86	141.367	4.951	0.650	0.663	1.312	0.000	0.000	0.000
	35	0.583	78.3	145.864	4.983	0.537	0.313	0.850	0.000	0.000	0.000
Artemisia	14	0.393	10.65	184.160	5.216	0.058	0.023	0.081	0.000	0.000	0.000
vulgaris	14	0.558	15.58	257.011	5.549	0.061	0.034	0.094	0.000	0.000	0.000
	14	0.447	8.09	252.971	5.533	0.032	0.014	0.046	0.000	0.000	0.000
	14	0.494	6.05	307.888	5.730	0.020	0.010	0.029	0.000	0.000	0.000
	14	0.493	12.84	313.094	5.747	0.041	0.020	0.061	0.000	0.000	0.000
	14	0.410	15.15	323.787	5.780	0.047	0.019	0.066	0.000	0.000	0.000
	14	0.343	10.97	316.503	5.757	0.035	0.012	0.047	0.000	0.000	0.000
	14	0.505	13.26	259.796	5.560	0.051	0.026	0.077	0.000	0.000	0.000
	14	0.348	6.08	1321.739	7.187	0.005	0.002	0.006	0.000	0.000	0.000
	14	1.273	4.39	1995.455	7.599	0.002	0.003	0.005	0.000	0.000	0.000
Artemisia	21	0.313	19.37	481.841	6.178	0.040	0.013	0.061	0.009	0.000	0.000
vulgaris	21	0.344	28.91	381.398	5.944	0.076	0.026	0.114	0.012	0.000	0.000
	21	0.359	35.16	360.246	5.887	0.098	0.035	0.146	0.014	0.000	0.000
	21	0.264	31.29	365.965	5.903	0.086	0.023	0.118	0.010	0.000	0.000
	21	0.337	18.13	370.757	5.916	0.049	0.017	0.072	0.007	0.000	0.000
	21	0.371	75.93	340.341	5.830	0.223	0.083	0.340	0.035	0.000	0.000
	21	0.292	25.51	493.424	6.201	0.052	0.015	0.073	0.006	0.000	0.000
	21	0.244	14.66	384.777	5.953	0.038	0.009	0.051	0.004	0.000	0.000
	21	0.494	13.02	329.620	5.798	0.040	0.020	0.063	0.004	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	21	0.297	19.01	346.898	5.849	0.055	0.016	0.075	0.004	0.000	0.000
Artemisia	28	0.384	107.69	284.068	5.649	0.379	0.146	0.683	0.158	0.000	0.000
vulgaris	28	0.400	129.08	391.745	5.971	0.330	0.132	0.544	0.083	0.000	0.000
	28	0.412	55.37	457.603	6.126	0.121	0.050	0.179	0.008	0.000	0.000
	28	0.407	25.42	688.889	6.535	0.037	0.015	0.060	0.008	0.000	0.000
	28	0.409	275.27	384.778	5.953	0.715	0.293	1.182	0.174	0.000	0.000
	28	0.332	181.39	465.580	6.143	0.390	0.129	0.680	0.161	0.000	0.000
	28	0.302	223.37	449.799	6.109	0.497	0.150	0.822	0.175	0.000	0.000
	28	0.549	40.6	183.794	5.214	0.221	0.121	0.448	0.106	0.000	0.000
	28	0.330	20.83	185.320	5.222	0.112	0.037	0.202	0.053	0.000	0.000
	28	0.703	108.03	250.708	5.524	0.431	0.303	0.933	0.199	0.000	0.000
	28	0.511	76.5	282.601	5.644	0.271	0.138	0.506	0.096	0.000	0.000
	28	0.722	226.75	365.078	5.900	0.621	0.448	1.572	0.502	0.000	0.000
	28	1.377	178.19	449.068	6.107	0.397	0.547	1.474	0.531	0.000	0.000
	28	0.449	142.97	226.040	5.421	0.633	0.284	1.382	0.466	0.000	0.000
Artemisia	35	0.735	423.39	325.434	5.785	1.301	0.957	3.663	1.406	0.000	0.000
vulgaris	35	0.682	622.46	370.777	5.916	1.679	1.145	4.926	2.102	0.000	0.000
	35	0.413	524.18	302.417	5.712	1.733	0.716	3.972	1.523	0.000	0.000
	35	0.889	499.34	344.206	5.841	1.451	1.290	4.857	2.117	0.000	0.000
	35	0.663	280.98	265.000	5.580	1.060	0.703	2.536	0.772	0.000	0.000
	35	1.011	174.19	220.076	5.394	0.792	0.800	2.212	0.621	0.000	0.000
	35	0.695	159.27	195.952	5.278	0.813	0.565	1.955	0.577	0.000	0.000
	35	0.862	210.46	208.665	5.341	1.009	0.870	2.270	0.392	0.000	0.000
	35	0.782	229.00	253.937	5.537	0.902	0.705	2.262	0.655	0.000	0.000
Bidens	14	0.409	14.21	264.028	5.576	0.054	0.013	0.022	0.013	0.000	0.000
cernua	14	0.448	15.48	360.923	5.889	0.043	0.008	0.019	0.008	0.000	0.000
	14	0.518	11.71	233.360	5.453	0.050	0.009	0.026	0.009	0.000	0.000
	14	0.340	13.94	252.125	5.530	0.055	0.010	0.019	0.010	0.000	0.000
	14	0.370	22.36	251.151	5.526	0.089	0.020	0.033	0.020	0.000	0.000
	14	0.353	13.75	311.368	5.741	0.044	0.011	0.016	0.011	0.000	0.000
	14	0.250	16.26	325.070	5.784	0.050	0.011	0.013	0.011	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	14	0.285	14.04	435.079	6.076	0.032	0.006	0.009	0.006	0.000	0.000
	14	0.382	18.88	246.250	5.506	0.077	0.016	0.029	0.016	0.000	0.000
	14	0.309	26.05	276.041	5.621	0.094	0.029	0.029	0.029	0.000	0.000
Bidens	21	0.347	46.84	379.271	5.938	0.124	0.043	0.221	0.055	0.000	0.000
cernua	21	0.315	81.7	349.593	5.857	0.234	0.074	0.394	0.087	0.000	0.000
	21	0.321	66.05	336.990	5.820	0.196	0.063	0.319	0.060	0.000	0.000
	21	0.295	62.38	425.222	6.053	0.147	0.043	0.249	0.059	0.000	0.000
	21	0.462	52.03	320.777	5.771	0.162	0.075	0.293	0.055	0.000	0.000
	21	0.412	88.61	375.148	5.927	0.236	0.097	0.429	0.095	0.000	0.000
	21	0.634	47.94	400.836	5.994	0.120	0.076	0.239	0.044	0.000	0.000
	21	0.284	84.52	384.357	5.952	0.220	0.063	0.373	0.091	0.000	0.000
	21	0.221	69.98	411.163	6.019	0.170	0.038	0.279	0.071	0.000	0.000
	21	0.306	101.16	276.016	5.620	0.367	0.112	0.599	0.121	0.000	0.000
Bidens	28	0.373	71.8	484.480	6.183	0.148	0.055	0.326	0.122	0.000	0.000
cernua	28	0.448	61.55	333.243	5.809	0.185	0.083	0.312	0.045	0.000	0.000
	28	0.278	32.99	552.596	6.315	0.060	0.017	0.108	0.031	0.000	0.000
	28	0.648	63.7	512.470	6.239	0.124	0.081	0.273	0.068	0.000	0.000
	28	0.163	135.62	474.528	6.162	0.286	0.047	0.509	0.177	0.000	0.000
	28	0.420	68.19	369.393	5.912	0.185	0.078	0.352	0.090	0.000	0.000
	28	0.538	3.49	32.739	3.489	0.107	0.057	0.223	0.059	0.000	0.000
	28	0.559	225.82	376.367	5.931	0.600	0.335	1.226	0.291	0.000	0.000
	28	0.882	89.54	517.872	6.250	0.173	0.153	0.467	0.142	0.000	0.000
	28	0.390	148.87	430.883	6.066	0.346	0.135	0.720	0.240	0.000	0.000
	28	0.418	71.58	342.980	5.838	0.209	0.087	0.353	0.057	0.000	0.000
	28	0.376	32.91	578.383	6.360	0.057	0.021	0.103	0.025	0.000	0.000
	28	0.419	44.31	539.708	6.291	0.082	0.034	0.141	0.025	0.000	0.000
Bidens	35	0.427	192.71	277.880	5.627	0.694	0.296	1.361	0.371	0.000	0.000
cernua	35	0.740	195.47	326.709	5.789	0.598	0.443	1.395	0.354	0.000	0.000
	35	0.583	402.02	345.794	5.846	1.163	0.678	2.498	0.657	0.000	0.000
	35	0.680	149.08	296.500	5.692	0.503	0.342	1.138	0.293	0.000	0.000
	35	0.316	139.21	368.378	5.909	0.378	0.120	0.873	0.376	0.000	0.000
	35	0.424	80.75	358.570	5.882	0.225	0.095	0.500	0.180	0.000	0.000
	35	0.466	80.52	375.910	5.929	0.214	0.100	0.446	0.132	0.000	0.000
	35	0.690	337.51	328.861	5.796	1.026	0.709	2.471	0.736	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	35	0.985	270.3	371.036	5.916	0.729	0.718	1.886	0.440	0.000	0.000
	35	0.693	153.87	420.985	6.043	0.366	0.253	0.927	0.308	0.000	0.000
	35	0.798	156.22	384.116	5.951	0.407	0.325	1.031	0.300	0.000	0.000
	35	0.355	143.92	302.544	5.712	0.476	0.169	0.778	0.133	0.000	0.000
Bidens	14	0.442	105.53	276.851	5.623	0.381	0.169	0.636	0.086	0.000	0.000
frondosa	14	0.293	102.79	243.365	5.495	0.422	0.124	0.654	0.108	0.000	0.000
	14	0.393	90.57	233.928	5.455	0.387	0.152	0.648	0.108	0.000	0.000
	14	0.324	77.17	295.308	5.688	0.261	0.085	0.408	0.062	0.000	0.000
	14	0.423	85.98	292.260	5.678	0.294	0.125	0.491	0.073	0.000	0.000
	14	0.399	125.67	280.670	5.637	0.448	0.179	0.752	0.125	0.000	0.000
	14	0.217	83.93	273.352	5.611	0.307	0.067	0.454	0.081	0.000	0.000
	14	0.402	101.13	238.537	5.475	0.424	0.171	0.696	0.101	0.000	0.000
	14	0.338	92.51	248.342	5.515	0.373	0.126	0.569	0.070	0.000	0.000
	14	0.541	78.94	213.196	5.362	0.370	0.200	0.661	0.090	0.000	0.000
Bidens	21	0.520	782.2	291.713	5.676	2.681	1.395	5.859	1.782	0.000	0.000
frondosa	21	0.557	514.95	280.016	5.635	1.839	1.024	3.921	1.058	0.000	0.000
	21	0.642	949.59	286.599	5.658	3.313	2.128	7.813	2.371	0.000	0.000
	21	0.318	401.53	323.528	5.779	1.241	0.394	2.392	0.756	0.000	0.000
	21	0.431	689.87	350.775	5.860	1.967	0.849	3.980	1.165	0.000	0.000
	21	0.298	928.23	311.811	5.742	2.977	0.888	5.683	1.818	0.000	0.000
	21	0.296	621.76	279.280	5.632	2.226	0.659	4.247	1.362	0.000	0.000
	21	0.456	783.5	341.975	5.835	2.291	1.045	4.927	1.591	0.000	0.000
	21	0.363	2243.31	849.546	6.745	2.641	0.959	5.545	1.945	0.000	0.000
	21	0.429	765.25	290.981	5.673	2.630	1.128	5.345	1.587	0.000	0.000
	21	0.368	1009.77	321.245	5.772	3.143	1.155	6.181	1.882	0.000	0.000
Bidens	28	0.674	1904.68	352.151	5.864	5.409	3.645	15.990	6.936	0.000	0.000
frondosa	28	0.779	1383.85	408.698	6.013	3.386	2.637	11.120	5.097	0.000	0.000
	28	0.692	2488.73	466.640	6.146	5.333	3.691	16.649	7.625	0.000	0.000
	28	0.562	1959.96	455.974	6.122	4.298	2.414	12.563	5.850	0.000	0.000
	28	0.480	1750.93	426.266	6.055	4.108	1.970	8.659	2.581	0.000	0.000
	28	1.373	2120.29	435.315	6.076	4.871	6.687	19.606	8.049	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	28	0.893	1939.86	482.937	6.180	4.017	3.586	13.814	6.212	0.000	0.000
	28	0.719	1654.52	521.043	6.256	3.175	2.282	9.711	4.254	0.000	0.000
	28	0.579	1734.59	487.436	6.189	3.559	2.062	10.052	4.432	0.000	0.000
	28	0.639	2614.52	508.760	6.232	5.139	3.286	16.195	7.770	0.000	0.000
	28	0.663	1854.38	497.073	6.209	3.731	2.474	11.316	5.112	0.000	0.000
	28	0.933	732.15	343.024	5.838	2.134	1.991	7.063	2.937	0.000	0.000
	28	0.861	1631.84	406.882	6.009	4.011	3.454	12.260	4.795	0.000	0.000
	28	0.993	1660.99	357.510	5.879	4.646	4.612	16.489	7.231	0.000	0.000
	28	1.042	2157.15	451.835	6.113	4.774	4.976	15.698	5.947	0.000	0.000
Bidens	35	0.780	4330.56	323.224	5.778	13.398	10.446	42.503	18.659	0.000	0.000
frondosa	35	0.626	3188.23	302.575	5.712	10.537	6.598	28.535	11.400	0.000	0.000
	35	0.528	3462.67	294.170	5.684	11.771	6.219	31.764	13.774	0.000	0.000
	35	0.668	3787.99	290.067	5.670	13.059	8.722	39.254	17.473	0.000	0.000
	35	0.674	3752.54	286.192	5.657	13.112	8.840	37.646	15.694	0.000	0.000
Centaurea	14	1.098	0.076	18.537	2.920	0.004	0.005	0.009	0.000	0.000	0.000
nigra	14	0.746	0.044	7.458	2.009	0.006	0.004	0.010	0.000	0.000	0.000
	14	0.634	0.052	6.341	1.847	0.008	0.005	0.013	0.000	0.000	0.000
Centaurea	21	0.902	2.43	158.824	5.068	0.015	0.014	0.029	0.000	0.000	0.000
nigra	21	0.284	2.91	142.647	4.960	0.020	0.006	0.026	0.000	0.000	0.000
	21	0.595	1.8	227.848	5.429	0.008	0.005	0.013	0.000	0.000	0.000
	21	0.216	1.49	97.386	4.579	0.015	0.003	0.019	0.000	0.000	0.000
	21	0.636	1.59	206.494	5.330	0.008	0.005	0.013	0.000	0.000	0.000
	21	0.662	3.31	162.255	5.089	0.020	0.014	0.034	0.000	0.000	0.000
	21	0.376	3.94	187.619	5.234	0.021	0.008	0.029	0.000	0.000	0.000
	21	0.400	2.62	134.359	4.901	0.020	0.008	0.027	0.000	0.000	0.000
	21	0.227	2.69	174.675	5.163	0.015	0.004	0.019	0.000	0.000	0.000
	21	0.260	3.19	180.226	5.194	0.018	0.005	0.022	0.000	0.000	0.000
	21	0.364	2.66	164.198	5.101	0.016	0.006	0.022	0.000	0.000	0.000
	21	0.372	3.12	109.474	4.696	0.029	0.011	0.039	0.000	0.000	0.000
Centaurea	28	0.387	13.76	171.785	5.146	0.080	0.031	0.111	0.000	0.000	0.000
nigra	28	0.281	13.06	237.887	5.472	0.055	0.015	0.070	0.000	0.000	0.000
	28	0.432	7.19	171.599	5.145	0.042	0.018	0.060	0.000	0.000	0.000
	28	0.456	12.49	225.045	5.416	0.056	0.025	0.081	0.000	0.000	0.000
	28	0.296	13.23	196.582	5.281	0.067	0.020	0.087	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	28	0.886	17.85	259.825	5.560	0.069	0.061	0.130	0.000	0.000	0.000
	28	0.499	7.8	180.974	5.198	0.043	0.022	0.065	0.000	0.000	0.000
	28	0.324	4.2	143.345	4.965	0.029	0.010	0.039	0.000	0.000	0.000
	28	0.344	17.35	137.589	4.924	0.126	0.043	0.170	0.000	0.000	0.000
Centaurea	35	0.306	7.1	84.423	4.436	0.084	0.026	0.110	0.000	0.000	0.000
nigra	35	0.345	49.61	167.658	5.122	0.296	0.102	0.398	0.000	0.000	0.000
	35	0.576	33.64	181.152	5.199	0.186	0.107	0.293	0.000	0.000	0.000
	35	0.457	41.21	161.102	5.082	0.256	0.117	0.373	0.000	0.000	0.000
	35	0.445	19.35	206.952	5.332	0.094	0.042	0.135	0.000	0.000	0.000
	35	0.570	34.44	186.062	5.226	0.185	0.106	0.291	0.000	0.000	0.000
	35	0.458	26.55	154.630	5.041	0.172	0.079	0.250	0.000	0.000	0.000
	35	0.504	21.24	178.638	5.185	0.119	0.060	0.179	0.000	0.000	0.000
	35	0.404	28.66	166.919	5.118	0.172	0.069	0.241	0.000	0.000	0.000
	35	0.441	14.4	116.035	4.754	0.124	0.055	0.179	0.000	0.000	0.000
	35	0.389	15.48	148.134	4.998	0.105	0.041	0.145	0.000	0.000	0.000
	35	0.315	34.76	146.977	4.990	0.237	0.075	0.311	0.000	0.000	0.000
	35	0.386	15.69	193.704	5.266	0.081	0.031	0.112	0.000	0.000	0.000
Chrysanthemum	14	0.493	8.57	297.569	5.696	0.029	0.014	0.043	0.000	0.000	0.000
leucanthemum	14	0.328	8.48	487.356	6.189	0.017	0.006	0.023	0.000	0.000	0.000
	14	0.383	9.04	298.350	5.698	0.030	0.012	0.042	0.000	0.000	0.000
	14	0.454	0.83	38.426	3.649	0.022	0.010	0.031	0.000	0.000	0.000
	14	0.370	1.27	117.593	4.767	0.011	0.004	0.015	0.000	0.000	0.000
	14	0.735	0.77	58.333	4.066	0.013	0.010	0.023	0.000	0.000	0.000
	14	0.809	0.68	100.000	4.605	0.007	0.006	0.012	0.000	0.000	0.000
	14	0.745	0.94	85.455	4.448	0.011	0.008	0.019	0.000	0.000	0.000
	14	0.313	0.73	76.042	4.331	0.010	0.003	0.013	0.000	0.000	0.000
	14	0.074	0.67	70.526	4.256	0.010	0.001	0.010	0.000	0.000	0.000
Chrysanthemum	21	0.172	14.24	445.000	6.098	0.032	0.006	0.038	0.000	0.000	0.000
leucanthemum	21	0.192	12.16	805.298	6.691	0.015	0.003	0.018	0.000	0.000	0.000
	21	0.414	11.29	719.108	6.578	0.016	0.007	0.022	0.000	0.000	0.000
	21	0.169	7.49	841.573	6.735	0.009	0.002	0.010	0.000	0.000	0.000
	21	0.174	8.77	762.609	6.637	0.012	0.002	0.014	0.000	0.000	0.000
	21	0.470	11.81	349.408	5.856	0.034	0.016	0.050	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	21	0.128	10.7	371.528	5.918	0.029	0.004	0.033	0.000	0.000	0.000
	21	0.303	10.44	632.727	6.450	0.017	0.005	0.022	0.000	0.000	0.000
	21	0.200	8.83	346.275	5.847	0.033	0.011	0.044	0.000	0.000	0.000
	21	0.425	8.07	128.914	4.859	0.063	0.027	0.089	0.000	0.000	0.000
	21	0.535	8.15	375.576	5.928	0.022	0.012	0.033	0.000	0.000	0.000
	21	0.375	7.35	316.810	5.758	0.023	0.009	0.032	0.000	0.000	0.000
Chrysanthemum	28	0.254	16.97	341.449	5.833	0.050	0.013	0.062	0.000	0.000	0.000
leucanthemum	28	0.253	16.65	409.091	6.014	0.041	0.010	0.051	0.000	0.000	0.000
	28	0.312	37.02	337.774	5.822	0.110	0.034	0.144	0.000	0.000	0.000
	28	0.508	15.77	476.435	6.166	0.033	0.017	0.050	0.000	0.000	0.000
	28	0.201	22.48	490.830	6.196	0.046	0.009	0.055	0.000	0.000	0.000
	28	0.330	33.27	346.202	5.847	0.096	0.032	0.128	0.000	0.000	0.000
	28	0.427	24.72	289.123	5.667	0.086	0.037	0.122	0.000	0.000	0.000
	28	0.399	20.99	297.309	5.695	0.071	0.028	0.099	0.000	0.000	0.000
	28	0.404	21.45	233.406	5.453	0.092	0.037	0.129	0.000	0.000	0.000
	28	0.517	17.12	286.288	5.657	0.060	0.031	0.091	0.000	0.000	0.000
	28	0.309	17.74	290.344	5.671	0.061	0.019	0.080	0.000	0.000	0.000
	28	0.190	32.24	386.108	5.956	0.084	0.016	0.099	0.000	0.000	0.000
	28	0.317	19.18	506.069	6.227	0.038	0.012	0.050	0.000	0.000	0.000
Chrysanthemum	35	0.354	54.7	127.357	4.847	0.430	0.152	0.582	0.000	0.000	0.000
leucanthemum	35	0.368	31.77	143.847	4.969	0.221	0.081	0.302	0.000	0.000	0.000
	35	0.358	29.38	138.064	4.928	0.213	0.076	0.289	0.000	0.000	0.000
	35	0.239	82.74	103.762	4.642	0.797	0.190	1.015	0.027	0.000	0.000
	35	0.020	88.55	115.510	4.749	0.767	0.016	0.849	0.067	0.000	0.000
	35	0.216	105.2	111.986	4.718	0.939	0.203	1.176	0.033	0.000	0.000
	35	0.396	114.21	133.845	4.897	0.853	0.338	1.222	0.030	0.000	0.000
	35	0.476	70.49	191.601	5.255	0.368	0.175	0.553	0.009	0.000	0.000
	35	0.343	29.01	171.353	5.144	0.169	0.058	0.227	0.000	0.000	0.000
	35	0.493	39.59	164.479	5.103	0.241	0.119	0.359	0.000	0.000	0.000
	35	0.484	38.24	143.759	4.968	0.266	0.129	0.409	0.014	0.000	0.000
	35	0.278	18.97	111.131	4.711	0.171	0.047	0.218	0.000	0.000	0.000
	35	0.172	31.57	269.139	5.595	0.117	0.020	0.138	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
Cichorium	14	0.478	7.15	178.750	5.186	0.040	0.019	0.059	0.000	0.000	0.000
intybus	14	0.257	5.2	171.053	5.142	0.030	0.008	0.038	0.000	0.000	0.000
	14	0.273	1.72	156.364	5.052	0.011	0.003	0.014	0.000	0.000	0.000
	14	0.427	2.9	145.729	4.982	0.020	0.009	0.028	0.000	0.000	0.000
	14	0.360	1.7	136.000	4.913	0.013	0.005	0.017	0.000	0.000	0.000
	14	0.605	2.69	166.049	5.112	0.016	0.010	0.026	0.000	0.000	0.000
	14	0.424	1.67	181.522	5.201	0.009	0.004	0.013	0.000	0.000	0.000
	14	0.178	1.01	138.356	4.930	0.007	0.001	0.009	0.000	0.000	0.000
	14	0.452	6.48	281.739	5.641	0.023	0.010	0.033	0.000	0.000	0.000
	14	0.541	5.84	166.382	5.114	0.035	0.019	0.054	0.000	0.000	0.000
	14	0.451	14.84	262.655	5.571	0.057	0.026	0.082	0.000	0.000	0.000
	14	0.464	2.1	187.500	5.234	0.011	0.005	0.016	0.000	0.000	0.000
	14	0.379	14.52	329.252	5.797	0.044	0.017	0.061	0.000	0.000	0.000
Cichorium	21	0.375	56.98	332.536	5.807	0.171	0.064	0.236	0.000	0.000	0.000
intybus	21	0.506	53.75	277.105	5.624	0.194	0.098	0.292	0.000	0.000	0.000
	21	0.408	29.99	313.211	5.747	0.096	0.039	0.135	0.000	0.000	0.000
	21	0.749	22.12	234.969	5.459	0.094	0.071	0.165	0.000	0.000	0.000
	21	0.790	56.57	368.823	5.910	0.153	0.121	0.275	0.000	0.000	0.000
	21	0.504	30.32	294.856	5.686	0.103	0.052	0.155	0.000	0.000	0.000
	21	0.353	31.58	348.642	5.854	0.091	0.032	0.123	0.000	0.000	0.000
	21	0.468	35.49	310.825	5.739	0.114	0.053	0.168	0.000	0.000	0.000
	21	0.309	42.54	329.895	5.799	0.129	0.040	0.169	0.000	0.000	0.000
	21	0.627	33.81	264.017	5.576	0.128	0.080	0.208	0.000	0.000	0.000
	21	0.544	36.41	318.019	5.762	0.114	0.062	0.177	0.000	0.000	0.000
	21	0.290	23.55	370.866	5.916	0.064	0.018	0.082	0.000	0.000	0.000
Cichorium	28	0.201	71.86	333.148	5.809	0.216	0.043	0.259	0.000	0.000	0.000
intybus	28	0.188	80.19	366.164	5.903	0.219	0.041	0.260	0.000	0.000	0.000
	28	0.277	116.06	332.645	5.807	0.349	0.097	0.446	0.000	0.000	0.000
	28	0.210	151.56	333.980	5.811	0.454	0.095	0.549	0.000	0.000	0.000
	28	0.305	95.57	353.701	5.868	0.270	0.082	0.353	0.000	0.000	0.000
	28	0.172	60.59	302.195	5.711	0.201	0.034	0.235	0.000	0.000	0.000
	28	0.307	178.36	234.962	5.459	0.759	0.233	0.992	0.000	0.000	0.000
	28	0.178	79.14	312.189	5.744	0.254	0.045	0.299	0.000	0.000	0.000
	28	0.158	85.04	449.947	6.109	0.189	0.030	0.219	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	28	0.237	76.38	411.974	6.021	0.185	0.044	0.229	0.000	0.000	0.000
	28	0.333	40.42	946.604	6.853	0.043	0.014	0.057	0.000	0.000	0.000
	28	0.276	48.72	487.688	6.190	0.100	0.028	0.128	0.000	0.000	0.000
Cichorium	35	0.317	144.9	359.821	5.886	0.403	0.128	0.530	0.000	0.000	0.000
intybus	35	0.348	92.32	489.242	6.193	0.189	0.066	0.254	0.000	0.000	0.000
	35	0.209	169.18	410.731	6.018	0.412	0.086	0.498	0.000	0.000	0.000
	35	0.257	248.84	460.900	6.133	0.540	0.139	0.679	0.000	0.000	0.000
	35	0.196	286.79	327.835	5.793	0.875	0.171	1.046	0.000	0.000	0.000
	35	1.193	76.79	368.297	5.909	0.209	0.249	0.457	0.000	0.000	0.000
	35	0.347	75.05	648.660	6.475	0.116	0.040	0.156	0.000	0.000	0.000
	35	0.595	79.12	226.900	5.425	0.349	0.208	0.556	0.000	0.000	0.000
	35	0.464	112.81	114.668	4.742	0.984	0.457	1.440	0.000	0.000	0.000
	35	0.486	136.87	163.622	5.098	0.837	0.407	1.243	0.000	0.000	0.000
	35	0.412	175.3	205.221	5.324	0.854	0.352	1.206	0.000	0.000	0.000
Cirsium	14	0.164	23.1	130.324	4.870	0.177	0.029	0.206	0.000	0.000	0.000
arvense	14	0.167	22.64	259.722	5.560	0.087	0.015	0.102	0.000	0.000	0.000
	14	0.339	18.12	204.261	5.319	0.089	0.030	0.119	0.000	0.000	0.000
	14	0.353	11.35	207.761	5.336	0.055	0.019	0.074	0.000	0.000	0.000
	14	0.167	14.33	197.928	5.288	0.072	0.012	0.085	0.000	0.000	0.000
	14	0.205	11.7	155.111	5.044	0.075	0.016	0.091	0.000	0.000	0.000
	14	0.339	18.12	211.707	5.355	0.086	0.029	0.115	0.000	0.000	0.000
	14	0.235	20.13	205.555	5.326	0.098	0.023	0.121	0.000	0.000	0.000
	14	0.249	24.81	175.212	5.166	0.142	0.035	0.177	0.000	0.000	0.000
	14	0.284	17.24	186.439	5.228	0.092	0.026	0.119	0.000	0.000	0.000
	14	0.239	17.61	220.456	5.396	0.080	0.019	0.099	0.000	0.000	0.000
	14	0.186	20.64	260.969	5.564	0.079	0.015	0.094	0.000	0.000	0.000
Cirsium	21	0.174	79.98	249.159	5.518	0.321	0.056	0.377	0.000	0.000	0.000
arvense	21	0.218	57.27	232.994	5.451	0.246	0.054	0.299	0.000	0.000	0.000
	21	0.230	41.22	241.760	5.488	0.171	0.039	0.210	0.000	0.000	0.000
	21	0.116	110.83	342.174	5.835	0.324	0.038	0.362	0.000	0.000	0.000
	21	0.189	37.04	265.520	5.582	0.140	0.026	0.166	0.000	0.000	0.000
	21	0.125	87.21	347.312	5.850	0.251	0.032	0.283	0.000	0.000	0.000
	21	0.151	46.97	362.703	5.894	0.130	0.020	0.149	0.000	0.000	0.000
	21	0.115	32.79	376.897	5.932	0.087	0.010	0.097	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	21	0.229	103.57	279.089	5.632	0.371	0.085	0.456	0.000	0.000	0.000
	21	0.103	68.7	337.924	5.823	0.203	0.021	0.224	0.000	0.000	0.000
	21	0.123	63.53	326.297	5.788	0.195	0.024	0.219	0.000	0.000	0.000
	21	0.111	75.98	304.285	5.718	0.250	0.028	0.277	0.000	0.000	0.000
Cirsium	28	0.293	36.45	583.200	6.369	0.063	0.018	0.081	0.000	0.000	0.000
arvense	28	0.172	167.36	287.511	5.661	0.582	0.100	0.682	0.000	0.000	0.000
	28	0.169	74.58	354.974	5.872	0.210	0.036	0.304	0.058	0.000	0.000
	28	0.238	104.2	432.365	6.069	0.241	0.057	0.348	0.050	0.000	0.000
	28	0.220	163.22	409.175	6.014	0.399	0.088	0.487	0.000	0.000	0.000
	28	0.414	148.32	267.677	5.590	0.554	0.230	0.784	0.000	0.000	0.000
	28	0.297	22.47	647.550	6.473	0.035	0.010	0.045	0.000	0.000	0.000
	28	0.213	137.29	499.055	6.213	0.275	0.059	0.334	0.000	0.000	0.000
	28	0.184	135.97	425.172	6.052	0.320	0.059	0.442	0.063	0.000	0.000
	28	0.317	78.6	580.074	6.363	0.136	0.043	0.265	0.086	0.000	0.000
	28	0.157	231.48	327.551	5.792	0.707	0.111	0.973	0.155	0.000	0.000
Cirsium	35	0.602	310.41	292.950	5.680	1.060	0.638	2.022	0.325	0.000	0.000
arvense	35	0.259	234.49	262.970	5.572	0.892	0.231	1.156	0.033	0.000	0.000
	35	0.353	158.68	281.797	5.641	0.563	0.199	0.864	0.102	0.000	0.000
	35	0.417	259.07	242.779	5.492	1.067	0.446	1.696	0.183	0.000	0.000
	35	0.173	151.8	211.009	5.352	0.719	0.124	0.844	0.000	0.000	0.000
	35	0.388	289.97	215.928	5.375	1.343	0.521	2.068	0.204	0.000	0.000
	35	0.440	193.9	161.583	5.085	1.200	0.528	1.943	0.215	0.000	0.000
	35	0.474	319.84	286.287	5.657	1.117	0.529	2.218	0.572	0.000	0.000
	35	0.545	272.02	205.453	5.325	1.324	0.722	2.673	0.627	0.000	0.000
	35	0.241	203.06	137.342	4.922	1.479	0.357	2.197	0.361	0.000	0.000
	35	0.589	144.66	192.854	5.262	0.750	0.442	1.378	0.186	0.000	0.000
	35	0.190	72.61	131.278	4.877	0.553	0.105	0.705	0.047	0.000	0.000
Erigeron	14	0.538	4.8	3692.308	8.214	0.001	0.003	0.003	0.000	0.000	0.000
canadensis	14	0.421	4.11	2163.158	7.679	0.002	0.001	0.002	0.000	0.000	0.000
	14	0.471	3.94	2317.647	7.748	0.002	0.001	0.003	0.000	0.000	0.000
	14	0.167	4.35	805.556	6.692	0.005	0.001	0.003	0.000	0.000	0.000
	14	1.500	0.23	383.333	5.949	0.001	0.001	0.006	0.000	0.000	0.000
	14	0.400	0.25	125.000	4.828	0.002	0.001	0.002	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	14	0.889	0.36	200.000	5.298	0.002	0.001	0.003	0.000	0.000	0.000
	14	0.800	0.33	132.000	4.883	0.003	0.002	0.003	0.000	0.000	0.000
Erigeron	21	0.423	10.75	307.143	5.727	0.035	0.002	0.005	0.000	0.000	0.000
canadensis	21	0.263	11.32	419.259	6.038	0.027	0.015	0.050	0.000	0.000	0.000
	21	0.255	6.79	692.857	6.541	0.010	0.007	0.034	0.000	0.000	0.000
	21	0.317	5.6	888.889	6.790	0.006	0.003	0.012	0.000	0.000	0.000
	21	0.470	6.29	629.000	6.444	0.010	0.002	0.008	0.000	0.000	0.000
	21	0.488	5.09	591.860	6.383	0.009	0.005	0.015	0.000	0.000	0.000
	21	1.419	5.23	843.548	6.738	0.006	0.004	0.013	0.000	0.000	0.000
	21	0.242	5.2	1575.758	7.362	0.003	0.009	0.015	0.000	0.000	0.000
	21	0.441	5.74	972.881	6.880	0.006	0.001	0.004	0.000	0.000	0.000
Erigeron	28	0.248	32.03	394.458	5.978	0.081	0.003	0.009	0.000	0.000	0.000
canadensis	28	0.097	7.53	666.372	6.502	0.011	0.020	0.101	0.000	0.000	0.000
	28	0.375	5.87	815.278	6.704	0.007	0.001	0.012	0.000	0.000	0.000
	28	0.947	5.31	2794.737	7.935	0.002	0.003	0.010	0.000	0.000	0.000
	28	0.127	10.65	750.000	6.620	0.014	0.002	0.004	0.000	0.000	0.000
	28	0.269	19.11	872.603	6.771	0.022	0.002	0.016	0.000	0.000	0.000
	28	0.556	0.94	116.049	4.754	0.008	0.006	0.028	0.000	0.000	0.000
	28	0.338	1.62	121.805	4.802	0.013	0.005	0.013	0.000	0.000	0.000
	28	0.568	2.05	132.258	4.885	0.016	0.005	0.018	0.000	0.000	0.000
	28	0.717	4.89	91.745	4.519	0.053	0.009	0.024	0.000	0.000	0.000
	28	0.949	1.81	132.117	4.884	0.014	0.038	0.092	0.000	0.000	0.000
	28	0.628	1.08	78.832	4.367	0.014	0.013	0.027	0.000	0.000	0.000
	28	0.350	11.27	402.500	5.998	0.028	0.009	0.022	0.000	0.000	0.000
Erigeron	35	0.385	44.84	504.387	6.223	0.089	0.034	0.123	0.000	0.000	0.000
canadensis	35	0.520	21.75	621.429	6.432	0.035	0.018	0.053	0.000	0.000	0.000
	35	0.427	36.09	786.275	6.667	0.046	0.020	0.066	0.000	0.000	0.000
	35	0.434	34.1	254.478	5.539	0.134	0.058	0.192	0.000	0.000	0.000
	35	0.849	14.9	281.664	5.641	0.053	0.045	0.098	0.000	0.000	0.000
	35	0.785	21.22	380.287	5.941	0.056	0.044	0.100	0.000	0.000	0.000
	35	0.458	41.92	345.875	5.846	0.121	0.056	0.177	0.000	0.000	0.000
	35	0.682	21.27	381.867	5.945	0.056	0.038	0.094	0.000	0.000	0.000
	35	0.665	18.23	368.283	5.909	0.050	0.033	0.082	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	35	0.489	17.04	137.753	4.925	0.124	0.061	0.184	0.000	0.000	0.000
	35	0.399	11.32	109.796	4.699	0.103	0.041	0.144	0.000	0.000	0.000
	35	0.404	16.39	119.635	4.784	0.137	0.055	0.192	0.000	0.000	0.000
Eupatorium	21	0.335	42.62	273.907	5.613	0.156	0.082	0.052	0.000	0.000	0.000
maculatum	21	0.461	72.56	291.289	5.674	0.249	0.064	0.115	0.000	0.000	0.000
	21	0.387	51.03	373.846	5.924	0.137	0.059	0.053	0.000	0.000	0.000
Eupatorium	28	0.543	53.51	425.358	6.053	0.126	0.068	0.297	0.103	0.000	0.000
maculatum	28	0.478	51.23	347.087	5.850	0.148	0.071	0.283	0.065	0.000	0.000
	28	0.638	48.71	382.639	5.947	0.127	0.081	0.272	0.063	0.000	0.000
	28	0.492	112.92	366.742	5.905	0.308	0.152	0.531	0.072	0.000	0.000
	28	0.457	46.2	369.896	5.913	0.125	0.057	0.218	0.036	0.000	0.000
	28	0.418	47.92	458.565	6.128	0.105	0.044	0.174	0.025	0.000	0.000
	28	0.356	122.55	305.306	5.721	0.401	0.143	0.725	0.180	0.000	0.000
	28	0.557	68.87	265.191	5.580	0.260	0.145	0.499	0.094	0.000	0.000
	28	1.021	28.89	501.563	6.218	0.058	0.059	0.138	0.022	0.000	0.000
	28	0.865	138.24	254.445	5.539	0.543	0.470	1.255	0.242	0.000	0.000
	28	0.716	179.27	257.980	5.553	0.695	0.497	1.460	0.267	0.000	0.000
	28	0.324	137.41	279.289	5.632	0.492	0.159	0.801	0.150	0.000	0.000
	28	0.531	164.47	269.270	5.596	0.611	0.324	1.196	0.261	0.000	0.000
	28	0.397	72.52	390.102	5.966	0.186	0.074	0.302	0.042	0.000	0.000
Eupatorium	35	0.488	516.94	286.600	5.658	1.804	0.880	3.095	0.412	0.000	0.000
maculatum	35	1.373	234.5	264.077	5.576	0.888	1.219	2.667	0.560	0.000	0.000
	35	0.442	282.84	109.653	4.697	2.579	1.140	4.736	1.017	0.000	0.000
	35	1.221	427.28	244.202	5.498	1.750	1.640	4.091	0.702	0.000	0.000
	35	0.624	300.57	236.446	5.466	1.271	0.794	2.777	0.712	0.000	0.000
	35	0.457	235.67	253.490	5.535	0.930	0.425	1.936	0.581	0.000	0.000
	35	1.108	302.67	295.288	5.688	1.025	1.136	2.456	0.295	0.000	0.000
	35	0.776	417.99	311.445	5.741	1.342	1.041	2.854	0.470	0.000	0.000
	35	0.696	181.14	323.407	5.779	0.560	0.390	1.246	0.297	0.000	0.000
	35	0.794	199.81	317.612	5.761	0.629	0.500	1.371	0.242	0.000	0.000
	35	0.781	185.62	368.294	5.909	0.504	0.394	1.212	0.315	0.000	0.000
	35	1.106	141.52	376.383	5.931	0.376	0.416	0.973	0.181	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
Eupatorium	14	0.479	9.93	528.191	6.269	0.019	0.009	0.031	0.004	0.000	0.000
rugosum	14	0.673	8.37	804.808	6.691	0.010	0.007	0.018	0.001	0.000	0.000
	14	0.187	17.63	470.133	6.153	0.038	0.007	0.052	0.007	0.000	0.000
	14	0.566	15.87	774.146	6.652	0.021	0.012	0.036	0.004	0.000	0.000
	14	0.354	8.51	859.596	6.756	0.010	0.004	0.017	0.003	0.000	0.000
	14	0.230	13.21	552.720	6.315	0.024	0.006	0.033	0.003	0.000	0.000
	14	0.195	15.89	515.909	6.246	0.031	0.006	0.042	0.006	0.000	0.000
	14	1.047	1.11	173.438	5.156	0.006	0.007	0.014	0.001	0.000	0.000
	14	0.706	1.56	229.412	5.436	0.007	0.005	0.014	0.002	0.000	0.000
	14	0.358	2.51	166.225	5.113	0.015	0.005	0.023	0.002	0.000	0.000
	14	0.213	3.28	211.613	5.355	0.016	0.003	0.021	0.003	0.000	0.000
	14	0.464	3.12	149.282	5.006	0.021	0.010	0.033	0.002	0.000	0.000
Eupatorium	21	0.319	96.79	338.901	5.826	0.286	0.091	0.546	0.169	0.000	0.000
rugosum	21	0.376	80.42	385.338	5.954	0.209	0.078	0.537	0.249	0.000	0.000
	21	0.162	87.6	259.709	5.560	0.337	0.055	0.606	0.213	0.000	0.000
	21	0.255	27.24	450.248	6.110	0.061	0.015	0.090	0.014	0.000	0.000
	21	0.533	19.04	520.219	6.254	0.037	0.020	0.069	0.013	0.000	0.000
	21	0.335	21.95	413.371	6.024	0.053	0.018	0.079	0.008	0.000	0.000
	21	0.311	42.3	334.387	5.812	0.127	0.039	0.195	0.029	0.000	0.000
	21	0.367	7.07	147.599	4.995	0.048	0.018	0.075	0.009	0.000	0.000
	21	0.350	6.52	131.984	4.883	0.049	0.017	0.075	0.009	0.000	0.000
	21	0.257	21.98	207.554	5.335	0.106	0.027	0.148	0.015	0.000	0.000
	21	0.161	37.94	133.404	4.893	0.284	0.046	0.395	0.065	0.000	0.000
	21	0.507	27.63	190.552	5.250	0.145	0.074	0.267	0.049	0.000	0.000
Eupatorium	28	0.727	96.94	851.097	6.747	0.114	0.083	0.280	0.083	0.000	0.000
rugosum	28	0.724	43.95	586.782	6.375	0.075	0.054	0.176	0.047	0.000	0.000
	28	0.478	112.75	706.011	6.560	0.160	0.076	0.311	0.075	0.000	0.000
	28	0.385	79.75	821.318	6.711	0.097	0.037	0.206	0.071	0.000	0.000
	28	0.500	146.56	438.409	6.083	0.334	0.167	0.576	0.074	0.000	0.000
	28	0.498	61.87	740.958	6.608	0.084	0.042	0.198	0.072	0.000	0.000
	28	0.350	115.43	647.029	6.472	0.178	0.063	0.328	0.087	0.000	0.000
	28	0.641	207.63	591.707	6.383	0.351	0.225	0.694	0.118	0.000	0.000
	28	0.351	104.23	692.558	6.540	0.151	0.053	0.271	0.068	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	28	0.400	119.87	516.014	6.246	0.232	0.093	0.397	0.072	0.000	0.000
	28	0.339	163	580.484	6.364	0.281	0.095	0.486	0.110	0.000	0.000
	28	0.182	70.59	122.915	4.811	0.574	0.105	1.056	0.377	0.000	0.000
	28	0.183	154.86	239.684	5.479	0.646	0.119	1.065	0.301	0.000	0.000
	28	0.288	152.31	217.368	5.382	0.701	0.202	1.105	0.202	0.000	0.000
Eupatorium	35	0.242	197.6	179.457	5.190	1.101	0.169	1.181	0.274	0.000	0.000
rugosum	35	0.496	229.59	328.455	5.794	0.699	0.000	1.375	0.313	0.000	0.000
	35	0.616	209.57	338.891	5.826	0.618	0.307	1.193	0.268	0.000	0.000
	35	0.575	637.03	292.686	5.679	2.177	1.341	4.775	1.257	0.000	0.000
	35	0.531	437.33	276.529	5.622	1.582	0.909	3.606	1.116	0.000	0.000
	35	0.452	302.4	261.185	5.565	1.158	0.524	2.447	0.765	0.000	0.000
	35	0.492	408.13	274.706	5.616	1.486	0.617	2.727	0.624	0.000	0.000
	35	0.220	196.1	112.044	4.719	1.750	0.862	3.241	0.629	0.000	0.000
	35	0.523	265.41	195.730	5.277	1.356	0.299	2.334	0.679	0.000	0.000
	35	0.197	232.6	229.230	5.435	1.015	0.530	2.117	0.572	0.000	0.000
	35	0.336	430.91	245.407	5.503	1.756	0.346	2.200	0.098	0.000	0.000
	35	0.527	447.23	195.050	5.273	2.293	0.770	4.722	1.660	0.000	0.000
Galinsoga	14	0.335	65.45	341.651	5.834	0.192	0.064	0.272	0.016	0.000	0.000
ciliata	14	0.370	30.05	399.707	5.991	0.075	0.028	0.110	0.008	0.000	0.000
	14	0.332	28.68	359.173	5.884	0.080	0.027	0.114	0.007	0.000	0.000
	14	0.377	20.77	348.139	5.853	0.060	0.023	0.087	0.005	0.000	0.000
	14	0.270	21.69	410.174	6.017	0.053	0.014	0.071	0.004	0.000	0.000
	14	0.340	23.77	368.985	5.911	0.064	0.022	0.092	0.006	0.000	0.000
	14	0.328	22.34	321.439	5.773	0.070	0.023	0.098	0.006	0.000	0.000
	14	0.357	27.52	294.174	5.684	0.094	0.033	0.135	0.008	0.000	0.000
	14	0.470	31.51	418.237	6.036	0.075	0.035	0.117	0.007	0.000	0.000
	14	0.627	126.09	384.796	5.953	0.328	0.205	0.576	0.043	0.000	0.000
	14	0.636	41.72	442.840	6.093	0.094	0.060	0.165	0.011	0.000	0.000
Galinsoga	21	0.477	345.66	350.675	5.860	0.986	0.047	1.394	0.337	0.024	0.000
ciliata	21	0.407	510.02	393.382	5.975	1.297	0.528	2.269	0.407	0.037	0.000
	21	0.461	151.63	480.450	6.175	0.316	0.146	0.570	0.103	0.006	0.000
	21	0.431	247.87	358.868	5.883	0.691	0.298	1.215	0.205	0.022	0.000
	21	0.517	218.51	357.101	5.878	0.612	0.316	1.125	0.181	0.016	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	21	0.368	133.24	395.488	5.980	0.337	0.124	0.555	0.091	0.002	0.000
	21	0.550	132.4	422.463	6.046	0.313	0.172	0.592	0.106	0.000	0.000
	21	0.045	286.84	400.167	5.992	0.717	0.032	1.001	0.231	0.021	0.000
	21	0.375	374.21	538.122	6.288	0.695	0.261	1.278	0.298	0.024	0.000
	21	0.487	339.77	356.004	5.875	0.954	0.465	1.681	0.231	0.031	0.000
	21	0.562	256.53	688.671	6.535	0.373	0.210	0.683	0.096	0.006	0.000
Galinsoga	28	0.685	907.76	600.331	6.397	1.512	1.036	3.871	1.140	0.183	0.000
ciliata	28	0.665	298.7	630.169	6.446	0.474	0.315	0.986	0.196	0.000	0.000
	28	0.625	841.58	770.607	6.647	1.092	0.683	2.770	0.910	0.085	0.000
	28	0.994	1190.97	657.268	6.488	1.812	1.802	5.023	1.279	0.130	0.000
	28	0.573	241.51	418.707	6.037	0.577	0.330	1.439	0.470	0.062	0.000
	28	0.454	959.08	357.106	5.878	2.686	1.218	5.611	1.327	0.381	0.000
	28	0.404	443.96	435.554	6.077	1.019	0.412	1.959	0.419	0.109	0.000
Galinsoga	35	0.268	420.03	681.314	6.524	0.617	0.335	1.546	0.524	0.071	0.000
ciliata	35	0.643	1358.42	150.638	5.015	9.018	1.152	13.122	2.475	0.477	0.000
	35	0.128	1259.97	610.687	6.415	2.063	1.748	7.368	2.812	0.745	0.000
	35	0.709	1203.19	776.252	6.654	1.550	1.072	4.435	1.431	0.421	0.000
	35	1.029	283.17	717.431	6.576	0.395	1.595	5.567	1.875	0.522	0.024
	35	1.061	437.7	633.980	6.452	0.690	0.419	1.273	0.393	0.067	0.000
	35	0.942	774.34	599.659	6.396	1.291	0.522	2.254	0.800	0.234	0.007
	35	1.190	1010.17	641.093	6.463	1.576	1.216	4.657	1.563	0.550	0.036
Hieracium	14	0.301	1.25	265.957	5.583	0.005	0.003	0.007	0.000	0.000	0.000
aurantiacum	14	0.553	0.48	154.839	5.042	0.003	0.002	0.006	0.000	0.000	0.000
	14	0.774	0.26	152.941	5.030	0.002	0.001	0.003	0.000	0.000	0.000
Hieracium	21	0.471	4.11	197.596	5.286	0.021	0.009	0.030	0.000	0.000	0.000
aurantiacum	21	0.442	2.68	149.721	5.009	0.018	0.008	0.026	0.000	0.000	0.000
	21	0.458	1.61	178.889	5.187	0.009	0.003	0.012	0.000	0.000	0.000
Hieracium	28	0.360	7.94	152.107	5.025	0.052	0.019	0.071	0.000	0.000	0.000
aurantiacum	28	0.324	18.29	163.669	5.098	0.112	0.030	0.142	0.000	0.000	0.000
	28	0.476	41.34	223.387	5.409	0.185	0.040	0.225	0.000	0.000	0.000
Hieracium	35	0.479	120.6	152.889	5.030	0.789	0.184	0.973	0.000	0.000	0.000
aurantiacum	35	0.267	57.25	235.781	5.463	0.243	0.044	0.286	0.000	0.000	0.000
	35	0.215	54.66	165.973	5.112	0.329	0.074	0.404	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	35	0.233	18.73	235.242	5.461	0.080	0.038	0.118	0.000	0.000	0.000
	35	0.179	41.44	208.346	5.339	0.199	0.057	0.256	0.000	0.000	0.000
	35	0.226	15.4	250.407	5.523	0.062	0.020	0.081	0.000	0.000	0.000
	35	0.287	42.82	203.035	5.313	0.211	0.065	0.275	0.000	0.000	0.000
	35	0.306	19.35	325.210	5.784	0.060	0.028	0.088	0.000	0.000	0.000
	35	0.281	32.38	173.155	5.154	0.187	0.053	0.240	0.000	0.000	0.000
	35	0.337	23.92	191.054	5.253	0.125	0.042	0.167	0.000	0.000	0.000
Hieracium	14	0.222	0.28	155.556	5.047	0.002	0.000	0.002	0.000	0.000	0.000
venosum	14	0.244	0.66	146.667	4.988	0.005	0.001	0.006	0.000	0.000	0.000
	14	0.250	0.89	278.125	5.628	0.003	0.001	0.004	0.000	0.000	0.000
	14	0.280	1.35	540.000	6.292	0.003	0.001	0.003	0.000	0.000	0.000
	14	0.087	1.66	360.870	5.889	0.005	0.000	0.005	0.000	0.000	0.000
	14	0.833	0.91	252.778	5.533	0.004	0.003	0.007	0.000	0.000	0.000
	14	0.074	0.73	271.375	5.604	0.003	0.002	0.005	0.000	0.000	0.000
Hieracium	21	0.285	3.19	211.258	5.353	0.015	0.004	0.019	0.000	0.000	0.000
venosum	21	0.347	4.96	281.818	5.641	0.018	0.006	0.024	0.000	0.000	0.000
Hieracium	28	0.303	8.06	157.422	5.059	0.051	0.016	0.067	0.000	0.000	0.000
venosum	28	0.376	8.05	189.412	5.244	0.043	0.016	0.059	0.000	0.000	0.000
	28	0.314	8.93	288.997	5.666	0.031	0.010	0.041	0.000	0.000	0.000
	28	0.471	32.48	271.466	5.604	0.038	0.018	0.056	0.000	0.000	0.000
Hieracium	35	0.845	19.59	325.125	5.784	0.100	0.084	0.184	0.000	0.000	0.000
venosum	35	0.996	15.61	417.697	6.035	0.047	0.047	0.094	0.000	0.000	0.000
	35	0.904	10.37	349.217	5.856	0.045	0.040	0.085	0.000	0.000	0.000
	35	1.155	9.55	436.073	6.078	0.022	0.025	0.047	0.000	0.000	0.000
	35	0.942	25.13	580.370	6.364	0.043	0.041	0.084	0.000	0.000	0.000
	35	0.504	25.14	321.073	5.772	0.078	0.040	0.118	0.000	0.000	0.000
	35	0.475	13.18	140.512	4.945	0.094	0.045	0.138	0.000	0.000	0.000
Hieracium	14	0.171	11.09	288.052	5.663	0.039	0.007	0.045	0.000	0.000	0.000
vulgatum	14	0.269	1.65	246.269	5.506	0.007	0.002	0.009	0.000	0.000	0.000
	14	0.211	2.52	231.193	5.443	0.011	0.002	0.013	0.000	0.000	0.000
	14	0.119	2	132.450	4.886	0.015	0.002	0.017	0.000	0.000	0.000
	14	0.157	2	240.964	5.485	0.008	0.001	0.010	0.000	0.000	0.000
	14	0.221	1.47	190.909	5.252	0.008	0.002	0.009	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	14	0.368	0.81	119.118	4.780	0.007	0.003	0.009	0.000	0.000	0.000
	14	0.290	0.81	130.645	4.872	0.006	0.002	0.008	0.000	0.000	0.000
	14	0.241	0.55	189.655	5.245	0.003	0.001	0.004	0.000	0.000	0.000
	14	0.212	0.61	184.848	5.220	0.003	0.001	0.004	0.000	0.000	0.000
	14	0.182	1.03	133.766	4.896	0.008	0.001	0.009	0.000	0.000	0.000
	14	0.195	1.53	198.701	5.292	0.008	0.002	0.009	0.000	0.000	0.000
Hieracium	21	0.141	2.32	108.920	4.691	0.021	0.003	0.024	0.000	0.000	0.000
vulgatum	21	0.504	1.5	123.967	4.820	0.012	0.006	0.018	0.000	0.000	0.000
	21	0.367	2.28	134.911	4.905	0.017	0.006	0.023	0.000	0.000	0.000
	21	0.101	2.69	123.394	4.815	0.022	0.002	0.024	0.000	0.000	0.000
	21	0.250	2.96	151.020	5.017	0.020	0.005	0.025	0.000	0.000	0.000
	21	0.174	3.07	206.040	5.328	0.015	0.003	0.018	0.000	0.000	0.000
	21	0.203	2.42	175.362	5.167	0.014	0.003	0.017	0.000	0.000	0.000
	21	0.239	1.85	138.060	4.928	0.013	0.003	0.017	0.000	0.000	0.000
	21	0.176	2.74	137.688	4.925	0.020	0.004	0.023	0.000	0.000	0.000
	21	0.138	10.5	344.262	5.841	0.031	0.004	0.035	0.000	0.000	0.000
	21	1.532	11.98	539.640	6.291	0.022	0.034	0.056	0.000	0.000	0.000
Hieracium	28	0.151	70.01	477.884	6.169	0.147	0.022	0.169	0.000	0.000	0.000
vulgatum	28	0.117	37.06	441.716	6.091	0.084	0.010	0.094	0.000	0.000	0.000
	28	0.096	72.18	389.951	5.966	0.185	0.018	0.203	0.000	0.000	0.000
	28	0.100	78.08	409.869	6.016	0.191	0.019	0.210	0.000	0.000	0.000
	28	0.166	37.63	356.008	5.875	0.106	0.018	0.123	0.000	0.000	0.000
	28	0.117	28.37	356.407	5.876	0.080	0.009	0.089	0.000	0.000	0.000
	28	0.176	20.05	211.275	5.353	0.095	0.017	0.112	0.000	0.000	0.000
	28	0.114	26.33	361.180	5.889	0.073	0.008	0.081	0.000	0.000	0.000
	28	0.095	49.28	541.538	6.294	0.091	0.009	0.100	0.000	0.000	0.000
	28	0.142	65.88	490.544	6.196	0.134	0.019	0.153	0.000	0.000	0.000
	28	0.229	32.13	169.194	5.131	0.190	0.043	0.233	0.000	0.000	0.000
	28	0.171	35.46	205.923	5.328	0.172	0.030	0.202	0.000	0.000	0.000
	28	0.106	29.38	535.155	6.283	0.055	0.006	0.061	0.000	0.000	0.000
	28	0.222	26.69	217.878	5.384	0.123	0.027	0.150	0.000	0.000	0.000
Hieracium	35	0.190	149.27	308.984	5.733	0.483	0.092	0.575	0.000	0.000	0.000
vulgatum	35	0.418	97.46	341.008	5.832	0.286	0.120	0.405	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	35	0.240	111.47	406.528	6.008	0.274	0.066	0.340	0.000	0.000	0.000
	35	0.125	70.37	360.133	5.886	0.195	0.024	0.220	0.000	0.000	0.000
	35	0.128	193.24	209.929	5.347	0.921	0.118	1.038	0.000	0.000	0.000
	35	0.168	94.63	248.699	5.516	0.381	0.064	0.444	0.000	0.000	0.000
	35	0.218	114.52	268.763	5.594	0.426	0.093	0.519	0.000	0.000	0.000
	35	0.176	125.47	230.983	5.442	0.543	0.095	0.639	0.000	0.000	0.000
	35	0.197	126.76	282.568	5.644	0.449	0.089	0.537	0.000	0.000	0.000
	35	0.340	43.94	458.664	6.128	0.096	0.033	0.128	0.000	0.000	0.000
	35	0.091	104.01	355.590	5.874	0.293	0.027	0.319	0.000	0.000	0.000
	35	0.090	62.3	450.145	6.110	0.138	0.013	0.151	0.000	0.000	0.000
	35	0.293	62.97	450.429	6.110	0.140	0.041	0.181	0.000	0.000	0.000
	35	0.183	35.7	86.066	4.455	0.415	0.076	0.491	0.000	0.000	0.000
	35	0.433	69.58	208.261	5.339	0.334	0.145	0.479	0.000	0.000	0.000
Lactuca	14	0.697	6.95	702.020	6.554	0.010	0.007	0.017	0.000	0.000	0.000
biennis	14	0.384	1.11	129.070	4.860	0.009	0.003	0.012	0.000	0.000	0.000
	14	0.338	1.12	172.308	5.149	0.007	0.002	0.009	0.000	0.000	0.000
	14	0.304	1.02	221.739	5.402	0.005	0.001	0.006	0.000	0.000	0.000
	14	0.180	3.58	402.247	5.997	0.009	0.002	0.011	0.000	0.000	0.000
	14	0.295	8.75	314.748	5.752	0.028	0.008	0.036	0.000	0.000	0.000
	14	0.158	8.42	204.866	5.322	0.041	0.007	0.048	0.000	0.000	0.000
	14	0.201	6.99	226.214	5.421	0.031	0.006	0.037	0.000	0.000	0.000
	14	0.170	3.61	256.028	5.545	0.014	0.002	0.017	0.000	0.000	0.000
	14	0.209	3.86	196.939	5.283	0.020	0.004	0.024	0.000	0.000	0.000
	14	0.256	2.82	343.902	5.840	0.008	0.002	0.010	0.000	0.000	0.000
	14	0.694	2.03	238.824	5.476	0.009	0.006	0.014	0.000	0.000	0.000
	14	0.265	1.09	106.863	4.672	0.010	0.003	0.013	0.000	0.000	0.000
	14	0.305	2.09	104.500	4.649	0.020	0.006	0.026	0.000	0.000	0.000
Lactuca	21	0.210	34.24	647.259	6.473	0.053	0.011	0.064	0.000	0.000	0.000
biennis	21	0.167	53.29	814.832	6.703	0.065	0.011	0.076	0.000	0.000	0.000
	21	0.375	18.17	190.861	5.252	0.095	0.036	0.131	0.000	0.000	0.000
	21	0.334	21.93	182.902	5.209	0.120	0.040	0.160	0.000	0.000	0.000
	21	0.487	11.43	175.038	5.165	0.065	0.032	0.097	0.000	0.000	0.000
	21	0.473	39.65	207.592	5.336	0.191	0.090	0.281	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	21	0.469	52.61	201.571	5.306	0.261	0.122	0.383	0.000	0.000	0.000
	21	0.502	22.26	179.516	5.190	0.124	0.062	0.186	0.000	0.000	0.000
	21	0.181	14.08	181.210	5.200	0.078	0.014	0.092	0.000	0.000	0.000
	21	0.210	15.42	297.683	5.696	0.052	0.011	0.063	0.000	0.000	0.000
	21	0.278	12.85	262.781	5.571	0.049	0.014	0.063	0.000	0.000	0.000
	21	0.173	8.51	111.680	4.716	0.076	0.013	0.089	0.000	0.000	0.000
	21	0.809	39.6	293.551	5.682	0.135	0.109	0.244	0.000	0.000	0.000
	21	0.348	11.55	235.234	5.461	0.049	0.017	0.066	0.000	0.000	0.000
	21	0.848	14.39	174.424	5.161	0.083	0.070	0.153	0.000	0.000	0.000
	21	0.405	8.22	158.687	5.067	0.052	0.021	0.073	0.000	0.000	0.000
	21	0.319	8.36	220.580	5.396	0.038	0.012	0.038	0.000	0.000	0.000
Lactuca	28	0.535	25.95	258.209	5.554	0.101	0.054	0.154	0.000	0.000	0.000
biennis	28	0.446	35.09	354.087	5.870	0.099	0.044	0.143	0.000	0.000	0.000
	28	0.793	27.7	318.757	5.764	0.087	0.069	0.156	0.000	0.000	0.000
	28	0.377	26.88	312.558	5.745	0.086	0.032	0.118	0.000	0.000	0.000
	28	0.374	21.85	298.090	5.697	0.073	0.027	0.101	0.000	0.000	0.000
	28	0.657	19.12	245.758	5.504	0.078	0.051	0.129	0.000	0.000	0.000
	28	0.713	17.19	293.846	5.683	0.059	0.042	0.100	0.000	0.000	0.000
	28	0.537	22.36	279.850	5.634	0.080	0.043	0.123	0.000	0.000	0.000
	28	0.641	41.23	313.060	5.746	0.132	0.084	0.216	0.000	0.000	0.000
	28	0.685	28.09	188.777	5.241	0.149	0.102	0.251	0.000	0.000	0.000
	28	0.315	22.39	185.809	5.225	0.121	0.038	0.158	0.000	0.000	0.000
Lactuca	35	0.335	176.31	262.327	5.570	0.672	0.225	0.898	0.000	0.000	0.000
biennis	35	0.330	121.21	283.201	5.646	0.428	0.141	0.569	0.000	0.000	0.000
	35	0.421	157.28	252.821	5.533	0.622	0.262	0.884	0.000	0.000	0.000
	35	0.229	140.07	347.568	5.851	0.403	0.092	0.495	0.000	0.000	0.000
	35	0.400	149.83	223.194	5.408	0.671	0.269	0.940	0.000	0.000	0.000
	35	0.632	143.79	260.678	5.563	0.552	0.349	0.900	0.000	0.000	0.000
	35	0.469	50.58	228.559	5.432	0.221	0.104	0.325	0.000	0.000	0.000
	35	0.558	84.09	234.954	5.459	0.358	0.200	0.558	0.000	0.000	0.000
	35	0.281	50.79	269.157	5.595	0.189	0.053	0.242	0.000	0.000	0.000
	35	0.393	57.63	355.521	5.874	0.162	0.064	0.226	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	35	0.706	45	298.607	5.699	0.151	0.106	0.257	0.000	0.000	0.000
	35	0.498	76.94	263.583	5.574	0.292	0.146	0.437	0.000	0.000	0.000
	35	0.458	65.71	250.706	5.524	0.262	0.120	0.382	0.000	0.000	0.000
Lactuca	14	0.167	22.69	416.330	6.031	0.055	0.009	0.064	0.000	0.000	0.000
canadensis	14	0.360	13.5	322.196	5.775	0.042	0.015	0.057	0.000	0.000	0.000
	14	0.215	25.65	335.733	5.816	0.076	0.016	0.093	0.000	0.000	0.000
	14	0.066	8.6	380.531	5.942	0.023	0.002	0.024	0.000	0.000	0.000
	14	0.255	29.99	369.335	5.912	0.081	0.021	0.102	0.000	0.000	0.000
	14	0.253	3.3	440.000	6.087	0.008	0.002	0.009	0.000	0.000	0.000
	14	0.167	2.33	970.833	6.878	0.002	0.000	0.003	0.000	0.000	0.000
	14	0.450	1.72	860.000	6.757	0.002	0.001	0.003	0.000	0.000	0.000
	14	0.028	2.86	794.444	6.678	0.004	0.000	0.004	0.000	0.000	0.000
	14	0.339	2.36	400.000	5.991	0.006	0.002	0.008	0.000	0.000	0.000
	14	0.213	4.95	618.750	6.428	0.008	0.002	0.010	0.000	0.000	0.000
Lactuca	21	0.103	52.8	314.510	5.751	0.168	0.017	0.185	0.000	0.000	0.000
canadensis	21	0.290	18.42	333.938	5.811	0.055	0.016	0.071	0.000	0.000	0.000
	21	0.057	76.66	322.345	5.776	0.238	0.014	0.251	0.000	0.000	0.000
	21	0.086	30.06	263.130	5.573	0.114	0.010	0.124	0.000	0.000	0.000
	21	0.033	93.97	303.786	5.716	0.309	0.010	0.319	0.000	0.000	0.000
	21	0.034	87.66	261.508	5.566	0.335	0.012	0.347	0.000	0.000	0.000
	21	0.098	75.02	307.800	5.729	0.244	0.024	0.268	0.000	0.000	0.000
	21	0.305	48.62	244.432	5.499	0.199	0.061	0.260	0.000	0.000	0.000
	21	1.404	14.64	449.631	6.108	0.033	0.046	0.078	0.000	0.000	0.000
	21	0.314	68	408.900	6.013	0.166	0.052	0.219	0.000	0.000	0.000
	21	0.318	46.15	375.509	5.928	0.123	0.039	0.162	0.000	0.000	0.000
	21	0.466	34.79	395.791	5.981	0.088	0.041	0.129	0.000	0.000	0.000
	21	0.252	41.81	379.057	5.938	0.110	0.028	0.138	0.000	0.000	0.000
	21	0.239	25.36	240.836	5.484	0.105	0.025	0.131	0.000	0.000	0.000
Lactuca	28	0.337	86.33	486.366	6.187	0.178	0.060	0.237	0.000	0.000	0.000
canadensis	28	0.244	109.91	444.620	6.097	0.247	0.060	0.308	0.000	0.000	0.000
	28	0.379	78.45	583.271	6.369	0.135	0.051	0.186	0.000	0.000	0.000
	28	0.307	74.88	464.804	6.142	0.161	0.049	0.211	0.000	0.000	0.000
	28	0.339	34.04	594.066	6.387	0.057	0.019	0.077	0.000	0.000	0.000
	28	0.378	102.79	468.719	6.150	0.219	0.083	0.302	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	28	0.399	129.91	535.270	6.283	0.243	0.097	0.340	0.000	0.000	0.000
	28	0.324	155.82	491.546	6.198	0.317	0.103	0.420	0.000	0.000	0.000
	28	0.377	104.08	486.355	6.187	0.214	0.081	0.295	0.000	0.000	0.000
	28	0.670	33.16	533.977	6.280	0.062	0.042	0.104	0.000	0.000	0.000
	28	0.337	118.41	343.915	5.840	0.344	0.116	0.460	0.000	0.000	0.000
	28	0.385	139.72	488.873	6.192	0.286	0.110	0.396	0.000	0.000	0.000
	28	0.157	58.87	268.323	5.592	0.219	0.035	0.254	0.000	0.000	0.000
	28	0.248	79.72	233.783	5.454	0.341	0.085	0.426	0.000	0.000	0.000
	28	0.336	74.72	251.160	5.526	0.298	0.100	0.398	0.000	0.000	0.000
Lactuca	35	0.401	157.9	473.180	6.159	0.334	0.134	0.468	0.000	0.000	0.000
canadensis	35	0.442	330.93	426.621	6.056	0.776	0.343	1.119	0.000	0.000	0.000
	35	0.396	151.08	325.183	5.784	0.465	0.184	0.785	0.137	0.000	0.000
	35	0.235	139.17	292.067	5.677	0.477	0.112	0.588	0.000	0.000	0.000
	35	0.258	156.55	379.607	5.939	0.412	0.106	0.519	0.000	0.000	0.000
	35	0.209	235.68	445.941	6.100	0.529	0.110	0.639	0.000	0.000	0.000
	35	0.296	227.16	441.002	6.089	0.515	0.153	0.668	0.000	0.000	0.000
	35	0.253	437.63	409.766	6.016	1.068	0.271	1.339	0.000	0.000	0.000
	35	0.862	180.9	678.290	6.520	0.267	0.230	0.497	0.000	0.000	0.000
	35	0.334	449.38	266.869	5.587	1.684	0.563	2.247	0.000	0.000	0.000
Lactuca	14	0.564	2.2	282.051	5.642	0.008	0.004	0.012	0.000	0.000	0.000
muralis	14	0.576	1.02	309.091	5.734	0.003	0.002	0.005	0.000	0.000	0.000
	14	1.528	2.05	386.792	5.958	0.005	0.008	0.013	0.000	0.000	0.000
	14	0.627	3.3	559.322	6.327	0.006	0.004	0.010	0.000	0.000	0.000
	14	0.237	2.74	464.407	6.141	0.006	0.001	0.007	0.000	0.000	0.000
	14	0.655	2.97	540.000	6.292	0.006	0.004	0.009	0.000	0.000	0.000
	14	0.840	0.49	196.000	5.278	0.003	0.002	0.005	0.000	0.000	0.000
	14	0.485	1.03	156.061	5.050	0.007	0.003	0.010	0.000	0.000	0.000
	14	0.384	1.64	146.429	4.987	0.011	0.004	0.016	0.000	0.000	0.000
	14	0.841	0.89	202.273	5.310	0.004	0.004	0.008	0.000	0.000	0.000
	14	0.714	1.02	182.143	5.205	0.006	0.004	0.010	0.000	0.000	0.000
	14	0.173	0.67	64.423	4.165	0.010	0.002	0.012	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	14	0.635	1.36	141.667	4.953	0.010	0.006	0.016	0.000	0.000	0.000
	14	0.533	1.98	188.571	5.239	0.011	0.006	0.016	0.000	0.000	0.000
	14	0.267	1.71	162.857	5.093	0.011	0.003	0.013	0.000	0.000	0.000
Lactuca	21	0.326	5.61	590.526	6.381	0.010	0.003	0.013	0.000	0.000	0.000
muralis	21	0.308	10.89	430.435	6.065	0.025	0.008	0.033	0.000	0.000	0.000
	21	0.484	4.96	196.825	5.282	0.025	0.012	0.037	0.000	0.000	0.000
	21	0.312	7.1	452.229	6.114	0.016	0.005	0.021	0.000	0.000	0.000
	21	0.400	5.39	308.000	5.730	0.018	0.007	0.025	0.000	0.000	0.000
	21	0.944	6.19	578.505	6.360	0.011	0.010	0.021	0.000	0.000	0.000
	21	0.170	11.64	360.372	5.887	0.032	0.006	0.038	0.000	0.000	0.000
	21	0.276	7.4	234.921	5.459	0.032	0.009	0.040	0.000	0.000	0.000
	21	0.412	3.08	235.115	5.460	0.013	0.005	0.019	0.000	0.000	0.000
	21	0.826	1.41	97.917	4.584	0.014	0.012	0.026	0.000	0.000	0.000
	21	0.855	2.67	193.478	5.265	0.014	0.012	0.026	0.000	0.000	0.000
	21	0.487	2.12	141.333	4.951	0.015	0.007	0.022	0.000	0.000	0.000
	21	0.896	1.63	169.792	5.135	0.010	0.009	0.018	0.000	0.000	0.000
Lactuca	28	0.411	18.3	305.509	5.722	0.060	0.025	0.085	0.000	0.000	0.000
muralis	28	0.697	15.99	290.200	5.671	0.055	0.038	0.094	0.000	0.000	0.000
	28	0.550	15.55	296.190	5.691	0.053	0.029	0.081	0.000	0.000	0.000
	28	0.316	10.87	303.631	5.716	0.036	0.011	0.047	0.000	0.000	0.000
	28	0.301	15.65	252.013	5.529	0.062	0.019	0.081	0.000	0.000	0.000
	28	1.154	11.13	286.118	5.656	0.039	0.045	0.084	0.000	0.000	0.000
	28	0.841	8.02	186.946	5.231	0.043	0.036	0.079	0.000	0.000	0.000
	28	0.681	6.84	180.475	5.196	0.038	0.026	0.064	0.000	0.000	0.000
	28	0.190	9.22	205.804	5.327	0.045	0.009	0.053	0.000	0.000	0.000
	28	0.295	9.82	195.618	5.276	0.050	0.015	0.065	0.000	0.000	0.000
	28	0.332	8.63	225.916	5.420	0.038	0.013	0.051	0.000	0.000	0.000
	28	0.366	6.36	200.631	5.301	0.032	0.012	0.043	0.000	0.000	0.000
Lactuca	35	0.415	31	194.577	5.271	0.159	0.066	0.225	0.000	0.000	0.000
muralis	35	0.466	47.66	236.315	5.465	0.202	0.094	0.296	0.000	0.000	0.000
	35	0.633	24.84	302.927	5.713	0.082	0.052	0.134	0.000	0.000	0.000
	35	0.498	16.66	193.541	5.265	0.086	0.043	0.129	0.000	0.000	0.000
	35	0.403	26.17	226.286	5.422	0.116	0.047	0.162	0.000	0.000	0.000
	35	0.365	38.7	233.738	5.454	0.166	0.061	0.226	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	35	0.316	27.84	260.333	5.562	0.107	0.034	0.141	0.000	0.000	0.000
	35	0.329	25.39	234.160	5.456	0.108	0.036	0.144	0.000	0.000	0.000
	35	0.393	27.29	240.525	5.483	0.113	0.045	0.158	0.000	0.000	0.000
	35	0.579	25.85	376.274	5.930	0.069	0.040	0.109	0.000	0.000	0.000
	35	0.431	32.46	247.220	5.510	0.131	0.057	0.188	0.000	0.000	0.000
	35	0.871	23.79	281.206	5.639	0.085	0.074	0.158	0.000	0.000	0.000
	35	0.565	27.24	308.494	5.732	0.088	0.050	0.138	0.000	0.000	0.000
	35	0.706	26.21	299.886	5.703	0.087	0.062	0.149	0.000	0.000	0.000
Lapsana	14	0.568	1.6	144.144	4.971	0.011	0.006	0.017	0.000	0.000	0.000
communis	14	0.417	1.73	205.952	5.328	0.008	0.004	0.012	0.000	0.000	0.000
	14	0.927	0.73	178.049	5.182	0.004	0.004	0.008	0.000	0.000	0.000
	14	0.200	0.8	114.286	4.739	0.007	0.001	0.008	0.000	0.000	0.000
	14	0.485	0.34	103.030	4.635	0.003	0.002	0.005	0.000	0.000	0.000
	14	0.271	0.66	137.500	4.924	0.005	0.001	0.006	0.000	0.000	0.000
	14	0.423	0.78	150.000	5.011	0.005	0.002	0.007	0.000	0.000	0.000
Lapsana	21	0.142	17.26	401.395	5.995	0.043	0.006	0.049	0.000	0.000	0.000
communis	21	0.191	18.22	483.289	6.181	0.038	0.007	0.045	0.000	0.000	0.000
	21	0.212	16.69	324.708	5.783	0.051	0.011	0.062	0.000	0.000	0.000
	21	0.318	12.27	322.895	5.777	0.038	0.012	0.050	0.000	0.000	0.000
	21	0.288	25.05	392.633	5.973	0.064	0.018	0.082	0.000	0.000	0.000
	21	0.263	7.69	280.657	5.637	0.027	0.007	0.035	0.000	0.000	0.000
	21	0.324	6.43	198.457	5.291	0.032	0.011	0.043	0.000	0.000	0.000
	21	0.298	5.67	222.353	5.404	0.026	0.008	0.033	0.000	0.000	0.000
	21	0.452	3.47	176.142	5.171	0.020	0.009	0.029	0.000	0.000	0.000
	21	0.242	4.88	262.366	5.570	0.019	0.005	0.023	0.000	0.000	0.000
	21	0.109	1.17	98.319	4.588	0.012	0.001	0.013	0.000	0.000	0.000
	21	0.382	2.9	136.792	4.918	0.021	0.008	0.029	0.000	0.000	0.000
	21	0.488	3.86	135.439	4.909	0.029	0.014	0.042	0.000	0.000	0.000
	21	0.220	2.83	214.394	5.368	0.013	0.003	0.016	0.000	0.000	0.000
	21	0.212	4.96	92.193	4.524	0.054	0.011	0.065	0.000	0.000	0.000
Lapsana	28	0.251	58.27	535.570	6.283	0.109	0.027	0.136	0.000	0.000	0.000
communis	28	0.342	99.63	481.304	6.176	0.207	0.071	0.278	0.000	0.000	0.000
	28	0.160	65.88	572.870	6.351	0.115	0.018	0.133	0.000	0.000	0.000
	28	0.127	17.12	452.910	6.116	0.038	0.005	0.043	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	28	0.237	35.8	460.746	6.133	0.078	0.018	0.096	0.000	0.000	0.000
	28	0.341	59.41	398.457	5.988	0.149	0.051	0.200	0.000	0.000	0.000
	28	0.216	114.66	478.947	6.172	0.239	0.052	0.291	0.000	0.000	0.000
	28	0.208	36.08	396.484	5.983	0.091	0.019	0.110	0.000	0.000	0.000
	28	0.847	32.51	551.952	6.313	0.059	0.050	0.109	0.000	0.000	0.000
	28	0.435	23.03	166.282	5.114	0.139	0.060	0.199	0.000	0.000	0.000
	28	0.403	14.15	165.885	5.111	0.085	0.034	0.120	0.000	0.000	0.000
Lapsana	35	0.629	82.35	362.616	5.893	0.227	0.143	0.370	0.000	0.000	0.000
communis	35	0.106	155.71	341.544	5.833	0.456	0.048	0.504	0.000	0.000	0.000
	35	0.451	245.78	351.868	5.863	0.699	0.315	1.014	0.000	0.000	0.000
	35	0.330	207.33	394.990	5.979	0.525	0.173	0.698	0.000	0.000	0.000
	35	0.556	234.84	357.933	5.880	0.656	0.365	1.021	0.000	0.000	0.000
	35	0.241	108.61	159.276	5.071	0.682	0.165	0.846	0.000	0.000	0.000
Leontodon	14	0.502	4.56	236.147	5.464	0.019	0.010	0.029	0.000	0.000	0.000
autumnalis	14	0.491	3.63	278.588	5.630	0.013	0.006	0.019	0.000	0.000	0.000
	14	0.506	5.22	338.521	5.825	0.015	0.008	0.023	0.000	0.000	0.000
	14	0.636	2.61	202.483	5.311	0.013	0.008	0.021	0.000	0.000	0.000
	14	0.510	8.74	394.582	5.978	0.022	0.011	0.033	0.000	0.000	0.000
	14	0.772	2.09	436.326	6.078	0.005	0.004	0.008	0.000	0.000	0.000
	14	0.802	9.55	341.804	5.834	0.028	0.022	0.050	0.000	0.000	0.000
	14	0.668	2.43	360.534	5.888	0.007	0.005	0.011	0.000	0.000	0.000
	14	0.477	5.37	492.661	6.200	0.011	0.005	0.016	0.000	0.000	0.000
	14	0.599	9.53	344.043	5.841	0.028	0.017	0.044	0.000	0.000	0.000
	14	0.557	6.22	320.619	5.770	0.019	0.011	0.030	0.000	0.000	0.000
	14	0.521	6.49	299.078	5.701	0.022	0.011	0.033	0.000	0.000	0.000
	14	0.630	5.86	293.000	5.680	0.020	0.013	0.033	0.000	0.000	0.000
Leontodon	21	0.385	34.59	388.215	5.962	0.089	0.034	0.123	0.000	0.000	0.000
autumnalis	21	0.269	21.2	311.307	5.741	0.068	0.018	0.086	0.000	0.000	0.000
	21	0.263	32.08	252.201	5.530	0.127	0.033	0.161	0.000	0.000	0.000
	21	0.503	9.9	194.499	5.270	0.051	0.026	0.077	0.000	0.000	0.000
	21	0.451	14.21	312.308	5.744	0.046	0.021	0.066	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	21	0.390	15.63	340.523	5.830	0.046	0.018	0.064	0.000	0.000	0.000
	21	0.257	28.71	442.373	6.092	0.065	0.017	0.082	0.000	0.000	0.000
	21	0.220	17.57	261.070	5.565	0.067	0.015	0.082	0.000	0.000	0.000
	21	0.226	60.48	316.815	5.758	0.191	0.043	0.234	0.000	0.000	0.000
	21	0.410	26.04	342.181	5.835	0.076	0.031	0.107	0.000	0.000	0.000
	21	2.405	29.17	258.829	5.556	0.113	0.027	0.038	0.000	0.000	0.000
	21	0.372	32	386.941	5.958	0.083	0.031	0.114	0.000	0.000	0.000
	21	0.203	30.2	461.069	6.134	0.066	0.013	0.079	0.000	0.000	0.000
Leontodon	28	0.143	48.19	654.755	6.484	0.074	0.011	0.084	0.000	0.000	0.000
autumnalis	28	0.527	32.91	471.490	6.156	0.070	0.037	0.107	0.000	0.000	0.000
	28	0.368	19.36	516.267	6.247	0.038	0.014	0.051	0.000	0.000	0.000
	28	0.197	13.16	489.219	6.193	0.027	0.005	0.032	0.000	0.000	0.000
	28	0.308	42.4	461.371	6.134	0.092	0.028	0.120	0.000	0.000	0.000
	28	0.255	58.25	272.578	5.608	0.214	0.055	0.268	0.000	0.000	0.000
	28	0.299	44.8	347.556	5.851	0.129	0.039	0.167	0.000	0.000	0.000
	28	0.229	26.9	534.791	6.282	0.050	0.012	0.062	0.000	0.000	0.000
	28	0.269	40.28	455.141	6.121	0.089	0.024	0.112	0.000	0.000	0.000
	28	0.329	96.33	481.169	6.176	0.200	0.066	0.266	0.000	0.000	0.000
	28	0.290	50.57	556.326	6.321	0.091	0.026	0.117	0.000	0.000	0.000
	28	0.281	85.72	574.916	6.354	0.149	0.042	0.191	0.000	0.000	0.000
	28	0.549	35.18	487.933	6.190	0.072	0.040	0.112	0.000	0.000	0.000
Leontodon	35	0.550	39.56	538.231	6.288	0.074	0.040	0.114	0.000	0.000	0.000
autumnalis	35	0.460	71.43	476.518	6.167	0.150	0.069	0.270	0.000	0.051	0.000
	35	0.454	119.04	476.351	6.166	0.250	0.113	0.363	0.000	0.000	0.000
	35	0.496	110.87	393.714	5.976	0.282	0.140	0.572	0.000	0.150	0.000
	35	0.411	74.68	513.971	6.242	0.145	0.060	0.205	0.000	0.000	0.000
	35	0.571	57.86	489.924	6.194	0.118	0.067	0.186	0.000	0.000	0.000
	35	0.630	83.91	562.023	6.332	0.149	0.094	0.243	0.000	0.000	0.000
	35	0.530	116.08	369.799	5.913	0.314	0.166	0.502	0.000	0.022	0.000
	35	0.353	170.94	357.690	5.880	0.478	0.169	0.647	0.000	0.000	0.000
	35	0.576	74.73	192.653	5.261	0.388	0.224	0.611	0.000	0.000	0.000
	35	0.667	52.88	177.093	5.177	0.299	0.199	0.498	0.000	0.000	0.000
	35	0.438	38.93	200.360	5.300	0.194	0.085	0.280	0.000	0.000	0.000
	35	0.285	42.55	190.295	5.249	0.224	0.064	0.287	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
Matricaria	14	0.775	2.1	243.056	5.493	0.009	0.007	0.015	0.000	0.000	0.000
matricarioides	14	0.992	1.9	269.122	5.595	0.007	0.007	0.014	0.000	0.000	0.000
	14	0.307	1.45	247.440	5.511	0.006	0.002	0.008	0.000	0.000	0.000
	14	0.322	1.48	164.444	5.103	0.009	0.003	0.012	0.000	0.000	0.000
	14	0.195	1.02	117.241	4.764	0.009	0.002	0.010	0.000	0.000	0.000
	14	0.526	2.15	377.193	5.933	0.006	0.003	0.009	0.000	0.000	0.000
	14	0.351	1.82	187.629	5.234	0.010	0.003	0.013	0.000	0.000	0.000
	14	0.125	2.22	308.333	5.731	0.007	0.001	0.008	0.000	0.000	0.000
	14	0.446	2.51	386.154	5.956	0.007	0.003	0.009	0.000	0.000	0.000
	14	0.162	2.42	327.027	5.790	0.007	0.001	0.009	0.000	0.000	0.000
	14	0.270	1.96	311.111	5.740	0.006	0.002	0.008	0.000	0.000	0.000
	14	0.400	1.37	249.091	5.518	0.006	0.002	0.008	0.000	0.000	0.000
	14	0.114	1.19	340.000	5.829	0.004	0.000	0.004	0.000	0.000	0.000
	14	0.194	1.69	469.444	6.152	0.004	0.001	0.004	0.000	0.000	0.000
	14	0.619	1.08	514.286	6.243	0.002	0.001	0.003	0.000	0.000	0.000
Matricaria	21	0.286	6.82	319.588	5.767	0.021	0.006	0.027	0.000	0.000	0.000
matricarioides	21	0.408	3.54	307.292	5.728	0.012	0.005	0.016	0.000	0.000	0.000
	21	0.246	2.8	312.849	5.746	0.009	0.002	0.011	0.000	0.000	0.000
	21	0.464	13.09	334.014	5.811	0.039	0.018	0.057	0.000	0.000	0.000
	21	0.269	3.69	431.579	6.067	0.009	0.002	0.011	0.000	0.000	0.000
	21	0.113	2.7	436.187	6.078	0.006	0.001	0.007	0.000	0.000	0.000
	21	0.301	13.9	259.813	5.560	0.054	0.016	0.070	0.000	0.000	0.000
	21	0.236	11.38	362.883	5.894	0.031	0.007	0.039	0.000	0.000	0.000
	21	0.349	8.51	406.399	6.007	0.021	0.007	0.028	0.000	0.000	0.000
	21	0.670	14.1	360.614	5.888	0.039	0.026	0.065	0.000	0.000	0.000
	21	0.449	7.09	201.420	5.305	0.035	0.016	0.051	0.000	0.000	0.000
	21	0.417	4.13	185.202	5.221	0.022	0.009	0.032	0.000	0.000	0.000
	21	0.254	3.19	224.648	5.415	0.014	0.004	0.018	0.000	0.000	0.000
Matricaria	28	0.237	21.04	592.676	6.385	0.036	0.008	0.044	0.000	0.000	0.000
matricarioides	28	0.252	14.47	498.966	6.213	0.029	0.007	0.036	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	28	0.358	5.27	331.447	5.803	0.016	0.006	0.022	0.000	0.000	0.000
	28	0.158	10.43	422.267	6.046	0.025	0.004	0.029	0.000	0.000	0.000
	28	0.234	21.81	477.243	6.168	0.046	0.011	0.056	0.000	0.000	0.000
	28	0.260	15.99	478.743	6.171	0.033	0.009	0.042	0.000	0.000	0.000
	28	0.330	17.39	562.783	6.333	0.031	0.010	0.041	0.000	0.000	0.000
	28	0.200	5.55	108.824	4.690	0.051	0.010	0.061	0.000	0.000	0.000
	28	0.159	16.54	444.624	6.097	0.037	0.006	0.043	0.000	0.000	0.000
	28	0.227	10.57	469.778	6.152	0.023	0.005	0.028	0.000	0.000	0.000
	28	0.512	4.15	107.235	4.675	0.039	0.020	0.059	0.000	0.000	0.000
	28	0.509	4.14	180.000	5.193	0.023	0.012	0.035	0.000	0.000	0.000
	28	0.571	6.35	274.892	5.616	0.023	0.013	0.036	0.000	0.000	0.000
	28	0.457	14.34	172.356	5.150	0.083	0.038	0.121	0.000	0.000	0.000
Matricaria	35	0.229	36.99	349.622	5.857	0.106	0.024	0.135	0.005	0.000	0.000
matricarioides	35	0.312	75.68	519.067	6.252	0.146	0.046	0.207	0.016	0.000	0.000
	35	0.188	19.56	379.070	5.938	0.052	0.010	0.066	0.004	0.000	0.000
	35	0.272	33.73	357.309	5.879	0.094	0.026	0.139	0.019	0.000	0.000
	35	0.238	36.67	387.632	5.960	0.095	0.023	0.140	0.023	0.000	0.000
	35	0.186	37.14	384.074	5.951	0.097	0.018	0.124	0.009	0.000	0.000
	35	0.439	24.68	250.558	5.524	0.099	0.043	0.163	0.017	0.004	0.000
	35	0.382	18.38	269.107	5.595	0.068	0.026	0.112	0.013	0.004	0.000
	35	0.220	33.55	279.817	5.634	0.120	0.026	0.159	0.013	0.000	0.000
	35	0.550	27.22	281.198	5.639	0.097	0.053	0.162	0.008	0.004	0.000
	35	0.483	18.09	462.660	6.137	0.039	0.019	0.070	0.010	0.002	0.000
	35	0.726	38.26	265.142	5.580	0.144	0.105	0.272	0.014	0.009	0.000
	35	0.877	44.61	284.140	5.649	0.157	0.138	0.295	0.000	0.000	0.000
Rudbeckia	14	0.529	0.13	76.471	4.337	0.002	0.001	0.003	0.000	0.000	0.000
hirta	14	0.053	0.23	121.053	4.796	0.002	0.000	0.002	0.000	0.000	0.000
	14	0.333	0.08	66.667	4.200	0.001	0.000	0.002	0.000	0.000	0.000
	14	0.231	0.23	44.231	3.789	0.005	0.001	0.006	0.000	0.000	0.000
	14	0.391	0.73	158.696	5.067	0.005	0.002	0.006	0.000	0.000	0.000
	14	0.632	0.53	278.947	5.631	0.002	0.001	0.003	0.000	0.000	0.000
	14	0.950	0.35	87.500	4.472	0.004	0.004	0.008	0.000	0.000	0.000
	14	0.333	0.35	72.917	4.289	0.005	0.002	0.006	0.000	0.000	0.000
	14	0.159	0.37	58.730	4.073	0.006	0.001	0.007	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	14	0.261	0.58	126.087	4.837	0.005	0.001	0.006	0.000	0.000	0.000
	14	0.043	0.57	247.826	5.513	0.002	0.000	0.002	0.000	0.000	0.000
	14	0.750	0.25	78.125	4.358	0.003	0.002	0.006	0.000	0.000	0.000
	14	0.412	0.26	152.941	5.030	0.002	0.001	0.002	0.000	0.000	0.000
Rudbeckia	21	0.620	6.8	149.451	5.007	0.046	0.028	0.074	0.000	0.000	0.000
hirta	21	0.387	10.56	209.524	5.345	0.050	0.020	0.070	0.000	0.000	0.000
	21	0.351	6.74	155.802	5.049	0.043	0.015	0.058	0.000	0.000	0.000
	21	0.702	2.43	185.496	5.223	0.013	0.009	0.022	0.000	0.000	0.000
	21	0.448	1.51	105.594	4.660	0.014	0.006	0.021	0.000	0.000	0.000
	21	0.271	1.63	169.792	5.135	0.010	0.003	0.012	0.000	0.000	0.000
	21	0.460	1.63	82.323	4.411	0.020	0.009	0.029	0.000	0.000	0.000
	21	0.225	1.1	107.843	4.681	0.010	0.002	0.013	0.000	0.000	0.000
Rudbeckia	28	1.569	27.81	281.763	5.641	0.099	0.155	0.254	0.000	0.000	0.000
hirta	28	0.725	14.68	322.637	5.777	0.046	0.033	0.079	0.000	0.000	0.000
	28	0.569	6.89	200.875	5.303	0.034	0.020	0.054	0.000	0.000	0.000
	28	0.868	18.69	182.698	5.208	0.102	0.089	0.191	0.000	0.000	0.000
	28	0.528	30.97	216.271	5.377	0.143	0.076	0.219	0.000	0.000	0.000
	28	0.567	10.76	146.395	4.986	0.074	0.042	0.115	0.000	0.000	0.000
	28	0.524	14.58	240.992	5.485	0.061	0.032	0.092	0.000	0.000	0.000
	28	0.937	8.68	156.396	5.052	0.056	0.052	0.108	0.000	0.000	0.000
	28	0.309	36.32	162.578	5.091	0.223	0.069	0.292	0.000	0.000	0.000
	28	0.482	21.2	126.492	4.840	0.168	0.081	0.248	0.000	0.000	0.000
	28	0.388	19.03	152.118	5.025	0.125	0.049	0.174	0.000	0.000	0.000
	28	0.544	14	158.371	5.065	0.088	0.048	0.137	0.000	0.000	0.000
	28	0.501	12.97	147.052	4.991	0.088	0.044	0.132	0.000	0.000	0.000
	28	0.282	34.05	184.154	5.216	0.185	0.052	0.237	0.000	0.000	0.000
Rudbeckia	35	0.569	63.94	173.703	5.157	0.368	0.209	0.578	0.000	0.000	0.000
hirta	35	0.496	106.34	199.512	5.296	0.533	0.264	0.797	0.000	0.000	0.000
	35	0.507	57.92	187.262	5.233	0.309	0.157	0.466	0.000	0.000	0.000
	35	1.189	47.77	243.973	5.497	0.196	0.233	0.429	0.000	0.000	0.000
	35	0.444	78.18	175.883	5.170	0.445	0.197	0.642	0.000	0.000	0.000
	35	0.902	44.47	193.600	5.266	0.230	0.207	0.437	0.000	0.000	0.000
	35	0.935	36.43	189.247	5.243	0.193	0.180	0.373	0.000	0.000	0.000
	35	0.848	41.94	181.323	5.200	0.231	0.196	0.428	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	35	0.609	42.37	242.530	5.491	0.175	0.106	0.281	0.000	0.000	0.000
	35	1.310	33.68	194.345	5.270	0.173	0.227	0.400	0.000	0.000	0.000
	35	0.570	44.36	243.469	5.495	0.182	0.104	0.286	0.000	0.000	0.000
	35	0.842	31.93	261.936	5.568	0.122	0.103	0.225	0.000	0.000	0.000
	35	0.481	32.31	191.070	5.253	0.169	0.081	0.251	0.000	0.000	0.000
	35	0.415	48.14	164.807	5.105	0.292	0.121	0.413	0.000	0.000	0.000
Senecio	14	0.376	3.44	275.420	5.618	0.012	0.005	0.017	0.000	0.000	0.000
vulgaris	14	0.333	3.33	308.048	5.730	0.011	0.004	0.014	0.000	0.000	0.000
	14	0.398	7.12	274.903	5.616	0.026	0.010	0.036	0.000	0.000	0.000
	14	0.538	5.07	216.667	5.378	0.023	0.013	0.036	0.000	0.000	0.000
	14	0.448	2.16	124.138	4.821	0.017	0.008	0.025	0.000	0.000	0.000
	14	0.524	2.51	202.419	5.310	0.012	0.007	0.019	0.000	0.000	0.000
	14	0.500	4.1	253.086	5.534	0.016	0.008	0.024	0.000	0.000	0.000
	14	0.363	2.97	326.374	5.788	0.009	0.003	0.012	0.000	0.000	0.000
	14	0.169	4.05	297.794	5.696	0.014	0.002	0.016	0.000	0.000	0.000
	14	0.265	5.48	250.228	5.522	0.022	0.006	0.028	0.000	0.000	0.000
	14	0.886	0.79	225.714	5.419	0.004	0.003	0.007	0.000	0.000	0.000
Senecio	21	0.352	11.98	262.030	5.568	0.046	0.016	0.062	0.000	0.000	0.000
vulgaris	21	0.204	24.25	217.762	5.383	0.111	0.023	0.134	0.000	0.000	0.000
	21	0.449	6.2	283.753	5.648	0.022	0.010	0.032	0.000	0.000	0.000
	21	0.336	1.77	220.423	5.396	0.008	0.003	0.011	0.000	0.000	0.000
	21	0.260	7.91	337.457	5.821	0.023	0.006	0.030	0.000	0.000	0.000
	21	0.237	13.39	314.319	5.750	0.043	0.010	0.053	0.000	0.000	0.000
	21	0.404	5.45	255.869	5.545	0.021	0.009	0.030	0.000	0.000	0.000
	21	0.288	9.7	268.698	5.594	0.036	0.010	0.047	0.000	0.000	0.000
	21	0.634	8.99	188.075	5.237	0.048	0.030	0.078	0.000	0.000	0.000
	21	0.568	8.28	207.000	5.333	0.040	0.023	0.063	0.000	0.000	0.000
	21	0.304	6.44	193.976	5.268	0.033	0.010	0.043	0.000	0.000	0.000
	21	0.453	7.33	310.593	5.738	0.024	0.011	0.034	0.000	0.000	0.000
	21	0.372	5.81	108.598	4.688	0.054	0.020	0.073	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
Senecio vulgaris	28	0.422	11.13	181.863	5.203	0.061	0.026	0.115	0.028	0.000	0.000
	28	0.343	13.69	191.737	5.256	0.071	0.025	0.101	0.005	0.000	0.000
	28	0.311	15.41	201.438	5.305	0.077	0.024	0.100	0.000	0.000	0.000
	28	0.468	17.7	255.411	5.543	0.069	0.032	0.102	0.000	0.000	0.000
	28	0.209	15.88	125.932	4.836	0.126	0.026	0.153	0.000	0.000	0.000
	28	0.340	29.49	147.745	4.995	0.200	0.068	0.268	0.000	0.000	0.000
	28	0.567	13.82	226.557	5.423	0.061	0.035	0.096	0.000	0.000	0.000
	28	0.615	14.93	212.376	5.358	0.070	0.043	0.114	0.000	0.000	0.000
	28	0.366	20.99	225.942	5.420	0.093	0.034	0.127	0.000	0.000	0.000
	28	0.335	21.76	152.702	5.028	0.143	0.048	0.190	0.000	0.000	0.000
	28	0.305	24.66	138.229	4.929	0.178	0.055	0.233	0.000	0.000	0.000
	28	0.404	15.12	219.767	5.393	0.069	0.028	0.097	0.000	0.000	0.000
	28	0.402	16.04	247.149	5.510	0.065	0.026	0.091	0.000	0.000	0.000
Senecio vulgaris	35	0.330	20.9	145.950	4.983	0.143	0.047	0.193	0.003	0.000	0.000
	35	0.387	19.83	227.931	5.429	0.087	0.034	0.126	0.005	0.000	0.000
	35	0.354	37.97	140.007	4.942	0.271	0.096	0.383	0.016	0.000	0.000
	35	0.333	20.83	162.989	5.094	0.128	0.043	0.170	0.000	0.000	0.000
	35	0.334	23.65	169.899	5.135	0.139	0.047	0.199	0.013	0.000	0.000
	35	0.454	50	138.083	4.928	0.362	0.164	0.541	0.015	0.000	0.000
	35	0.638	34.26	140.583	4.946	0.244	0.155	0.399	0.000	0.000	0.000
	35	0.510	42.56	139.313	4.937	0.306	0.156	0.474	0.013	0.000	0.000
	35	0.384	37.62	182.444	5.206	0.206	0.079	0.288	0.002	0.000	0.000
	35	0.238	40.62	137.695	4.925	0.295	0.070	0.365	0.000	0.000	0.000
	35	0.373	20.56	156.350	5.052	0.132	0.049	0.189	0.008	0.000	0.000
	35	0.397	31.36	162.656	5.092	0.193	0.077	0.279	0.009	0.000	0.000
	35	0.346	37.57	169.387	5.132	0.222	0.077	0.299	0.000	0.000	0.000
	35	0.437	31.1	120.730	4.794	0.258	0.113	0.370	0.000	0.000	0.000
Solidago canadensis	14	0.318	3.35	304.269	5.718	0.011	0.004	0.015	0.000	0.000	0.000
	14	0.314	3.33	349.057	5.855	0.010	0.003	0.013	0.000	0.000	0.000
	14	0.447	5.99	377.204	5.933	0.016	0.007	0.023	0.000	0.000	0.000
	14	0.265	0.73	107.353	4.676	0.007	0.002	0.009	0.000	0.000	0.000
	14	0.375	0.99	206.250	5.329	0.005	0.002	0.007	0.000	0.000	0.000
	14	1.463	0.59	143.902	4.969	0.004	0.006	0.010	0.000	0.000	0.000
	14	0.167	1.65	458.333	6.128	0.004	0.001	0.004	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	14	0.194	1.3	361.111	5.889	0.004	0.001	0.004	0.000	0.000	0.000
	14	0.271	6.28	586.916	6.375	0.011	0.003	0.014	0.000	0.000	0.000
	14	0.391	8.5	357.143	5.878	0.024	0.009	0.033	0.000	0.000	0.000
	14	0.255	7.44	486.275	6.187	0.015	0.004	0.019	0.000	0.000	0.000
Solidago	21	0.485	10.2	282.548	5.644	0.036	0.018	0.054	0.000	0.000	0.000
canadensis	21	0.325	5.2	313.253	5.747	0.017	0.005	0.022	0.000	0.000	0.000
	21	0.297	21.08	269.910	5.598	0.078	0.023	0.110	0.008	0.000	0.000
	21	0.305	7.51	231.077	5.443	0.033	0.010	0.047	0.004	0.000	0.000
	21	0.450	12.94	282.533	5.644	0.046	0.021	0.071	0.004	0.000	0.000
	21	0.312	18.45	222.826	5.406	0.083	0.026	0.119	0.011	0.000	0.000
	21	0.497	9.47	205.423	5.325	0.046	0.023	0.073	0.004	0.000	0.000
	21	1.041	4.88	331.973	5.805	0.015	0.015	0.030	0.000	0.000	0.000
Solidago	28	0.341	27.34	564.876	6.337	0.048	0.017	0.079	0.014	0.000	0.000
canadensis	28	0.167	19.56	626.923	6.441	0.031	0.005	0.042	0.006	0.000	0.000
	28	0.239	40.44	483.732	6.182	0.084	0.020	0.129	0.026	0.000	0.000
	28	0.239	28.26	524.304	6.262	0.054	0.013	0.091	0.024	0.000	0.000
	28	0.249	27.59	572.407	6.350	0.048	0.012	0.073	0.012	0.000	0.000
	28	0.156	26.52	551.351	6.312	0.048	0.008	0.065	0.009	0.000	0.000
	28	0.294	10.96	766.434	6.642	0.014	0.004	0.042	0.023	0.000	0.000
	28	0.672	7.14	96.097	4.565	0.074	0.050	0.154	0.030	0.000	0.000
	28	0.309	21.98	162.214	5.089	0.136	0.042	0.232	0.054	0.000	0.000
	28	0.866	41.33	371.339	5.917	0.111	0.096	0.212	0.004	0.000	0.000
	28	0.757	27.23	441.329	6.090	0.062	0.047	0.117	0.009	0.000	0.000
	28	0.502	28.55	248.477	5.515	0.115	0.058	0.182	0.009	0.000	0.000
	28	0.239	15.92	101.595	4.621	0.157	0.037	0.255	0.061	0.000	0.000
Solidago	35	0.573	41.29	161.541	5.085	0.256	0.146	0.440	0.038	0.000	0.000
canadensis	35	0.502	62.62	221.429	5.400	0.283	0.142	0.550	0.125	0.000	0.000
	35	0.443	56.06	241.742	5.488	0.232	0.103	0.419	0.084	0.000	0.000
	35	0.576	104.71	195.354	5.275	0.536	0.309	1.045	0.200	0.000	0.000
	35	0.240	72.26	223.162	5.408	0.324	0.078	0.498	0.096	0.000	0.000
	35	0.322	77.67	215.093	5.371	0.361	0.116	0.611	0.133	0.000	0.000
	35	0.305	112.26	255.369	5.543	0.440	0.134	0.698	0.125	0.000	0.000
	35	0.672	140.69	179.589	5.191	0.783	0.527	1.348	0.038	0.000	0.000
	35	0.590	53.74	258.241	5.554	0.208	0.123	0.408	0.077	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	35	0.402	71.66	237.994	5.472	0.301	0.121	.552	0.129	0.000	0.000
	35	0.442	57.33	245.735	5.504	0.233	0.103	0.420	0.083	0.000	0.000
	35	0.812	51.04	214.364	5.368	0.238	0.193	0.513	0.082	0.000	0.000
	35	0.958	85.58	212.410	5.359	0.403	0.386	0.893	0.104	0.000	0.000
	35	0.049	66.15	244.096	5.498	0.271	0.013	0.366	0.082	0.000	0.000
	35	0.854	73.72	195.492	5.276	0.377	0.322	0.789	0.090	0.000	0.000
Solidago	14	0.899	3.58	200.000	5.298	0.018	0.016	0.034	0.000	0.000	0.000
graminifolia	14	1.105	3.03	352.326	5.865	0.009	0.010	0.018	0.000	0.000	0.000
	14	0.425	0.55	137.500	4.924	0.004	0.002	0.006	0.000	0.000	0.000
	14	0.714	0.36	102.857	4.633	0.004	0.003	0.006	0.000	0.000	0.000
	14	0.727	1.05	119.318	4.782	0.009	0.006	0.015	0.000	0.000	0.000
	14	0.733	1.37	228.333	5.431	0.006	0.004	0.010	0.000	0.000	0.000
	14	0.221	2.3	154.362	5.039	0.015	0.003	0.018	0.000	0.000	0.000
	14	0.149	1.42	151.064	5.018	0.009	0.001	0.011	0.000	0.000	0.000
	14	0.880	1.3	120.370	4.791	0.011	0.010	0.020	0.000	0.000	0.000
	14	0.664	1.61	142.478	4.959	0.011	0.008	0.019	0.000	0.000	0.000
Solidago	21	4.329	3.39	210.559	5.350	0.016	0.070	0.088	0.002	0.000	0.000
graminifolia	21	3.377	2.93	276.415	5.622	0.011	0.036	0.046	0.000	0.000	0.000
	21	1.318	2.9	341.176	5.832	0.009	0.011	0.020	0.000	0.000	0.000
	21	0.989	2.36	253.763	5.536	0.009	0.009	0.019	0.000	0.000	0.000
	21	0.852	2.1	344.262	5.841	0.006	0.005	0.011	0.000	0.000	0.000
	21	3.931	1.55	267.241	5.588	0.006	0.023	0.029	0.000	0.000	0.000
	21	1.283	1.02	221.739	5.402	0.005	0.006	0.011	0.000	0.000	0.000
	21	0.566	4.88	238.049	5.472	0.021	0.012	0.034	0.002	0.000	0.000
	21	0.659	6.07	178.529	5.185	0.034	0.022	0.059	0.003	0.000	0.000
	21	0.369	4.05	143.617	4.967	0.028	0.010	0.039	0.000	0.000	0.000
	21	0.746	4.86	280.925	5.638	0.017	0.013	0.030	0.000	0.000	0.000
	21	0.694	7.12	190.374	5.249	0.037	0.026	0.074	0.010	0.000	0.000
Solidago	28	1.072	11.73	195.500	5.276	0.060	0.064	0.130	0.006	0.000	0.000
graminifolia	28	1.100	11.85	231.445	5.444	0.051	0.056	0.195	0.087	0.000	0.000
	28	1.917	10.2	264.935	5.579	0.039	0.074	0.116	0.004	0.000	0.000
	28	2.205	6.1	223.443	5.409	0.027	0.060	0.091	0.003	0.000	0.000
	28	1.539	8.33	167.606	5.122	0.050	0.077	0.128	0.002	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	28	1.009	7.64	140.183	4.943	0.055	0.055	0.110	0.000	0.000	0.000
	28	1.439	5.66	173.620	5.157	0.033	0.047	0.080	0.000	0.000	0.000
	28	1.471	7.85	188.702	5.240	0.042	0.061	0.108	0.005	0.000	0.000
	28	0.327	11.86	277.103	5.624	0.043	0.014	0.063	0.007	0.000	0.000
	28	1.244	6.99	159.226	5.070	0.044	0.055	0.110	0.012	0.000	0.000
	28	0.988	11.74	230.196	5.439	0.051	0.050	0.128	0.027	0.000	0.000
	28	0.739	16.38	233.666	5.454	0.070	0.052	0.136	0.014	0.000	0.000
	28	0.428	30.85	238.962	5.476	0.129	0.055	0.195	0.011	0.000	0.000
	28	0.665	16.49	166.062	5.112	0.099	0.066	0.185	0.020	0.000	0.000
Solidago	35	0.778	20.85	252.421	5.531	0.083	0.064	0.155	0.008	0.000	0.000
graminifolia	35	1.489	15.86	254.167	5.538	0.062	0.093	0.194	0.039	0.000	0.000
	35	1.297	64.64	164.646	5.104	0.393	0.509	0.968	0.066	0.000	0.000
	35	1.693	16.82	224.566	5.414	0.075	0.127	0.226	0.024	0.000	0.000
	35	0.439	12.37	191.783	5.256	0.065	0.028	0.121	0.028	0.000	0.000
	35	0.550	28.77	240.753	5.484	0.120	0.066	0.267	0.082	0.000	0.000
	35	0.753	22.48	240.943	5.485	0.093	0.070	0.181	0.017	0.000	0.000
	35	0.760	29.46	263.036	5.572	0.112	0.085	0.229	0.032	0.000	0.000
	35	0.706	30.82	166.775	5.117	0.185	0.130	0.333	0.018	0.000	0.000
	35	0.797	59.89	111.589	4.715	0.537	0.428	1.029	0.064	0.000	0.000
	35	1.938	23.23	146.932	4.990	0.158	0.306	0.502	0.038	0.000	0.000
	35	0.814	34.21	157.941	5.062	0.217	0.176	0.435	0.042	0.000	0.000
	35	1.069	23.64	202.397	5.310	0.117	0.125	0.261	0.019	0.000	0.000
	35	0.793	21.32	162.997	5.094	0.131	0.104	0.247	0.012	0.000	0.000
Sonchus	14	0.431	4.45	208.236	5.339	0.021	0.009	0.031	0.000	0.000	0.000
asper	14	0.138	6.84	470.750	6.154	0.015	0.002	0.017	0.000	0.000	0.000
	14	0.221	9.27	410.359	6.017	0.023	0.005	0.028	0.000	0.000	0.000
	14	0.283	8.11	499.077	6.213	0.016	0.005	0.021	0.000	0.000	0.000
	14	0.500	1.68	221.053	5.398	0.008	0.004	0.011	0.000	0.000	0.000
	14	0.105	3.04	533.333	6.279	0.006	0.001	0.006	0.000	0.000	0.000
	14	0.366	1.36	331.707	5.804	0.004	0.002	0.006	0.000	0.000	0.000
	14	0.245	2.06	388.679	5.963	0.005	0.001	0.007	0.000	0.000	0.000
	14	0.477	2.22	341.538	5.833	0.007	0.003	0.010	0.000	0.000	0.000
	14	0.659	2.22	504.545	6.224	0.004	0.003	0.007	0.000	0.000	0.000
	14	0.276	1.97	339.655	5.828	0.006	0.002	0.007	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	14	0.231	1.85	284.615	5.651	0.007	0.002	0.008	0.000	0.000	0.000
	14	0.087	2.12	460.870	6.133	0.005	0.000	0.005	0.000	0.000	0.000
	14	0.238	3.85	458.333	6.128	0.008	0.002	0.010	0.000	0.000	0.000
	14	0.181	3.12	433.333	6.072	0.007	0.001	0.009	0.000	0.000	0.000
	14	0.136	1.67	206.173	5.329	0.008	0.001	0.009	0.000	0.000	0.000
Sonchus	21	0.193	20.04	477.712	6.169	0.042	0.008	0.050	0.000	0.000	0.000
asper	21	0.357	21.21	283.822	5.648	0.075	0.027	0.101	0.000	0.000	0.000
	21	0.192	17.72	365.889	5.902	0.048	0.009	0.058	0.000	0.000	0.000
	21	0.323	29.26	306.195	5.724	0.096	0.031	0.126	0.000	0.000	0.000
	21	0.529	8.71	484.967	6.184	0.018	0.010	0.027	0.000	0.000	0.000
	21	0.249	22.06	421.717	6.044	0.052	0.013	0.065	0.000	0.000	0.000
	21	0.259	8.97	493.943	6.202	0.018	0.005	0.023	0.000	0.000	0.000
	21	0.393	2.9	87.613	4.473	0.033	0.001	0.005	0.000	0.000	0.000
	21	0.348	21.7	335.394	5.815	0.065	0.023	0.087	0.000	0.000	0.000
	21	0.356	4.75	64.979	4.174	0.073	0.026	0.099	0.000	0.000	0.000
	21	0.397	7.81	574.265	6.353	0.014	0.005	0.019	0.000	0.000	0.000
	21	0.193	5.51	408.148	6.012	0.014	0.003	0.016	0.000	0.000	0.000
	21	0.029	26.02	250.192	5.522	0.104	0.003	0.107	0.000	0.000	0.000
Sonchus	28	0.180	57.21	517.738	6.249	0.111	0.020	0.130	0.000	0.000	0.000
asper	28	0.246	28.24	521.996	6.258	0.054	0.013	0.067	0.000	0.000	0.000
	28	0.324	142.73	248.399	5.515	0.575	0.186	0.761	0.000	0.000	0.000
	28	0.429	14.46	389.757	5.966	0.037	0.016	0.053	0.000	0.000	0.000
	28	0.587	52.89	246.804	5.509	0.214	0.126	0.340	0.000	0.000	0.000
	28	0.521	68.56	400.234	5.992	0.171	0.089	0.261	0.000	0.000	0.000
	28	0.897	36.73	509.431	6.233	0.072	0.065	0.137	0.000	0.000	0.000
	28	0.945	45.31	395.375	5.980	0.115	0.108	0.223	0.000	0.000	0.000
	28	0.769	65.43	427.368	6.058	0.153	0.118	0.271	0.000	0.000	0.000
	28	1.202	49.93	355.627	5.874	0.140	0.169	0.309	0.000	0.000	0.000
	28	0.674	62.62	357.624	5.879	0.175	0.118	0.293	0.000	0.000	0.000
	28	0.811	36.79	468.662	6.150	0.079	0.064	0.142	0.000	0.000	0.000
	28	0.714	43.2	510.035	6.234	0.085	0.061	0.145	0.000	0.000	0.000
Sonchus	35	0.283	68.41	287.196	5.660	0.238	0.067	0.353	0.037	0.010	0.000
asper	35	0.455	35.48	387.336	5.959	0.092	0.042	0.134	0.000	0.001	0.000
	35	0.611	44.4	434.868	6.075	0.102	0.062	0.165	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	35	0.479	102.6	238.162	5.473	0.431	0.206	0.683	0.040	0.006	0.000
	35	0.706	47.8	259.641	5.559	0.184	0.130	0.985	0.551	0.110	0.010
	35	0.392	39.65	270.648	5.601	0.147	0.058	0.204	0.000	0.000	0.000
	35	0.306	31.02	341.630	5.834	0.091	0.028	0.119	0.000	0.000	0.000
	35	0.255	62.7	268.408	5.593	0.234	0.060	0.355	0.062	0.000	0.000
	35	0.335	62.69	222.147	5.403	0.282	0.095	0.392	0.016	0.000	0.000
	35	0.424	95.17	167.464	5.121	0.568	0.241	0.810	0.000	0.000	0.000
	35	0.421	49.8	187.571	5.234	0.266	0.112	0.377	0.000	0.000	0.000
	35	0.798	115.52	356.543	5.876	0.324	0.258	0.621	0.024	0.014	0.000
	35	0.639	123	336.433	5.818	0.366	0.234	0.666	0.041	0.026	0.000
	35	0.498	102.72	252.632	5.532	0.407	0.203	0.686	0.034	0.043	0.000
Tanacetum	14	0.207	2.26	245.652	5.504	0.009	0.002	0.011	0.000	0.000	0.000
vulgare	14	0.242	2.45	191.406	5.254	0.013	0.003	0.016	0.000	0.000	0.000
	14	0.407	3.13	223.571	5.410	0.014	0.006	0.020	0.000	0.000	0.000
	14	0.220	1.01	110.989	4.709	0.009	0.002	0.011	0.000	0.000	0.000
	14	0.101	5.43	305.056	5.720	0.018	0.002	0.020	0.000	0.000	0.000
	14	0.261	2.84	255.856	5.545	0.011	0.003	0.014	0.000	0.000	0.000
	14	0.917	1.2	500.000	6.215	0.002	0.002	0.005	0.000	0.000	0.000
	14	2.111	1.49	1655.556	7.412	0.001	0.002	0.003	0.000	0.000	0.000
	14	0.301	2.09	286.301	5.657	0.007	0.002	0.010	0.000	0.000	0.000
	14	0.703	1.98	535.135	6.283	0.004	0.003	0.006	0.000	0.000	0.000
	14	0.725	1.53	300.000	5.704	0.005	0.004	0.009	0.000	0.000	0.000
	14	0.488	4.77	197.107	5.284	0.024	0.012	0.036	0.000	0.000	0.000
	14	0.412	3.88	136.620	4.917	0.028	0.012	0.040	0.000	0.000	0.000
Tanacetum	21	0.279	6.78	245.297	5.502	0.028	0.008	0.035	0.000	0.000	0.000
vulgare	21	0.262	7.12	263.119	5.573	0.027	0.007	0.034	0.000	0.000	0.000
	21	0.274	8.84	336.634	5.819	0.026	0.007	0.033	0.000	0.000	0.000
	21	0.295	7.79	370.952	5.916	0.021	0.006	0.027	0.000	0.000	0.000
	21	0.196	16.56	328.571	5.795	0.050	0.010	0.060	0.000	0.000	0.000
	21	1.823	7.32	296.476	5.692	0.025	0.045	0.070	0.000	0.000	0.000
	21	0.355	9.35	251.344	5.527	0.037	0.013	0.050	0.000	0.000	0.000
	21	0.192	12.77	401.068	5.994	0.032	0.006	0.038	0.000	0.000	0.000
	21	0.260	8.01	217.073	5.380	0.037	0.010	0.047	0.000	0.000	0.000
	21	0.313	3.91	214.835	5.370	0.018	0.006	0.024	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	21	0.442	3.97	192.718	5.261	0.021	0.009	0.030	0.000	0.000	0.00
	21	0.292	11.57	267.824	5.590	0.043	0.013	0.056	0.000	0.000	0.000
Tanacetum	28	0.342	20.06	248.575	5.516	0.081	0.028	0.108	0.000	0.000	0.000
vulgare	28	0.462	13.82	301.089	5.707	0.046	0.021	0.067	0.000	0.000	0.000
	28	0.558	5.14	454.867	6.120	0.011	0.006	0.018	0.000	0.000	0.000
	28	0.499	23.64	170.933	5.141	0.138	0.069	0.207	0.000	0.000	0.000
	28	0.458	66.92	116.140	4.755	0.576	0.264	0.840	0.000	0.000	0.000
	28	0.450	42.67	119.826	4.786	0.356	0.160	0.516	0.000	0.000	0.000
	28	0.521	33.91	126.153	4.837	0.269	0.140	0.409	0.000	0.000	0.000
	28	0.440	38.55	125.325	4.831	0.308	0.135	0.497	0.054	0.000	0.000
	28	0.328	38.93	126.519	4.840	0.308	0.101	0.409	0.000	0.000	0.000
	28	0.499	36.5	225.866	5.420	0.162	0.081	0.242	0.000	0.000	0.000
	28	0.458	40.25	198.569	5.291	0.203	0.093	0.296	0.000	0.000	0.000
	28	0.456	26.34	151.292	5.019	0.174	0.079	0.254	0.000	0.000	0.000
	28	0.789	42.79	211.204	5.353	0.203	0.160	0.363	0.000	0.000	0.000
Tanacetum	35	0.775	188.24	223.271	5.408	0.843	0.653	1.756	0.260	0.000	0.000
vulgare	35	0.836	121.15	374.845	5.927	0.323	0.270	0.789	0.196	0.000	0.000
	35	0.513	47.44	547.174	6.305	0.087	0.045	0.167	0.036	0.000	0.000
	35	0.717	72.77	355.322	5.873	0.205	0.147	0.408	0.057	0.000	0.000
	35	0.474	85.52	185.229	5.222	0.462	0.219	0.755	0.074	0.000	0.000
	35	0.687	79.48	194.613	5.271	0.408	0.281	0.748	0.059	0.000	0.000
	35	0.532	46.48	171.260	5.143	0.271	0.145	0.458	0.043	0.000	0.000
	35	0.948	35.68	340.458	5.830	0.105	0.099	0.204	0.000	0.000	0.000
	35	0.607	41.24	302.346	5.712	0.136	0.083	0.229	0.010	0.000	0.000
	35	0.575	31.07	205.218	5.324	0.151	0.087	0.252	0.013	0.000	0.000
	35	0.575	44.93	287.460	5.661	0.156	0.090	0.260	0.014	0.000	0.000
	35	0.835	73.23	193.935	5.268	0.378	0.315	0.727	0.034	0.000	0.000
	35	0.805	29.92	212.500	5.359	0.141	0.113	0.254	0.000	0.000	0.000
	35	0.553	73.88	218.193	5.385	0.339	0.187	0.550	0.024	0.000	0.000
Taraxacum	14	0.426	0.75	122.951	4.812	0.006	0.003	0.009	0.000	0.000	0.000
officinale	14	0.289	2.11	185.088	5.221	0.011	0.003	0.015	0.000	0.000	0.000
	14	0.737	1.97	129.605	4.864	0.015	0.011	0.026	0.000	0.000	0.000
	14	0.494	0.8	98.765	4.593	0.008	0.004	0.012	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	14	0.672	2.96	119.838	4.786	0.025	0.017	0.041	0.000	0.000	0.000
	14	0.273	2.65	219.008	5.389	0.012	0.003	0.015	0.000	0.000	0.000
Taraxacum	21	0.359	4.32	469.565	6.152	0.00	0.003	0.013	0.000	0.000	0.000
officinale	21	0.238	12.68	485.824	6.186	0.026	0.006	0.032	0.000	0.000	0.000
	21	0.423	9.27	284.356	5.650	0.03	0.014	0.046	0.000	0.000	0.000
	21	0.340	7.02	345.813	5.846	0.020	0.007	0.027	0.000	0.000	0.000
	21	0.376	6.77	285.654	5.655	0.024	0.009	0.033	0.000	0.000	0.000
	21	0.202	5.71	303.723	5.716	0.019	0.004	0.023	0.000	0.000	0.000
Taraxacum	28	0.380	43.92	202.117	5.309	0.217	0.083	0.300	0.000	0.000	0.000
officinale	28	0.524	15.28	153.260	5.032	0.100	0.052	0.152	0.000	0.000	0.000
	28	0.784	44.25	214.910	5.370	0.206	0.162	0.367	0.000	0.000	0.000
	28	0.421	12.34	153.292	5.032	0.081	0.034	0.114	0.000	0.000	0.000
	28	0.535	19.61	170.078	5.136	0.115	0.062	0.177	0.000	0.000	0.000
Taraxacum	35	0.530	103.07	221.418	5.400	0.466	0.247	0.712	0.000	0.000	0.000
officinale	35	0.648	116.34	248.430	5.515	0.468	0.304	0.772	0.000	0.000	0.000
	35	0.645	85.52	145.319	4.979	0.589	0.380	0.968	0.000	0.000	0.000
	35	0.521	51.81	221.979	5.403	0.233	0.122	0.355	0.000	0.000	0.000
	35	0.518	53.16	232.954	5.451	0.228	0.118	0.347	0.000	0.000	0.000
	35	0.591	49.12	238.215	5.473	0.206	0.122	0.328	0.000	0.000	0.000
	35	0.387	41.47	287.786	5.662	0.144	0.056	0.200	0.000	0.000	0.000
	35	0.517	40.69	244.973	5.501	0.166	0.086	0.252	0.000	0.000	0.000
	35	0.417	37.61	332.832	5.808	0.113	0.047	0.160	0.000	0.000	0.000
	35	0.383	22.7	155.693	5.048	0.146	0.056	0.202	0.000	0.000	0.000
Tragopogon	14	0.330	13.55	277.664	5.626	0.049	0.016	0.065	0.000	0.000	0.000
pratensis	14	0.200	4.7	254.054	5.538	0.019	0.004	0.022	0.000	0.000	0.000
	14	0.196	5.58	295.238	5.688	0.019	0.004	0.023	0.000	0.000	0.000
	14	0.266	6.63	304.128	5.717	0.022	0.006	0.028	0.000	0.000	0.000
	14	0.228	7.22	432.335	6.069	0.017	0.004	0.021	0.000	0.000	0.000
	14	0.157	5.43	275.635	5.619	0.020	0.003	0.023	0.000	0.000	0.000
	14	0.124	5.71	284.080	5.649	0.020	0.003	0.023	0.000	0.000	0.000
	14	0.131	1.56	157.576	5.060	0.010	0.001	0.011	0.000	0.000	0.000
	14	0.343	1.44	205.714	5.326	0.007	0.002	0.009	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
	14	2.483	2.63	176.510	5.173	0.015	0.037	0.052	0.000	0.000	0.000
	14	0.509	1.68	150.000	5.011	0.011	0.006	0.017	0.000	0.000	0.000
	14	0.333	4.65	140.909	4.948	0.033	0.011	0.044	0.000	0.000	0.000
	14	0.193	1.63	90.055	4.500	0.018	0.004	0.022	0.000	0.000	0.000
	14	0.466	4.61	142.284	4.958	0.032	0.015	0.048	0.000	0.000	0.000
Tragopogon	21	0.248	6.62	150.455	5.014	0.044	0.011	0.055	0.000	0.000	0.000
pratensis	21	3.049	6.99	229.180	5.435	0.031	0.093	0.124	0.000	0.000	0.000
	21	0.338	6.37	187.353	5.233	0.034	0.012	0.046	0.000	0.000	0.000
	21	0.333	5.28	115.536	4.750	0.046	0.015	0.061	0.000	0.000	0.000
	21	0.568	10	191.205	5.253	0.052	0.030	0.082	0.000	0.000	0.000
	21	0.474	8.08	207.179	5.334	0.039	0.019	0.058	0.000	0.000	0.000
	21	0.655	3.9	118.182	4.772	0.033	0.022	0.055	0.000	0.000	0.000
	21	0.739	6.81	104.608	4.650	0.065	0.048	0.113	0.000	0.000	0.000
	21	0.538	5.43	105.029	4.654	0.052	0.028	0.080	0.000	0.000	0.000
	21	0.424	7.12	95.828	4.563	0.074	0.032	0.106	0.000	0.000	0.000
	21	0.492	9.59	111.382	4.713	0.086	0.042	0.129	0.000	0.000	0.000
	21	0.632	5.92	107.246	4.675	0.055	0.035	0.090	0.000	0.000	0.000
Tragopogon	28	0.454	9.82	152.248	5.026	0.065	0.029	0.094	0.000	0.000	0.000
pratensis	28	0.456	8.47	179.830	5.192	0.047	0.022	0.069	0.000	0.000	0.000
	28	0.431	10.58	190.975	5.252	0.055	0.024	0.079	0.000	0.000	0.000
	28	0.460	15.1	234.109	5.456	0.065	0.030	0.094	0.000	0.000	0.000
	28	0.434	8.99	169.623	5.134	0.053	0.023	0.076	0.000	0.000	0.000
	28	0.829	25.14	275.356	5.618	0.091	0.076	0.167	0.000	0.000	0.000
	28	0.336	5.7	145.038	4.977	0.039	0.013	0.053	0.000	0.000	0.000
	28	0.405	6.19	180.466	5.196	0.034	0.014	0.048	0.000	0.000	0.000
	28	0.178	7.31	182.750	5.208	0.040	0.007	0.047	0.000	0.000	0.000
	28	0.457	13.53	139.917	4.941	0.097	0.044	0.141	0.000	0.000	0.000
	28	0.514	11.85	165.966	5.112	0.071	0.037	0.108	0.000	0.000	0.000
	28	0.502	11.1	176.190	5.172	0.063	0.032	0.095	0.000	0.000	0.000
	28	0.404	13.11	153.154	5.031	0.086	0.035	0.120	0.000	0.000	0.000
	28	0.705	13.02	145.964	4.983	0.089	0.063	0.152	0.000	0.000	0.000

Species	Harvest day	Root/Shoot (g/g)	Leaf area (cm^2)	SLA (cm^2/g)	LN(SLA) (cm^2/g)	Leaf d.w. (g)	Root d.w. (g)	Total d.w. (g)	Stem d.w. (g)	Flower d.w. (g)	Seeds d.w. (g)
Tragopogon pratensis	35	0.833	44.09	158.997	5.069	0.277	0.231	0.508	0.000	0.000	0.000
	35	0.989	39.58	206.039	5.328	0.192	0.190	0.382	0.000	0.000	0.000
	35	1.009	46.97	166.856	5.117	0.282	0.284	0.565	0.000	0.000	0.000
	35	0.424	60.37	182.995	5.209	0.330	0.140	0.470	0.000	0.000	0.000
	35	0.791	47.11	134.255	4.900	0.351	0.278	0.628	0.000	0.000	0.000
	35	0.879	19.51	160.049	5.075	0.122	0.107	0.229	0.000	0.000	0.000
	35	1.160	11.75	136.469	4.916	0.086	0.100	0.186	0.000	0.000	0.000
	35	1.060	16.4	164.000	5.100	0.100	0.106	0.206	0.000	0.000	0.000
	35	0.288	19.43	184.872	5.220	0.105	0.030	0.135	0.000	0.000	0.000
	35	0.719	28.49	146.103	4.984	0.195	0.140	0.335	0.000	0.000	0.000
	35	0.715	29.6	172.796	5.152	0.171	0.122	0.294	0.000	0.000	0.000
	35	0.696	27.55	158.061	5.063	0.174	0.121	0.296	0.000	0.000	0.000
	35	0.791	26.55	171.512	5.145	0.155	0.123	0.277	0.000	0.000	0.000
	35	0.610	30.55	149.828	5.009	0.204	0.124	0.328	0.000	0.000	0.000

Appendix 5. Data set of 31 species used in chapter II

Species	Harvest Day	SLA	RGR	Toxicity (LC_{50})	Toxicity ($1/LC_{50}$)	root:shoot	Total Nitrog.	Leaf Nitrog.	Leaf Phen.	Root Phen.	Total Phen.
Achillea	14	273.056	0.175	10	0.1	0.527	4.952	5.53	0.788	2.762	1.261
millefolium	21	205.047	0.175	6	0.167	0.278	4.443	5.007	0.462	0.492	0.468
	28	213.236	0.175	7	0.143	0.512	4.653	5.377	0.443	0.539	0.472
	35	192.686	0.175	3	0.333	0.474	4.299	4.387	0.661	0.622	0.649
Arctium	14	233.793	0.11	17	0.059	0.287	5.345	5.599	0.756	1	0.822
lappa	21	204.577	0.11	19	0.053	0.202	.	5.136	0.582	0.759	0.658
	28	277.571	0.11	100	.	0.293	4.204	4.553	0.67	1.007	0.799
	35	144.922	0.11	100	.	0.345	4.148	4.086	1.296	1.548	1.386
Arctium	14	215.276	0.141	113	.	0.381	5.055	5.308	0.581	0.556	0.575
minus	21	167.641	0.141	68	0.015	0.705	3.64	3.827	0.785	0.921	0.809
	28	127.301	0.141	105	.	0.591	3.283	3.54	0.68	0.94	0.744
	35	144.845	0.141	17	0.059	0.565	3.363	3.548	0.707	0.637	0.689
Artemia	14	389.829	0.226	37	0.027	0.526	4.222	4.993	1.161	0.392	0.918
vulgaris	21	382.117	0.226	22	0.045	0.367	4.489	5.761	0.795	0.389	0.651
	28	337.885	0.226	100	.	0.52	4.079	5.648	0.793	0.628	0.674
	35	269.922	0.226	100	.	0.763	3.743	5.67	0.608	0.677	0.594
Bidens	14	290.056	0.108	16	0.063	0.366	4.56	5.673	0.946	0.366	0.741
cernua	21	363.229	0.108	15	0.067	0.36	5.228	7.014	0.946	0.401	0.722
	28	369.093	0.108	19	0.053	0.455	5.181	7.552	0.753	0.379	0.56
	35	344.136	0.108	3	0.333	0.597	4.687	7.404	0.907	0.2	0.562
Bidens	14	258.222	0.191	100	.	0.364	6.12	8.136	1.247	0.42	1.017
frondosa	21	336.594	0.191	100	.	0.439	5.194	8.135	1.417	0.372	0.969
	28	436.463	0.191	100	.	0.792	3.924	8.111	1.094	0.525	0.793
	35	298.963	0.191	100	.	0.814	3.566	7.979	1.24	0.693	0.802
Centaurea	14	9.571	0.152	.	.	0.826	.	.	1.609	0.558	1.15
nigra	21	157.903	0.152	49	0.02	0.441	.	.	1.604	0.734	1.347
	28	187.593	0.152	39	0.026	0.434	.034	4.323	1.558	1.077	1.413
	35	157.23	0.152	19	0.053	0.43	5.461	5.886	1.541	0.828	1.326
Chrysanthemum	14	117.984	0.151	20	0.05	0.453	5.104	6.013	0.742	0.53	0.676
leucanthemum	21	442.135	0.151	52	0.019	0.299	5.43	5.506	0.683	0.626	0.67

Species	Harvest Day	SLA	RGR	Toxicity (LC_{50})	Toxicity ($1/LC_{50}$)	root:shoot	Total Nitrog.	Leaf Nitrog.	Leaf Phen.	Root Phen.	Total Phen.
	28	351.378	0.151	4	0.25	0.34	5.836	6.648	0.642	0.407	0.583
	35	143.099	0.151	17	0.059	0.323	5.122	6.038	0.704	0.451	0.643
Cichorium	14	185.144	0.141	69	0.014	0.407	5.86	5.999	0.865	0.683	0.811
intybus	21	311.072	0.141	63	0.016	0.494	5.979	7.533	1.125	0.422	0.889
	28	381.749	0.141	61	0.016	0.236	5.298	5.923	0.468	0.42	0.459
	35	306.966	0.141	100	.	0.403	4.801	5.387	0.567	0.286	0.491
Cirsium	14	197.891	0.116	29	0.034	0.244	5.009	5.437	0.64	0.54	0.621
arvense	21	301.619	0.116	.	.	0.157	5.012	5.371	0.65	0.366	0.611
	28	420.972	0.116	100	.	0.238	4.536	5.275	0.651	0.536	0.607
	35	211.332	0.116	99	.	0.389	4.313	5.312	0.648	0.46	0.564
Erigeron	14	608.769	0.165	38	0.026	0.648	.	.	1.023	.	0.702
canadensis	21	695.708	0.165	6	0.167	0.486	.	5.631	1.273	0.534	1.049
	28	306.974	0.165	23	0.043	0.474	5.244	5.983	1.137	0.523	0.953
	35	302.679	0.165	30	0.033	0.541	4.948	5.592	0.958	0.451	0.789
Eupatorium	14	.	0.198	.	.	.	.	.	.	.	.
maculatum	21	310.127	0.198	.	.	0.394	4.41	5.886	1.449	0.971	1.215
	28	334.094	0.198	100	.	0.557	3.789	5.271	1.899	0.608	1.225
	35	271.309	0.198	22	0.045	0.831	3.571	5.178	2.587	0.506	1.443
Eupatorium	14	375.759	0.21	16	0.063	0.456	.	.	0.635	1.035	0.841
rugosum	21	263.661	0.21	41	0.024	0.328	4.067	5.039	2.381	0.526	1.705
	28	459.465	0.21	33	0.03	0.432	4.096	5.441	2.364	0.349	1.638
	35	252.074	0.21	14	0.071	0.403	3.825	5.308	1.872	0.644	1.257
Galinsoga	14	369.284	0.156	28	0.036	0.404	6.058	8.052	0.619	0.385	0.547
ciliata	21	421.662	0.156	100	.	0.409	5.754	7.474	0.953	0.202	0.749
	28	534.595	0.156	46	0.022	0.614	4.206	7.099	0.806	0.51	0.59
	35	551.091	0.156	24	0.042	0.719	3.851	6.913	0.577	0.555	0.442
Hieracium	14	184.674	0.157	21	0.048	0.543	.	.	0.743	0.51	0.681
aurantiacum	21	174.267	0.157	38	0.026	0.419	.	.	0.972	0.579	0.83
	28	152.107	0.157	46	0.022	0.409	.	.	0.954	0.607	0.809
	35	206.072	0.157	17	0.059	0.259	4.67	4.623	1.172	0.507	1.034
Hieracium	14	262.035	0.147	100	.	0.284	.	.	0.469	1.275	0.686
venosum	21	211.258	0.147	30	0.033	0.316	.	.	0.819	0.18	0.677
	28	221.99	0.147	49	0.02	0.366	4.826	4.177	1.24	0.56	1.071

Species	Harvest Day	SLA	RGR	Toxicity (LC_{50})	Toxicity ($1/LC_{50}$)	root:shoot	Total Nitrog.	Leaf Nitrog.	Leaf Phen.	Root Phen.	Total Phen.
	5	331.828	0.147	40	0.025	0.832	5.181	4.298	0.884	0.556	0.746
Hieracium	14	183.41	0.179	96	.	0.22	.	4.74	1.39	0.964	1.32
vulgatum	21	173.658	0.179	21	0.048	0.348	.	3.683	1.299	0.655	1.131
	28	346.007	0.179	100	.	0.143	4.083	3.841	1.099	0.685	1.046
	35	291.022	0.179	32	0.031	0.214	3.643	3.163	1.867	0.594	1.654
Lactuca	14	217.395	0.146	57	0.018	0.316	.	4.424	1.187	0.36	1.009
biennis	21	231.845	0.146	100	.	0.388	4.515	4.568	1.142	0.414	0.922
	28	271.986	0.146	30	0.033	0.552	.053	5.382	1.131	0.681	0.971
	35	268.944	0.146	42	0.024	0.439	5.094	5.567	.	.	.
Lactuca	14	497.018	0.172	68	0.015	0.228	.	6.046	0.973	0.416	0.87
canadensis	21	322.704	0.172	63	0.016	0.286	.	7.121	0.842	0.441	0.783
	28	444.527	0.172	82	0.012	0.348	5.32	5.928	0.768	0.51	0.704
	35	400.496	0.172	100	.	0.379	5.355	6.117	1.002	0.554	0.879
Lactuca	14	226.985	0.133	38	0.026	0.604	.	.	1.929	0.582	1.457
muralis	21	267.824	0.133	27	0.037	0.515	.	4.072	1.972	0.442	1.5
	28	239.375	0.133	24	0.042	0.511	4.333	4.142	2.806	0.611	2.072
	35	255.526	0.133	100	.	0.498	4.49	4.997	3.459	0.537	2.52
Lapsana	14	143.996	0.206	26	0.038	0.47	.	.	1.353	0.521	1.092
communis	21	222.718	0.206	100	.	0.276	4.395	4.496	1.318	0.579	1.161
	28	393.98	0.206	18	0.056	0.324	4.216	4.433	1.002	0.301	0.836
	35	315.235	0.206	100	.	0.386	4.199	4.387	1.347	0.503	1.118
Leontodon	14	325.237	0.114	10	0.1	0.59	.	5.666	1.038	0.499	0.839
autumnalis	21	319.702	0.114	100	.	0.489	5.502	6.208	0.553	0.429	0.522
	28	474.781	0.114	100	.	0.311	5.742	6.476	0.447	0.46	0.45
	35	349.739	0.114	.	.	0.494	5.366	6.002	0.723	0.549	0.676
Matricaria	14	281.319	0.13	40	0.025	0.387	4.278	5.17	0.783	0.383	0.671
matricarioides	21	307.918	0.13	47	0.0213	0.343	4.356	5.057	0.685	0.534	0.643
	28	318.518	0.13	29	0.0345	0.319	5.257	5.964	0.616	0.469	0.58
	35	335.287	0.13	28	0.0357	0.392	5.487	6.654	0.616	0.457	0.557
Rudbeckia	14	104.121	0.221	74	0.0135	0.391	.	.	0.846	0.511	0.754
hirta	21	139.577	0.221	49	0.0204	0.433	4.278	4.321	1.914	0.716	1.543
	28	184.612	0.221	100	.	0.628	4.144	4.617	1.203	0.722	1.03
	35	200.953	0.221	26	0.038	0.723	4.716	5.775	0.939	0.369	0.712

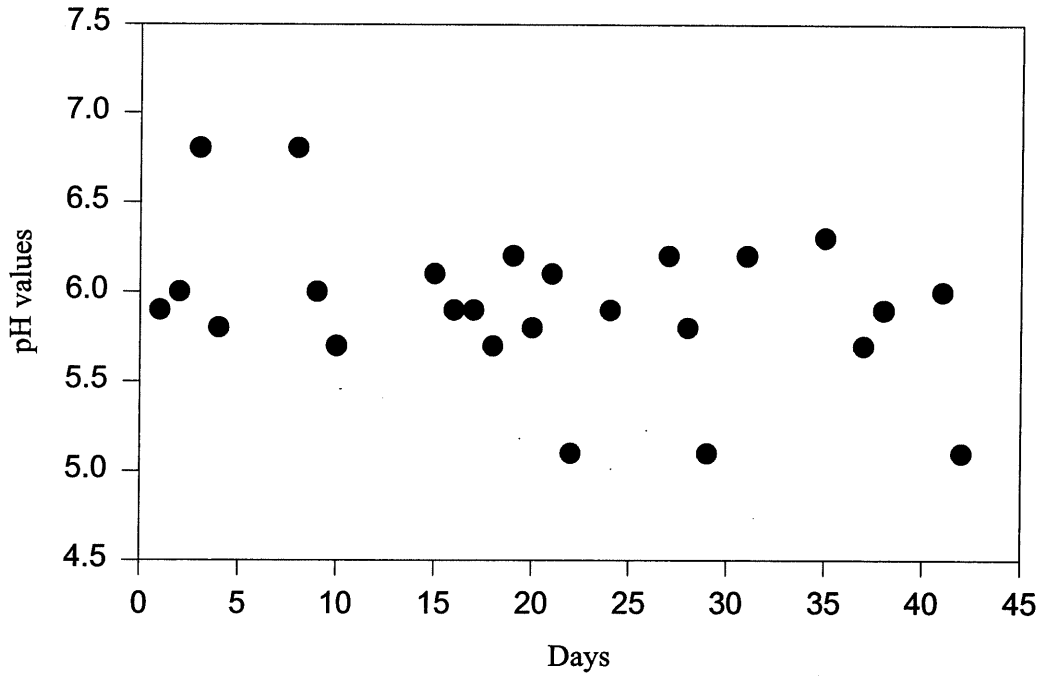
Species	Harvest Day	SLA	RGR	Toxicity (LC_{50})	Toxicity ($1/LC_{50}$)	root:shoot	Total Nitrog.	Leaf Nitrog.	Leaf Phen.	Root Phen.	Total Phen.
Senecio vulgaris	14	243.248	0.13	4	0.25	0.436	5.156	5.581	0.667	0.482	0.613
	21	234.899	0.13	7	0.143	0.374	5.117	5.284	0.68	0.576	0.653
	28	189.843	0.13	29	0.034	0.391	4.661	4.777	0.54	0.192	0.439
	35	154.848	0.13	11	0.091	.394	5.845	6.265	0.602	0.194	0.484
Solidago canadensis	14	305.372	0.182	21	0.048	0.405	.	5.006	0.637	0.572	0.619
	21	264.146	0.182	22	0.045	0.464	4.434	6.308	0.659	0.538	0.627
	28	354.591	0.182	100	.	0.387	4.139	5.339	1.008	0.584	0.806
	35	218.322	0.182	7	0.143	0.516	4.459	6.418	0.747	0.362	0.596
Solidago graminifolia	14	159.8	0.151	27	0.037	0.652 .	6.122	0.682	0.516	0.616	
	21	238.312	0.151	31	0.032	1.593	3.356	4.889	0.931	0.401	0.645
	28	202.442	0.151	23	0.043	1.153	4.306	6.164	0.694	0.289	0.537
	35	192.917	0.151	42	0.024	0.991 .	7.048	1.013	0.51	0.772	
Sonchus asper	14	364.228	0.177	5	0.2	0.286	5.494	6.105	1.102	0.814	1.039
	21	301.732	0.177	11	0.091	0.294	5.732	6.191	0.996	0.766	0.948
	28	400.24	0.177	48	0.021	0.639	4.558	5.474	0.682	0.366	0.566
	35	277.052	0.177	0.2	5	0.472	4.553	5.684	0.585	0.347	0.543
Tanacetum vulgare	14	287.887	0.178	.	.	0.546 .	5.61	0.906	0.466	0.788	
	21	275.418	0.178	3	0.333	0.415 .	5.75	0.58	0.406	0.532	
	28	181.512	0.178	65	0.015	0.481	4.054	4.771	1.101	0.645	0.955
	35	257.005	0.178	18	0.056	0.674	3.745	4.65	1.12	0.701	0.887
Taraxacum officinale	14	140.356	0.156	7	0.143	0.482	.	.	1.294	0.513	1.024
	21	353.345	0.156	8	0.125	0.323 .	5.426	0.814	0.511	0.74	
	28	176.966	0.156	95	0.1	0.529	4.73	4.627	0.803	0.589	0.727
	35	226.776	0.156	98	.	0.516	4.227	3.876	1.343	0.489	1.038
Tragopogon pratensis	14	210.36	0.111	28	0.036	0.426	4.638	4.586	0.798	0.707	0.772
	21	137.06	0.111	58	0.017	0.707	5.129	4.863	0.831	0.801	0.82
	28	174.875	0.111	30	0.033	0.469	4.361	4.017	0.703	0.692	0.699
	35	165.284	0.111	100	.	0.793	5.685	4.965	0.652	0.418	0.55

Appendix 6. List of species germination rates used in chapter III.

Tribe		Genus	Species	germination time (days)
Anthemideae		*Achillea*	*millefolium*	3-7
		Artemisia	*vulgaris*	3
		Chrysanthemum	*leucanthemum*	5
		Matricaria	*matricarioides*	3
		Tanacetum	*vulgare*	3
Astereae		*Erigeron*	*canadensis*	3
		Solidago	*canadensis*	6-9
Cichorieae		*Cichorium*	*intybus*	4
		Hieracium	*aurantiacum*	4-5
		H.	*vulgatum*	11
		Lactuca	*canadensis*	6-8
		Lapsana	*communis*	3
		Leontodon	*autumnalis*	3-6
		Taraxacum	*officinale*	6
		Tragopogon	*pratensis*	3
Cynareae	Carduinae	*Arctium*	*lappa*	3
		A.	*minus*	3
Heliantheae	Coreopsidinare	*Bidens*	*cernua*	5-7
Helianthinae		*Rudbeckia*	*hirta*	3
Senecioneae		*Tussilago*	*farfara*	4-7

Appendix 7. Daily measurements of pH during the growth period from June-July (chapter III). 1/8 dilute solution.

	June							July															
Date	18	19	20	21	25	26	27	2	3	4	5	7	8	9	10	12	15	16	17	19	23	25	26	29	30
pH	5.9	6.0	6.8	5.8	6.8	6.0	5.7	6.1	5.9	5.9	5.7	6.2	5.8	6.1	5.1	5.9	6.2	5.8	5.1	6.2	6.3	5.7	5.9	6.0	5.1



Daily pH changes in the external nutrient solution during the experimental period from June-July (chapter III). 1/8 dilute solution. Numerical values are given in the table above.

Appendix 8a. Primary data set of 20 species used in chapter III.

Species	Harvest Day	Leaf d.w. (g)	Stem d.w. (g)	Root d.w. (g)	Total d.w. (g)	Leaf (cm^2)	SLA (cm^2/g)	Ln(SLA) (cm^2/g)	Root/Shoot (g/g)
Achillea	20	0.001	0.000	0.013	0.013	0.310	442.857	6.093	18.000
millefolium	20	0.001	0.001	0.020	0.022	0.250	312.500	5.745	25.125
	20	0.003	0.001	0.004	0.008	0.670	239.286	5.478	1.500
	20	0.004	0.001	0.003	0.007	0.980	245.000	5.501	0.675
	20	0.005	0.001	0.004	0.010	1.580	322.449	5.776	0.796
	20	0.004	0.001	0.008	0.013	1.140	316.667	5.758	2.222
	20	0.016	0.002	0.015	0.034	2.560	156.098	5.050	0.921
	20	0.003	0.001	0.007	0.011	0.670	203.030	5.313	1.970
	20	0.003	0.001	0.002	0.005	0.390	139.286	4.937	0.643
	20	0.003	0.001	0.006	0.009	0.530	165.625	5.110	1.719
	20	0.003	0.001	0.003	0.006	0.970	312.903	5.746	0.903
	20	0.005	0.001	0.003	0.009	1.160	223.077	5.408	0.635
Achillea	40	0.300	0.030	0.497	0.826	29.210	97.529	4.580	1.660
millefolium	40	0.015	0.002	0.025	0.043	1.490	97.386	4.579	1.627
	40	0.416	0.039	0.649	1.104	38.650	92.976	4.532	1.560
	40	0.003	0.001	0.007	0.011	0.048	19.200	2.955	2.920
	40	0.020	0.004	0.062	0.085	2.340	115.842	4.752	3.054
	40	0.066	0.009	0.037	0.112	4.830	73.293	4.294	0.560
	40	0.002	0.001	0.005	0.007	0.330	157.143	5.057	2.286
Arctium	20	0.052	0.014	0.080	0.145	9.830	188.676	5.240	1.526
lappa	20	0.072	0.015	0.106	0.193	11.210	155.479	5.047	1.473
	20	0.107	0.023	0.144	0.274	16.900	158.092	5.063	1.347
	20	0.140	0.031	0.185	0.355	25.100	179.799	5.192	1.323
	20	0.116	0.025	0.163	0.304	22.180	191.372	5.254	1.403
Arctium	40	0.304	0.069	0.602	0.975	46.430	152.730	5.029	1.981
lappa	40	0.201	0.054	0.275	0.530	28.790	143.234	4.964	1.370
	40	0.820	0.185	1.657	2.662	104.230	127.187	4.846	2.022
	40	0.477	0.111	0.819	1.407	62.480	130.930	4.875	1.716
Arctium	20	0.085	0.018	0.095	0.197	14.360	169.140	5.131	1.113
minus	20	0.094	0.020	0.120	0.233	17.250	184.295	5.217	1.282
	20	0.139	0.024	0.241	0.404	19.450	139.527	4.938	1.727

Species	Harvest Day	Leaf d.w. (g)	Stem d.w. (g)	Root d.w. (g)	Total d.w. (g)	Leaf (cm^2)	SLA (cm^2/g)	Ln(SLA) (cm^2/g)	Root/Shoot (g/g)
	20	0.118	0.024	0.151	0.293	13.450	114.468	4.740	1.282
	20	0.014	0.005	0.012	0.031	1.860	132.857	4.889	0.879
	20	0.033	0.007	0.046	0.086	5.570	168.788	5.129	1.382
	20	0.087	0.016	0.128	0.231	15.420	176.632	5.174	1.467
	20	0.034	0.007	0.053	0.095	6.910	202.047	5.308	1.561
Arctium	40	0.333	0.077	0.801	1.211	48.160	144.538	4.974	2.405
minus	40	0.043	0.019	0.176	0.237	6.610	152.656	5.028	4.053
	40	0.519	0.108	1.033	1.660	70.900	136.662	4.918	1.991
	40	0.231	0.064	0.606	0.901	31.700	137.051	4.920	2.619
	40	0.095	0.028	0.374	0.497	13.940	146.122	4.984	3.923
	40	0.273	0.089	0.778	1.140	38.290	140.256	4.943	2.851
	40	0.083	0.023	0.217	0.323	12.880	155.744	5.048	2.626
Artemisia	20	0.030	0.008	0.058	0.095	7.770	260.738	5.564	1.946
vulgaris	20	0.051	0.011	0.092	0.155	14.590	284.405	5.650	1.799
	20	0.023	0.005	0.062	0.090	4.900	214.912	5.370	2.737
	20	0.000	0.001	0.001	0.002	0.220	220.000	7.696	9.000
	20	0.012	0.003	0.020	0.036	1.940	161.667	5.086	1.683
	20	0.019	0.006	0.020	0.045	4.760	246.632	5.508	1.021
	20	0.014	0.003	0.028	0.045	3.630	264.964	5.580	2.029
Artemisia	40	0.043	0.013	0.303	0.359	9.520	220.882	5.398	7.032
vulgaris	40	0.125	0.049	0.409	0.584	20.800	166.002	5.112	3.266
	40	0.193	0.126	0.627	0.946	33.360	173.299	5.155	3.259
	40	0.268	0.154	0.663	1.085	40.770	152.411	5.027	2.479
	40	0.170	0.133	0.335	0.638	27.040	159.340	5.071	1.975
	40	0.022	0.008	0.047	0.078	3.500	156.951	5.056	2.103
Bidens	20	0.091	0.026	0.128	0.245	16.980	187.211	5.232	1.412
cernua	20	0.119	0.030	0.131	0.280	24.130	202.944	5.313	1.100
	20	0.023	0.005	0.051	0.079	5.970	255.128	5.542	2.158
	20	0.036	0.008	0.058	0.101	7.390	208.169	5.338	1.628
	20	0.040	0.007	0.071	0.117	7.950	201.266	5.305	1.785
	20	0.012	0.003	0.024	0.039	2.610	210.484	5.349	1.911
	20	0.019	0.005	0.065	0.088	3.190	167.895	5.123	3.400
	20	0.016	0.003	0.049	0.068	2.650	167.722	5.122	3.101
	20	0.025	0.007	0.026	0.057	4.040	163.563	5.097	1.053

Species	Harvest Day	Leaf d.w. (g)	Stem d.w. (g)	Root d.w. (g)	Total d.w. (g)	Leaf (cm^2)	SLA (cm^2/g)	Ln(SLA) (cm^2/g)	Root/Shoot (g/g)
	20	0.034	0.008	0.066	0.108	5.400	159.292	5.071	1.932
Bidens	40	0.376	0.299	0.415	1.090	51.390	136.821	4.919	1.105
cernua	40	0.283	0.156	0.299	0.738	39.260	138.924	4.934	1.057
	40	0.236	0.116	0.361	0.713	32.950	139.737	4.940	1.531
	40	0.315	0.195	0.602	1.111	56.410	179.364	5.189	1.913
	40	0.284	0.152	0.430	0.866	44.410	156.263	5.052	1.512
	40	0.248	0.127	0.262	0.638	44.840	180.588	5.196	1.057
	40	0.325	0.203	0.324	0.852	76.930	236.489	5.466	0.994
Chrysanthemum	20	0.009	0.002	0.025	0.036	2.100	241.379	5.486	2.908
leucanthemum	20	0.002	0.001	0.009	0.012	0.600	315.789	5.755	4.737
	20	0.013	0.001	0.015	0.029	1.990	157.937	5.062	1.167
	20	0.005	0.001	0.006	0.012	1.000	192.308	5.259	1.173
	20	0.007	0.001	0.002	0.010	1.460	205.634	5.326	0.324
	20	0.004	0.001	0.002	0.007	0.670	163.415	5.096	0.439
	20	0.004	0.001	0.004	0.009	1.060	294.444	5.685	1.222
	20	0.002	0.000	0.002	0.005	0.490	204.167	5.319	1.000
	20	0.004	0.000	0.003	0.007	0.600	153.846	5.036	0.821
	20	0.003	0.000	0.003	0.007	0.970	303.125	5.714	0.938
Chrysanthemum	40	0.123	0.019	0.061	0.204	11.010	89.222	4.491	0.497
leucanthemum	40	0.006	0.001	0.009	0.016	0.640	108.475	4.687	1.593
	40	0.255	0.044	0.136	0.435	17.290	67.937	4.219	0.535
	40	0.525	0.146	0.620	1.290	53.410	101.811	4.623	1.181
	40	0.509	0.139	0.639	1.286	44.170	86.863	4.464	1.256
	40	0.289	0.070	0.250	0.609	29.640	102.561	4.630	0.865
Cichorium	20	0.013	0.002	0.026	0.041	4.900	365.672	5.902	1.948
intybus	20	0.064	0.006	0.070	0.140	16.960	264.174	5.577	1.087
	20	0.211	0.018	0.326	0.555	50.000	236.967	5.468	1.546
	20	0.002	0.001	0.002	0.005	0.350	205.882	5.327	1.235
	20	0.035	0.004	0.047	0.086	11.360	323.647	5.780	1.333
	20	0.089	0.006	0.108	0.203	24.590	275.364	5.618	1.207
	20	0.038	0.004	0.056	0.097	10.610	282.181	5.643	1.484
Cichorium	40	0.336	0.041	0.961	1.338	101.000	300.595	5.706	2.859
intybus	40	0.454	0.034	1.047	1.534	82.890	182.577	5.207	2.305
	40	0.209	0.021	1.235	1.465	39.090	187.392	5.233	5.920

Species	Harvest Day	Leaf d.w. (g)	Stem d.w. (g)	Root d.w. (g)	Total d.w. (g)	Leaf (cm^2)	SLA (cm^2/g)	Ln(SLA) (cm^2/g)	Root/Shoot (g/g)
	40	1.484	0.147	3.893	5.524	228.760	154.193	5.038	2.624
	40	0.510	0.051	1.862	2.422	87.300	171.244	5.143	3.651
	40	0.455	0.048	1.900	2.403	68.750	151.066	5.018	4.176
	40	0.357	0.031	1.509	1.897	78.270	219.551	5.392	4.233
	40	0.260	0.015	1.178	1.452	45.700	176.040	5.171	4.538
Erigeron	20	0.001	0.000	0.001	0.003	0.230	176.923	5.176	0.923
canadensis	20	0.000	0.000	0.001	0.001	0.030	75.000	4.317	1.500
	20	0.002	0.000	0.003	0.005	0.410	273.333	5.611	1.933
	20	0.005	0.001	0.005	0.011	1.050	218.750	5.388	0.958
	20	0.005	0.001	0.013	0.019	1.110	209.434	5.344	2.358
	20	0.002	0.001	0.002	0.004	0.280	164.706	5.104	0.941
	20	0.001	0.000	0.001	0.001	0.070	140.000	4.942	1.400
	20	0.001	0.000	0.001	0.002	0.090	150.000	5.011	1.833
	20	0.004	0.001	0.005	0.010	1.190	290.244	5.671	1.293
	20	0.003	0.001	0.003	0.006	0.900	321.429	5.773	0.964
	20	0.002	0.001	0.003	0.006	0.650	282.609	5.644	1.304
Erigeron	40	0.020	0.005	0.033	0.058	3.890	191.626	5.256	1.626
canadensis	40	0.004	0.001	0.003	0.008	1.090	302.778	5.713	0.917
	40	0.083	0.023	0.193	0.299	11.200	135.266	4.907	2.332
	40	0.129	0.041	0.210	0.380	20.350	157.752	5.061	1.626
	40	0.001	0.001	0.001	0.003	0.160	133.333	4.893	1.083
	40	0.101	0.029	0.170	0.299	12.990	128.360	4.855	1.675
	40	0.054	0.016	0.131	0.201	10.470	194.610	5.271	2.431
Tussilago	20	0.073	0.014	0.082	0.169	15.000	205.198	5.324	1.120
farfara	20	0.009	0.002	0.020	0.031	1.370	155.682	5.048	2.284
	20	0.123	0.045	0.097	0.264	16.820	136.971	4.920	0.790
	20	0.011	0.002	0.017	0.031	2.340	205.263	5.324	1.491
	20	0.004	0.001	0.006	0.011	0.880	220.000	5.394	1.450
	20	0.013	0.003	0.019	0.034	2.120	165.625	5.110	1.445
	20	0.000	0.001	0.003	0.004	0.080	266.667	5.586	9.667
Tussilago	40	0.205	0.060	0.287	0.551	25.710	125.598	4.833	1.400
farfara	40	0.193	0.097	0.344	0.634	23.830	123.728	4.818	1.786
	40	0.310	0.135	0.361	0.806	45.030	145.071	4.977	1.162

Species	Harvest Day	Leaf d.w. (g)	Stem d.w. (g)	Root d.w. (g)	Total d.w. (g)	Leaf (cm^2)	SLA (cm^2/g)	Ln(SLA) (cm^2/g)	Root/Shoot (g/g)
	40	0.594	0.278	0.703	1.575	88.950	149.697	5.009	1.182
	40	0.384	0.092	0.666	1.142	59.760	155.706	5.048	1.736
	40	0.107	0.047	0.116	0.270	18.100	168.529	5.127	1.081
Hieracium	20	0.022	0.002	0.014	0.038	4.850	222.477	5.405	0.633
vulgatum	20	0.007	0.001	0.006	0.014	1.600	225.352	5.418	0.831
	20	0.007	0.001	0.005	0.014	1.740	241.667	5.488	0.750
	20	0.008	0.002	0.006	0.016	1.730	221.795	5.402	0.808
	20	0.016	0.002	0.011	0.029	4.040	258.974	5.557	0.712
	20	0.001	0.000	0.002	0.004	0.270	192.857	5.262	1.429
	20	0.002	0.001	0.002	0.005	0.340	226.667	5.423	1.467
Hieracium	40	0.112	0.014	0.060	0.186	18.770	167.589	5.122	0.539
vulgatum	40	0.038	0.004	0.031	0.073	5.530	145.144	4.978	0.803
	40	0.171	0.023	0.089	0.284	26.040	151.925	5.023	0.521
	40	0.130	0.020	0.079	0.229	27.230	209.623	5.345	0.606
	40	0.135	0.017	0.053	0.205	25.750	190.882	5.252	0.394
	40	0.153	0.019	0.090	0.262	24.130	157.301	5.058	0.587
Hieracium	20	0.001	0.000	0.002	0.004	0.310	238.462	5.474	1.692
aurantiacum	20	0.002	0.000	0.003	0.005	0.640	304.762	5.720	1.286
	20	0.011	0.001	0.004	0.015	1.150	109.524	4.696	0.352
	20	0.002	0.000	0.004	0.007	0.450	187.500	5.234	1.542
	20	0.001	0.000	0.003	0.004	0.240	266.667	5.586	3.000
	20	0.002	0.000	0.001	0.003	0.300	176.471	5.173	0.706
	20	0.003	0.000	0.004	0.007	0.580	232.000	5.447	1.560
	20	0.081	0.001	0.001	0.083	1.630	200.248	3.008	0.015
	20	0.006	0.001	0.003	0.011	1.510	247.541	5.512	0.541
	20	0.002	0.001	0.005	0.007	0.210	123.529	4.816	2.765
Hieracium	40	0.088	0.017	0.041	0.146	17.190	194.677	5.271	0.460
aurantiacum	40	0.002	0.001	0.001	0.004	0.260	136.842	4.919	0.632
	40	0.002	0.001	0.002	0.004	0.210	131.250	4.877	1.188
	40	0.026	0.004	0.030	0.060	5.490	215.294	5.372	1.192
	40	0.057	0.006	0.050	0.113	9.520	165.854	5.111	0.864
	40	0.082	0.010	0.087	0.178	18.340	224.205	5.413	1.057
	40	0.012	0.002	0.005	0.018	1.980	172.174	5.149	0.443

Species	Harvest Day	Leaf d.w. (g)	Stem d.w. (g)	Root d.w. (g)	Total d.w. (g)	Leaf (cm^2)	SLA (cm^2/g)	Ln(SLA) (cm^2/g)	Root/Shoot (g/g)
Lactuca	20	0.022	0.015	0.023	0.060	6.930	315.000	5.753	1.064
canadensis	20	0.026	0.002	0.036	0.064	13.850	528.626	6.270	1.385
	20	0.015	0.001	0.019	0.034	6.120	416.327	6.031	1.265
	20	0.003	0.000	0.003	0.006	0.810	324.000	5.781	1.280
	20	0.049	0.003	0.052	0.104	15.130	309.407	5.735	1.070
	20	0.038	0.002	0.027	0.066	10.880	285.564	5.654	0.698
	20	0.022	0.001	0.021	0.044	6.280	284.163	5.650	0.959
	20	0.008	0.001	0.005	0.013	2.200	282.051	5.642	0.603
Lactuca	40	0.105	0.005	0.129	0.239	32.520	309.714	5.736	1.230
canadensis	40	0.116	0.010	0.363	0.490	31.870	274.741	5.616	3.132
	40	0.127	0.006	0.197	0.329	21.170	166.824	5.117	1.552
	40	0.008	0.001	0.018	0.027	1.110	142.308	4.958	2.295
	40	0.012	0.001	0.016	0.028	1.940	161.667	5.086	1.308
	40	0.172	0.007	0.290	0.469	31.970	185.441	5.223	1.680
	40	0.147	0.007	0.179	0.333	34.430	234.377	5.457	1.219
Lapsana	20	0.004	0.001	0.005	0.010	0.440	112.821	4.726	1.385
communis	20	0.004	0.001	0.002	0.007	1.010	288.571	5.665	0.657
	20	0.002	0.001	0.005	0.008	0.610	277.273	5.625	2.136
	20	0.013	0.003	0.014	0.030	3.800	292.308	5.678	1.062
	20	0.015	0.005	0.022	0.041	3.720	254.795	5.540	1.486
	20	0.000	0.000	0.003	0.003	0.150	375.000	5.927	6.750
Lapsana	40	0.172	0.016	0.311	0.499	35.700	207.438	5.335	1.807
communis	40	0.026	0.007	0.010	0.043	5.740	222.481	5.405	0.372
	40	0.079	0.014	0.013	0.106	12.630	160.483	5.078	0.171
	40	0.165	0.029	0.100	0.294	28.520	173.058	5.154	0.606
	40	0.033	0.005	0.056	0.094	6.250	189.970	5.247	1.702
	40	0.023	0.005	0.044	0.073	5.010	219.737	5.392	1.947
	40	0.021	0.006	0.092	0.119	2.750	132.212	4.884	4.442
Leontodon	20	0.037	0.005	0.031	0.073	7.560	202.681	5.312	0.834
autumnalis	20	0.019	0.002	0.014	0.035	4.540	240.212	5.482	0.725
	20	0.004	0.001	0.008	0.014	0.800	186.047	5.226	1.953
	20	0.051	0.007	0.040	0.098	9.380	184.646	5.218	0.791
	20	0.001	0.001	0.003	0.005	0.210	161.538	5.085	2.000

Species	Harvest Day	Leaf d.w. (g)	Stem d.w. (g)	Root d.w. (g)	Total d.w. (g)	Leaf (cm^2)	SLA (cm^2/g)	Ln(SLA) (cm^2/g)	Root/Shoot (g/g)
	20	0.009	0.002	0.012	0.023	2.490	264.894	5.579	1.234
	20	0.004	0.001	0.006	0.011	0.790	219.444	5.391	1.722
Leontodon	40	0.385	0.069	0.334	0.787	47.640	123.901	4.819	0.869
autumnalis	40	0.314	0.040	0.423	0.777	35.910	114.254	4.738	1.345
	40	0.305	0.039	0.450	0.794	34.290	112.426	4.722	1.474
	40	0.132	0.011	0.204	0.347	22.320	169.734	5.134	1.550
	40	0.028	0.002	0.057	0.087	4.270	150.352	5.013	1.996
	40	0.484	0.074	0.864	1.423	54.820	113.241	4.730	1.785
	40	0.449	0.063	0.744	1.255	57.160	127.305	4.847	1.656
Matricaria	20	0.025	0.006	0.024	0.054	3.990	162.195	5.089	0.959
matricarioides	20	0.002	0.001	0.018	0.021	0.210	140.000	4.942	12.267
	20	0.070	0.012	0.088	0.170	14.950	213.877	5.365	1.252
	20	0.006	0.001	0.007	0.014	1.100	189.655	5.245	1.241
	20	0.000	0.001	0.003	0.004	0.050	166.667	5.116	10.333
	20	0.003	0.001	0.006	0.010	0.540	216.000	5.375	2.280
	20	0.024	0.006	0.024	0.053	4.960	211.064	5.352	1.030
	20	0.002	0.000	0.002	0.004	0.680	400.000	5.991	1.294
Matricaria	40	0.381	0.074	0.891	1.346	48.190	126.350	4.839	2.336
matricarioides	40	0.001	0.000	0.007	0.008	0.280	200.000	5.298	4.714
	40	0.035	0.005	0.047	0.086	8.260	239.420	5.478	1.351
	40	0.022	0.003	0.031	0.056	5.030	233.953	5.455	1.460
	40	0.201	0.052	0.374	0.627	29.070	144.915	4.976	1.866
	40	0.090	0.017	0.150	0.257	16.150	179.644	5.191	1.672
	40	0.131	0.028	0.186	0.345	19.430	148.321	4.999	1.419
	40	0.172	0.038	0.340	0.551	24.300	140.951	4.948	1.973
Rudbeckia	20	0.006	0.002	0.002	0.010	1.170	198.305	5.290	0.305
hirta	20	0.004	0.001	0.003	0.008	1.060	258.537	5.555	0.659
	20	0.023	0.005	0.025	0.053	5.920	263.111	5.573	1.129
	20	0.000	0.001	0.001	0.001	0.060	600.000	6.397	6.000
	20	0.002	0.002	0.004	0.008	0.460	200.000	5.298	1.652
	20	0.001	0.000	0.000	0.001	0.080	160.000	5.075	0.200
Rudbeckia	40	0.204	0.030	0.193	0.428	24.030	117.852	4.769	0.949
hirta	40	0.048	0.009	0.034	0.091	9.130	190.605	5.250	0.708
	40	0.177	0.046	0.342	0.565	26.880	151.607	5.021	1.927

Species	Harvest Day	Leaf d.w. (g)	Stem d.w. (g)	Root d.w. (g)	Total d.w. (g)	Leaf (cm^2)	SLA (cm^2/g)	Ln(SLA) (cm^2/g)	Root/Shoot (g/g)
	40	0.017	0.004	0.013	0.035	2.030	118.713	4.777	0.772
	40	0.074	0.017	0.146	0.237	12.530	170.476	5.139	1.989
	40	0.042	0.007	0.045	0.094	5.120	121.040	4.796	1.057
	40	0.003	0.000	0.005	0.007	0.380	152.000	5.024	1.840
Solidago	20	0.003	0.001	0.003	0.007	0.630	203.226	5.314	0.935
canadensis	20	0.011	0.001	0.012	0.024	2.470	220.536	5.396	1.054
	20	0.002	0.001	0.003	0.005	0.500	277.778	5.627	1.500
	20	0.014	0.002	0.014	0.030	2.950	210.714	5.351	1.000
	20	0.003	0.001	0.004	0.008	0.700	205.882	5.327	1.118
	20	0.001	0.001	0.001	0.002	0.300	500.000	6.215	1.500
	20	0.003	0.001	0.003	0.006	0.620	248.000	5.513	1.160
	20	0.001	0.000	0.002	0.003	0.160	160.000	5.075	1.800
	20	0.001	0.000	0.001	0.002	0.070	140.000	4.942	2.400
	20	0.000	0.000	0.000	0.001	0.070	700.000	6.551	2.000
	20	0.000	0.000	0.001	0.001	0.130	1300.000	7.170	9.000
	20	0.002	0.000	0.002	0.004	0.200	125.000	4.828	1.313
	20	0.000	0.001	0.001	0.002	0.180	450.000	6.109	3.250
	20	0.000	0.000	0.001	0.001	0.060	150.000	5.011	1.750
Solidago	40	0.171	0.022	0.150	0.342	22.310	130.850	4.874	0.879
canadensis	40	0.136	0.019	0.135	0.290	17.570	129.668	4.865	0.999
	40	0.037	0.009	0.026	0.072	4.630	125.815	4.835	0.715
	40	0.026	0.003	0.028	0.057	2.510	98.047	4.585	1.109
	40	0.009	0.002	0.006	0.017	1.220	141.860	4.955	0.709
	40	0.019	0.002	0.026	0.048	2.150	110.825	4.708	1.351
	40	0.122	0.032	0.191	0.346	15.130	123.611	4.817	1.560
Tanacetum	20	0.004	0.001	0.006	0.011	0.690	197.143	5.284	1.829
vulgare	20	0.032	0.006	0.022	0.061	7.060	219.255	5.390	0.696
	20	0.010	0.002	0.008	0.019	1.280	124.272	4.822	0.738
	20	0.005	0.000	0.004	0.009	1.270	249.020	5.518	0.706
	20	0.022	0.003	0.010	0.036	3.410	155.000	5.043	0.468
	20	0.002	0.001	0.001	0.005	0.520	273.684	5.612	0.737
	20	0.002	0.001	0.003	0.005	0.220	110.000	4.700	1.250
	20	0.002	0.001	0.004	0.006	0.280	140.000	4.942	1.950
	20	0.001	0.000	0.002	0.004	0.190	237.500	5.470	3.000

Species	Harvest Day	Leaf d.w. (g)	Stem d.w. (g)	Root d.w. (g)	Total d.w. (g)	Leaf (cm^2)	SLA (cm^2/g)	Ln(SLA) (cm^2/g)	Root/Shoot (g/g)
	20	0.001	0.001	0.001	0.003	0.150	136.364	4.915	1.182
	20	0.001	0.000	0.001	0.002	0.080	114.286	4.739	0.857
Tanacetum	40	0.068	0.009	0.057	0.134	9.200	134.700	4.903	0.833
vulgare	40	0.237	0.050	0.423	0.710	25.620	107.919	4.681	1.780
	40	0.432	0.063	0.606	1.101	54.930	127.241	4.846	1.403
	40	0.021	0.003	0.037	0.061	2.780	134.300	4.900	1.787
	40	0.155	0.033	0.180	0.368	21.900	141.382	4.951	1.164
	40	0.133	0.026	0.188	0.346	12.480	94.189	4.545	1.420
	40	0.071	0.013	0.216	0.301	7.230	101.831	4.623	3.045
Taraxacum	20	0.062	0.006	0.065	0.133	20.250	327.670	5.792	1.058
officinale	20	0.046	0.004	0.043	0.093	16.650	361.957	5.892	0.941
	20	0.073	0.007	0.066	0.147	17.310	235.831	5.463	0.902
	20	0.005	0.001	0.011	0.017	1.520	316.667	5.758	2.292
	20	0.032	0.004	0.048	0.084	10.130	312.654	5.745	1.488
	20	0.023	0.003	0.035	0.062	6.580	281.197	5.639	1.500
	20	0.007	0.001	0.012	0.020	2.830	398.592	5.988	1.732
	20	0.062	0.006	0.048	0.116	18.490	300.162	5.704	0.784
Taraxacum	40	0.216	0.032	0.526	0.774	38.690	179.203	5.189	2.436
officinale	40	0.088	0.005	0.019	0.112	19.060	216.591	5.378	0.219
	40	0.071	0.012	0.112	0.194	13.880	195.218	5.274	1.572
	40	0.085	0.009	0.106	0.199	21.170	250.533	5.524	1.250
	40	0.089	0.008	0.236	0.333	15.970	180.248	5.194	2.668
	40	0.142	0.018	0.400	0.560	22.430	157.958	5.062	2.820
	40	0.403	0.065	0.847	1.315	58.980	146.280	4.986	2.102
Tragopogon	20	0.063	0.014	0.190	0.266	7.790	124.640	4.825	3.034
pratensis	20	0.031	0.007	0.036	0.073	4.180	136.156	4.914	1.176
	20	0.035	0.010	0.045	0.090	5.150	145.480	4.980	1.263
	20	0.042	0.010	0.078	0.130	6.160	146.667	4.988	1.852
	20	0.047	0.006	0.059	0.112	6.660	142.308	4.958	1.250
	20	0.015	0.000	0.012	0.027	3.310	228.276	5.431	0.841
	20	0.078	0.000	0.094	0.172	10.800	137.931	4.927	1.195
Tragopogon	40	0.098	0.000	0.356	0.453	6.940	71.107	4.264	3.644
pratensis	40	0.149	0.000	0.508	0.657	14.270	95.772	4.562	3.411
	40	0.105	0.000	0.243	0.348	12.430	118.947	4.779	2.325

Appendix 8b. Data set of 20 species used in chapter III.

Species	Harvest Day	SLA (cm^2)	Root:shoot (g/g)	RGR (g/g/day)	Phenolics Total	Toxicity (LC_{50})	Leaf Nitrogen
Achillea millefolium	20	242.946	4.592	0.103	1.448	.	.
	40	80.870	1.952	0.103	1.425	20.3	0.825
Arctium lappa	20	174.017	1.414	0.079	0.789	.	2.889
	40	138.154	1.772	0.079	1.291	100	1.003
Arctium minus	20	158.505	1.337	0.075	0.634	.	2.026
	40	144.557	2.924	0.075	1.205	100	2.054
Artemisia vulgaris	20	323.453	2.888	0.123	0.685	.	4.458
	40	170.096	3.353	0.123	1.327	29.4	1.875
Bidens cernua	20	190.431	1.948	0.107	0.766	.	2.77
	40	163.915	1.310	0.107	2.426	41.6	2.001
Chrysanthemum	20	215.708	1.473	0.172	1.008	.	.
leucanthemum	40	91.746	0.988	0.172	1.063	100	1.123
Cichorium intybus	20	274.861	1.406	0.159	0.623	.	2.773
	40	188.374	3.788	0.159	0.811	100	1.109
Erigeron canadensis	20	194.597	1.401	0.140	1.408	.	.
	40	170.119	1.670	0.140	1.263	77.2	1.702
Tussilago farfara	20	189.351	2.607	0.151	0.670	.	1.724
	40	143.837	1.391	0.151	1.120	13.5	0.66
Hieracium vulgatum	20	226.330	0.947	0.134	0.810	.	.
	40	168.954	0.575	0.134	1.615	100	1.891
Hieracium aurantiacum	20	158.629	1.346	0.073	0.812	.	.
	40	173.952	0.834	0.073	1.296	100	.
Lactuca canadensis	20	335.117	1.040	0.077	0.706	.	.
	40	202.976	1.774	0.077	0.801	100	1.492
Lapsana communis	20	251.344	2.246	0.121	1.138	.	.
	40	183.754	1.578	0.121	0.989	37.9	0.728
Leontodon autumnalis	20	205.930	1.323	0.161	0.632	.	3.569
	40	128.721	1.525	0.161	0.837	100	1.325
Matricaria	20	202.248	3.406	0.112	0.647	.	.
matricarioides	40	172.122	2.099	0.112	0.765	100	2.145

Species	Harvest Day	SLA (cm^2)	Root:shoot (g/g)	RGR (g/g/day)	Phenolics Total	Toxicity	Leaf Nitrogen
Rudbeckia hirta	20	252.474	1.657	0.147	0.733	.	.
	40	143.744	1.320	0.147	1.562	100	0.973
Solidago canadensis	20	270.992	2.127	0.166	0.662	.	.
	40	122.193	1.046	0.166	1.431	64.6	1.279
Tanacetum vulgare	20	169.108	1.219	0.182	2.107	.	.
	40	118.946	1.633	0.182	1.368	21.1	0.913
Taraxacum officinale	20	313.442	1.337	0.085	1.179	.	1.466
	40	186.697	1.867	0.085	1.182	100	0.868
Tragopogon pratensis	20	148.896	1.516	0.076	0.879	.	.
	40	93.218	3.127	0.076	0.772	100	1.395

Appendix 9. Daily measurements of pH, conductance (ms) and nitrate during the growth period from October-December (chapter IV). Light intensity =500 μmol/m^2/s.

	Full-strength					1/5 dilute				
Date	pH	ms	(-) mV	ln (M)	NO_3^- (M)	pH	ms	(-) Mv	ln (M)	NO_3^- (M)
30-Oct	5.65	1.92	92.8	-4.758	0.0086	5.5	1.01	133.8	-6.410	0.00164
	5.55	1.9	93	-4.766	0.0085	5.64	1.03	134.0	-6.418	0.00163
	5.62	1.85	92.5	-4.746	0.0087	5.6	0.9	133.9	-6.414	0.00164
31-Oct	5.71	1.78	93.3	-4.778	0.0084	5.7	1.02	134.1	-6.422	0.00163
	5.58	1.95	93.1	-4.77	0.0085	5.6	0.85	134.3	-6.43	0.00161
	5.5	1.81	93.5	-4.786	0.0083	6.0	0.89	134.5	-6.438	0.00160
1-Nov	5.8	1.93	93.8	-4.798	0.0082	5.62	0.75	134.6	-6.442	0.00159
	5.7	1.93	93.6	-4.79	0.0083	5.45	0.7	134.8	-6.45	0.00158
	5.5	1.89	93.5	-4.786	0.0083	5.55	0.76	134.7	-6.446	0.00159
2-Nov	6.01	1.8	93.8	-4.798	0.0082	5.6	0.78	134.7	-6.446	0.00159
	5.6	1.93	93.7	-4.794	0.0083	5.6	0.73	134.9	-6.454	0.00157
	5.5	1.92	93.3	-4.778	0.0084	5.4	0.65	134.8	-6.45	0.00158
3-Nov	5.7	1.86	93.9	-4.802	0.0082	5.5	1.02	135.1	-6.462	0.00156
	5.5	1.89	93.1	-4.77	0.0085	5.8	0.99	135.5	-6.479	0.00154
	5.6	1.95	93.7	-4.794	0.0083	5.5	1.03	135.5	-6.479	0.00154
4-Nov	5.65	1.9	94	-4.806	0.0082	5.6	0.86	136.3	-6.511	0.00149
	5.64	1.88	94.1	-4.81	0.0081	5.5	0.8	136.3	-6.511	0.00149
	5.61	1.82	93.9	-4.802	0.0082	5.5	0.64	136	-6.499	0.00151
5-Nov	5.54	1.8	90.9	-4.681	0.0093	5.4	0.81	136.8	-6.531	0.00146
	5.6	2.6	91	-4.685	0.0092	5.49	0.82	136.7	-6.527	0.00146
	5.64	1.82	91.1	-4.689	0.0092	5.5	0.75	136.5	-6.519	0.00148
6-Nov	5.75	1.92	91.3	-4.697	0.0091	5.59	0.75	134.3	-6.43	0.00161
	5.5	2.2	91.2	-4.693	0.0092	5.5	0.81	134.5	-6.438	0.00160
	5.6	2.3	91.3	-4.697	0.0091	5.6	0.69	134.6	-6.442	0.00159
7-Nov	5.9	1.81	92.7	-4.754	0.0086	5.5	0.74	134.5	-6.438	0.00160
	5.7	1.91	93.1	-4.77	0.0085	5.5	0.82	134.6	-6.442	0.00159
	5.6	2.2	92.8	-4.758	0.0086	5.5	0.84	134.8	-6.45	0.00158
8-Nov	5.7	1.88	92.9	-4.762	0.0086	5.6	0.74	134.8	-6.45	0.00158
	5.6	1.88	93.6	-4.79	0.0083	5.4	0.68	134.6	-6.442	0.00159
	5.8	2.55	93.5	-4.786	0.0083	5.71	0.9	134.9	-6.454	0.00157
9-Nov	5.6	1.88	93.2	-4.774	0.0084	5.75	0.9	135.1	-6.462	0.00156
	5.62	1.88	93.6	-4.79	0.0083	5.77	0.91	135.3	-6.47	0.00155
	5.6	1.82	94.1	-4.81	0.0081	5.72	0.78	135.3	-6.47	0.00155
13-Nov	5.55	1.82	91.8	-4.717	0.0089	5.6	0.68	134	-6.418	0.00163
	5.65	1.89	91.2	-4.693	0.0092	5.58	0.77	134.1	-6.422	0.00163
	5.7	1.8	91.5	-4.705	0.009	5.55	0.74	134.1	-6.422	0.00163
14-Nov	5.6	1.92	92.3	-4.738	0.0088	5.62	0.73	134.2	-6.426	0.00162
	5.6	2.3	92.5	-4.746	0.0087	5.6	0.73	134.5	-6.438	0.00160
	5.68	1.6	93.5	-4.786	0.0083	5.53	0.75	134.4	-6.434	0.00161

	Full-strength					1/5 dilute				
Date	pH	ms	(-) mV	ln (M)	NO_3^- (M)	pH	ms	(-) Mv	ln (M)	NO_3^- (M)
15-Nov	5.65	1.76	93.3	-4.778	0.0084	5.66	0.7	134.8	-6.45	0.00158
	5.65	1.92	92.8	-4.758	0.0086	5.54	0.7	134.9	-6.454	0.00157
	5.6	1.91	93.1	-4.77	0.0085	5.57	0.73	134.8	-6.45	0.00158
16-Nov	5.61	1.86	93	-4.766	0.0085	5.59	0.75	135	-6.458	0.00157
	5.62	1.9	92.5	-4.746	0.0087	5.45	0.76	135.3	-6.47	0.00155
	5.58	1.95	93.1	-4.77	0.0085	5.5	0.8	135.1	-6.462	0.00156
20-Nov	5.6	1.9	91.4	-4.701	0.0091	5.44	0.74	134.3	-6.43	0.00161
	5.5	1.89	92.5	-4.746	0.0087	5.78	0.88	134.1	-6.422	0.00163
	5.6	1.8	91.7	-4.713	0.009	5.64	0.83	134.3	-6.43	0.00161
21-Nov	5.5	1.81	92	-4.726	0.0089	5.6	0.72	134.7	-6.446	0.00159
	5.61	2.2	93.1	-4.77	0.0085	5.51	0.65	134.6	-6.442	0.00159
	5.61	1.75	93.5	-4.786	0.0083	5.44	0.55	134.8	-6.45	0.00158
22-Nov	5.72	1.92	96	-4.887	0.0075	5.57	0.56	134.8	-6.45	0.00158
	5.6	1.93	95	-4.846	0.0079	5.79	0.54	134.9	-6.454	0.00157
	5.6	1.88	95.1	-4.85	0.0078	5.5	0.59	135	-6.458	0.00157
23-Nov	5.63	1.76	96.7	-4.915	0.0073	5.62	0.78	135	-6.458	0.00157
	5.65	1.92	96.1	-4.891	0.0075	5.46	0.79	135.4	-6.475	0.00154
	5.6	1.91	95.9	-4.883	0.0076	5.53	0.77	135.1	-6.462	0.00156
27-Nov	5.5	1.86	93	-4.766	0.0085	5.54	0.79	133.9	-6.414	0.00164
	5.62	1.9	92.5	-4.746	0.0087	6	0.8	133.5	-6.398	0.00166
	5.58	1.95	93.1	-4.77	0.0085	5.8	0.79	133.6	-6.402	0.00166
28-Nov	5.61	1.9	93.5	-4.786	0.0083	5.55	0.77	134.1	-6.422	0.00163
	5.8	1.89	92.5	-4.746	0.0087	5.91	0.91	134.3	-6.43	0.00161
	5.6	1.8	93.2	-4.774	0.0084	5.69	0.65	134.1	-6.422	0.00163
29-Nov	5.61	1.81	94.1	-4.81	0.0081	5.29	0.8	134.5	-6.438	0.00160
	5.65	1.92	93.7	-4.794	0.0083	5.4	0.87	134.8	-6.45	0.00158
	5.63	1.75	93.9	-4.802	0.0082	5.6	0.82	134.7	-6.446	0.00159
30-Nov	5.61	1.92	96	-4.887	0.0075	5.49	0.79	135.2	-6.466	0.00155
	5.62	1.93	95.7	-4.875	0.0076	5.82	0.75	135.6	-6.483	0.00153
	5.5	1.88	96.5	-4.907	0.0074	5.8	0.84	135.7	-6.487	0.00152
4-Dec	5.62	1.76	93.3	-4.778	0.0084	5.54	0.83	133	-6.378	0.00170
	5.65	1.92	92.8	-4.758	0.0086	5.6	0.62	133.9	-6.414	0.00164
	5.8	1.91	93.1	-4.77	0.0085	5.46	0.56	133.5	-6.398	0.00166
5-Dec	5.6	1.86	93.6	-4.79	0.0083	5.5	0.51	133.5	-6.398	0.00166
	5.62	1.9	93.9	-4.802	0.0082	5.4	0.48	134.1	-6.422	0.00163
	5.5	1.95	93.1	-4.77	0.0085	5.6	0.47	133.9	-6.414	0.00164
6-Dec	5.8	1.9	94.3	-4.818	0.0081	5.5	0.35	134.4	-6.434	0.00161
	5.6	1.89	94.5	-4.826	0.008	5.8	0.5	134.6	-6.442	0.00159
	5.6	1.8	94.4	-4.822	0.008	5.7	0.31	134.8	-6.45	0.00158
7-Dec	5.5	1.81	95.1	-4.85	0.0078	5.45	0.89	135.1	-6.462	0.00156
	5.6	1.92	95.1	-4.85	0.0078	5.4	0.8	135.9	-6.495	0.00151
	5.63	1.75	95.1	-4.85	0.0078	5.5	0.6	135.4	-6.475	0.00154
11-Dec	5.6	1.92	92.3	-4.738	0.0088	5.6	0.7	133.3	-6.39	0.00168
	5.62	1.93	92.5	-4.746	0.0087	5.85	0.8	133.5	-6.398	0.00166
	5.6	1.88	93.5	-4.786	0.0083	5.5	0.79	133.6	-6.402	0.00166
12-Dec	5.8	1.76	93.3	-4.778	0.0084	5.6	0.65	134.2	-6.426	0.00162
	5.55	1.92	92.8	-4.758	0.0086	5.4	0.64	134.6	-6.442	0.00159

	Full-strength					1/5 dilute				
Date	pH	ms	(-) mV	ln (M)	NO_3^- (M)	pH	ms	(-) Mv	ln (M)	NO_3^- (M)
	5.6	1.91	93.7	-4.794	0.0083	5.6	0.63	134.5	-6.438	0.0016
13-Dec	5.6	1.86	94	-4.806	0.0082	5.5	0.54	134.9	-6.454	0.00157
	5.55	1.9	94.1	-4.81	0.0081	5.4	0.55	135.3	-6.47	0.00155
	5.55	1.95	94.6	-4.83	0.008	5.6	0.45	135.1	-6.462	0.00156
14-Dec	5.55	1.9	94.9	-4.842	0.0079	5.43	0.35	135.3	-6.47	0.00155
	5.6	1.89	95.1	-4.85	0.0078	5.78	0.29	135.8	-6.491	0.00152
	5.55	1.8	95	-4.846	0.0079	5.65	0.2	136	-6.499	0.00151
18-Dec	5.48	1.81	92.1	-4.73	0.0088	5.5	0.9	133.8	-6.41	0.00164
	5.63	1.92	92.3	-4.738	0.0088	5.64	0.89	133.7	-6.406	0.00165
	5.61	1.75	92.1	-4.73	0.0088	5.65	0.88	133.8	-6.41	0.00164
19-Dec	5.55	1.93	93.6	-4.79	0.0083	5.6	0.94	134.3	-6.43	0.00161
	5.55	1.92	93.1	-4.77	0.0085	5.5	0.88	134.8	-6.45	0.00158
	5.52	1.95	92.8	-4.758	0.0086	5.73	0.82	134.5	-6.438	0.0016
20-Dec	5.7	1.89	94.5	-4.826	0.008	5.6	0.79	134.9	-6.454	0.00157
	6	1.94	94.3	-4.818	0.0081	5.62	0.68	135.3	-6.47	0.00155
	5.8	1.92	94.7	-4.834	0.008	5.7	0.76	135.4	-6.475	0.00154
21-Dec	5.54	1.93	95.1	-4.85	0.0078	5.7	0.74	135.8	-6.491	0.00152
	5.6	1.9	95.1	-4.85	0.0078	5.5	0.72	135.9	-6.495	0.00151
	5.51	1.92	95.3	-4.858	0.0078	5.78	0.72	135.4	-6.475	0.00154
26-Dec	5.57	1.93	93.3	-4.778	0.0084	5.64	0.73	133.2	-6.386	0.00169
	5.5	1.91	93.9	-4.802	0.0082	5.71	0.74	133.5	-6.398	0.00166
	5.52	1.89	93.7	-4.794	0.0083	5.6	0.76	133.4	-6.394	0.00167
27-Dec	5.5	1.96	95.6	-4.871	0.0077	5.66	0.72	134.4	-6.434	0.00161
	5.6	1.94	95.4	-4.863	0.0077	5.64	0.76	134.3	-6.43	0.00161
	5.63	1.92	95.5	-4.867	0.0077	5.57	0.77	134.8	-6.45	0.00158
28-Dec	5.5	1.93	96.1	-4.891	0.0075	5.64	0.76	135.3	-6.47	0.00155
	5.65	1.88	96.3	-4.899	0.0075	5.64	0.75	135.8	-6.491	0.00152
	5.48	1.76	96.5	-4.907	0.0074	5.53	0.76	135.7	-6.487	0.00152

Appendix 9. Daily measurements of pH, conductance (ms) and nitrate during the growth period from October-December (chapter IV). Light intensity =500 µmol/m^2/s.

	1/10 dilute					1/50 dilute				
Date	pH	ms	(-) Mv	ln (M)	NO_3^- (M)	pH	ms	(-) Mv	ln (M)	NO_3^- (M)
30-Oct	5.55	0.3	151.1	-7.107	0.00082	5.68	0.1	191.2	-8.723	0.0001628
	5.57	0.3	151.3	-7.115	0.00081	5.65	0.09	191.3	-8.727	0.0001621
	5.63	0.29	151	-7.103	0.00082	5.81	0.1	191.2	-8.723	0.0001628

	1/10 dilute					1/50 dilute				
Date	pH	ms	(-) Mv	ln (M)	NO_3^- (M)	pH	ms	(-) Mv	ln (M)	NO_3^- (M)
31-Oct	5.63	0.28	151.3	-7.115	0.00081	5.6	0.05	191.3	-8.727	0.0001621
	5.65	0.25	151.5	-7.123	0.00081	5.7	0.05	191.2	-8.723	0.0001628
	5.6	0.26	151.4	-7.119	0.00081	5.6	0.06	191.3	-8.727	0.0001621
1-Nov	5.5	0.24	151.9	-7.139	0.00079	5.55	0.07	191.4	-8.731	0.0001614
	5.74	0.22	151.7	-7.131	0.0008	5.8	0.08	191.3	-8.727	0.0001621
	5.71	0.21	151.9	-7.139	0.00079	5.35	0.1	191.4	-8.731	0.0001614
2-Nov	5.72	0.18	152.1	-7.148	0.00079	5.55	0.04	191.5	-8.735	0.0001608
	5.69	0.16	152.1	-7.148	0.00079	5.42	0.001	191.5	-8.735	0.0001608
	5.7	0.15	152.3	-7.156	0.00078	5.5	0.002	191.5	-8.735	0.0001608
3-Nov	5.43	0.1	152.7	-7.172	0.00077	5.51	0.002	191.5	-8.735	0.0001608
	5.64	0.2	152.1	-7.148	0.00079	5.6	0.003	191.4	-8.731	0.0001614
	5.63	0.23	152.4	-7.16	0.00078	5.6	0.01	191.6	-8.739	0.0001601
4-Nov	5.65	0.2	152.9	-7.18	0.00076	5.46	0.01	191.7	-8.743	0.0001595
	5.7	0.25	152.7	-7.172	0.00077	5.5	0.06	191.5	-8.735	0.0001608
	5.69	0.26	152.9	-7.18	0.00076	5.6	0.05	191.7	-8.743	0.0001595
5-Nov	5.6	0.24	153.3	-7.196	0.00075	5.7	0.01	191.5	-8.735	0.0001608
	5.62	0.26	153.1	-7.188	0.00076	5.5	0.08	191.7	-8.743	0.0001595
	5.7	0.28	153.4	-7.2	0.00075	5.4	0.1	191.9	-8.751	0.0001582
6-Nov	5.68	0.26	153.3	-7.196	0.00075	5.49	0.09	191.7	-8.743	0.0001595
	5.7	0.24	153.1	-7.188	0.00076	5.5	0.1	191.8	-8.747	0.0001589
	5.65	0.23	153.4	-7.2	0.00075	5.59	0.05	191.7	-8.743	0.0001595
7-Nov	5.5	0.21	153.1	-7.188	0.00076	5.8	0.05	191.9	-8.751	0.0001582
	5.66	0.29	153.7	-7.212	0.00074	5.7	0.06	192	-8.756	0.0001576
	5.6	0.25	153.8	-7.216	0.00073	5.6	0.07	192	-8.756	0.0001576
8-Nov	5.65	0.24	153.4	-7.2	0.00075	5.5	0.08	192.3	-8.768	0.0001557
	5.62	0.27	153.2	-7.192	0.00075	5.6	0.1	192.1	-8.76	0.0001570
	5.6	0.23	153.9	-7.22	0.00073	5.7	0.04	192	-8.756	0.0001576
9-Nov	5.6	0.26	153.9	-7.22	0.00073	5.7	0.001	192.5	-8.776	0.0001544
	5.65	0.29	153.8	-7.216	0.00073	6.05	0.002	192.1	-8.76	0.0001570
	5.7	0.28	153.9	-7.22	0.00073	5.7	0.1	192.3	-8.768	0.0001557
13-Nov	5.58	0.26	151.2	-7.111	0.00082	5.46	0.09	191.5	-8.735	0.0001608
	5.6	0.25	151.3	-7.115	0.00081	5.59	0.1	191.3	-8.727	0.0001621
	5.55	0.26	151.1	-7.107	0.00082	5.56	0.05	191.5	-8.735	0.0001608
14-Nov	5.5	0.28	151.7	-7.131	0.0008	5.6	0.05	191.7	-8.743	0.0001595
	5.67	0.25	151.9	-7.139	0.00079	5.75	0.06	191.7	-8.743	0.0001595
	5.61	0.21	151.5	-7.123	0.00081	5.78	0.07	191.9	-8.751	0.0001582
15-Nov	5.65	0.23	151.9	-7.139	0.00079	5.7	0.08	192.3	-8.768	0.0001557
	5.5	0.25	152.2	-7.152	0.00078	5.6	0.1	192.5	-8.776	0.0001544
	5.65	0.21	152.3	-7.156	0.00078	5.61	0.04	192.6	-8.78	0.0001538
16-Nov	5.6	0.22	152.6	-7.168	0.00077	5.62	0.001	192.9	-8.792	0.0001520
	5.56	0.21	152.9	-7.18	0.00076	5.5	0.002	192.8	-8.788	0.0001526
	5.58	0.16	153.1	-7.188	0.00076	5.45	0.1	192.7	-8.784	0.0001532
20-Nov	5.58	0.18	151.4	-7.119	0.00081	5.52	0.09	191.3	-8.727	0.0001621
	5.6	0.16	151.2	-7.111	0.00082	5.75	0.1	191.4	-8.731	0.0001614
	5.63	0.2	151.5	-7.123	0.00081	5.62	0.05	191.4	-8.731	0.0001614
21-Nov	5.5	0.2	152.3	-7.156	0.00078	5.5	0.05	191.9	-8.751	0.0001582
	5.6	0.16	152.1	-7.148	0.00079	5.5	0.06	192.1	-8.76	0.0001570

	1/10 dilute					1/50 dilute				
Date	pH	ms	(-) Mv	ln (M)	NO_3^- (M)	pH	ms	(-) Mv	ln (M)	NO_3^- (M)
	5.5	0.13	151.9	-7.139	0.00079	5.46	0.07	192.1	-8.76	0.0001570
22-Nov	5.66	0.19	152.6	-7.168	0.00077	5.35	0.08	192.3	-8.768	0.0001557
	5.6	0.14	152.9	-7.18	0.00076	5.71	0.1	192.8	-8.788	0.0001526
	5.6	0.16	152.5	-7.164	0.00077	5.61	0.04	192.9	-8.792	0.0001520
23-Nov	5.65	0.18	153.1	-7.188	0.00076	5.5	0.001	192.8	-8.788	0.0001526
	5.55	0.16	153.9	-7.22	0.00073	5.46	0.002	193.4	-8.812	0.0001490
	5.63	0.17	153.4	-7.2	0.00075	5.5	0.1	193.6	-8.82	0.0001478
27-Nov	5.7	0.19	151.3	-7.115	0.00081	5.52	0.09	191.3	-8.727	0.0001621
	5.45	0.25	151.3	-7.115	0.00081	5.34	0.1	191.3	-8.727	0.0001621
	5.48	0.24	151.4	-7.119	0.00081	5.46	0.05	191.4	-8.731	0.0001614
28-Nov	5.56	0.22	152.1	-7.148	0.00079	5.53	0.05	192.2	-8.764	0.0001563
	5.55	0.11	152.5	-7.164	0.00077	5.8	0.06	192.3	-8.768	0.0001557
	5.8	0.16	152.1	-7.148	0.00079	5.59	0.07	192.5	-8.776	0.0001544
29-Nov	5.6	0.19	152.9	-7.18	0.00076	5.35	0.08	193.1	-8.8	0.0001508
	5.5	0.22	152.9	-7.18	0.00076	5.6	0.1	193.4	-8.812	0.0001489
	5.5	0.28	152.7	-7.172	0.00077	5.5	0.04	193.1	-8.8	0.0001508
30-Nov	5.55	0.24	153.3	-7.196	0.00075	5.49	0.001	193.5	-8.816	0.0001483
	5.75	0.26	153.9	-7.22	0.00073	5.82	0.002	193.6	-8.82	0.0001478
	5.5	0.21	153.8	-7.216	0.00073	5.5	0.1	193.3	-8.808	0.0001495
4-Dec	5.8	0.1	152	-7.144	0.00079	5.44	0.09	191.4	-8.731	0.0001614
	5.7	0.16	151.6	-7.127	0.0008	5.49	0.1	191.5	-8.735	0.0001608
	5.5	0.2	151.5	-7.123	0.00081	5.5	0.05	191.3	-8.727	0.0001621
5-Dec	5.6	0.23	152.3	-7.156	0.00078	5.5	0.05	191.9	-8.751	0.0001582
	5.4	0.16	152.7	-7.172	0.00077	5.46	0.06	191.8	-8.747	0.0001589
	5.5	0.2	152.9	-7.18	0.00076	5.48	0.07	192	-8.756	0.0001576
6-Dec	5.49	0.16	153.5	-7.204	0.00074	5.6	0.08	192.3	-8.768	0.0001557
	5.7	0.19	153.9	-7.22	0.00073	5.72	0.1	192.4	-8.772	0.0001550
	5.5	0.18	153.7	-7.212	0.00074	5.5	0.04	192.3	-8.768	0.0001557
7-Dec	5.51	0.17	154.1	-7.228	0.00073	5.6	0.001	192.9	-8.792	0.0001520
	5.5	0.13	154.7	-7.252	0.00071	5.6	0.002	192.9	-8.792	0.0001520
	5.48	0.2	154.9	-7.26	0.0007	5.4	0.01	192.8	-8.788	0.0001526
11-Dec	5.87	0.28	151.3	-7.115	0.00081	5.5	0.1	191.4	-8.731	0.0001614
	5.76	0.25	151.2	-7.111	0.00082	5.4	0.09	191.4	-8.731	0.0001614
	5.7	0.26	151.4	-7.119	0.00081	5.7	0.1	191.3	-8.727	0.0001621
12-Dec	5.6	0.24	153.1	-7.188	0.00076	5.5	0.05	192.5	-8.776	0.0001544
	5.5	0.16	153.4	-7.2	0.00075	5.5	0.05	192.1	-8.76	0.0001570
	5.45	0.19	153.1	-7.188	0.00076	5.49	0.06	192.3	-8.768	0.0001557
13-Dec	5.5	0.18	153.9	-7.22	0.00073	5.48	0.07	193.1	-8.8	0.0001508
	5.51	0.16	153.8	-7.216	0.00073	5.43	0.08	193.3	-8.808	0.0001495
	5.6	0.17	154.1	-7.228	0.00073	5.6	0.1	193.1	-8.8	0.0001508
14-Dec	5.6	0.19	155.3	-7.276	0.00069	5.4	0.04	193.6	-8.82	0.0001478
	5.71	0.16	155.2	-7.272	0.00069	5.63	0.001	193.6	-8.82	0.0001478
	5.76	0.17	155.5	-7.285	0.00069	5.45	0.002	193.5	-8.816	0.0001483
18-Dec	5.58	0.18	151.6	-7.127	0.0008	5.4	0.05	191.3	-8.727	0.0001621
	5.64	0.22	151.3	-7.115	0.00081	5.45	0.1	191.5	-8.735	0.0001608
	5.77	0.24	151.2	-7.111	0.00082	5.8	0.06	191.5	-8.735	0.0001608

	1/10 dilute					1/50 dilute				
Date	pH	ms	(-) Mv	ln (M)	NO_3^- (M)	pH	ms	(-) Mv	ln (M)	NO_3^- (M)
19-Dec	5.77	0.21	152.3	-7.156	0.00078	5.41	0.09	192.1	-8.76	0.0001570
	5.67	0.13	152.6	-7.168	0.00077	5.62	0.07	192.3	-8.768	0.0001557
	5.65	0.15	153	-7.184	0.00076	5.66	0.09	191.9	-8.751	0.0001582
20-Dec	5.67	0.13	153.7	-7.212	0.00074	5.73	0.1	192.8	-8.788	0.0001526
	5.71	0.12	153.5	-7.204	0.00074	5.74	0.06	192.9	-8.792	0.0001520
	5.68	0.15	153.9	-7.22	0.00073	5.5	0.08	193.2	-8.804	0.0001501
21-Dec	5.61	0.16	154.1	-7.228	0.00073	5.4	0.1	193.1	-8.8	0.0001508
	5.57	0.19	154.6	-7.248	0.00071	5.59	0.04	193.1	-8.8	0.0001508
	5.63	0.16	154.3	-7.236	0.00072	5.63	0.001	193.6	-8.82	0.0001478
26-Dec	5.6	0.18	151.3	-7.115	0.00081	5.62	0.002	191.6	-8.739	0.0001601
	5.7	0.18	151.1	-7.107	0.00082	5.34	0.05	191.5	-8.735	0.0001608
	5.56	0.16	151.3	-7.115	0.00081	5.6	0.1	191.6	-8.739	0.0001601
27-Dec	5.54	0.15	152.5	-7.164	0.00077	5.7	0.06	192.3	-8.768	0.0001557
	5.65	0.13	152.1	-7.148	0.00079	5.5	0.08	192.6	-8.78	0.0001538
	5.68	0.18	152.7	-7.172	0.00077	5.57	0.09	192.4	-8.772	0.0001551
28-Dec	5.69	0.17	152.9	-7.18	0.00076	5.6	0.07	193.3	-8.808	0.0001495
	5.56	0.18	152.7	-7.172	0.00077	5.62	0.09	193.3	-8.808	0.0001495
	5.55	0.16	153.3	-7.196	0.00075	5.6	0.1	193.4	-8.812	0.0001489

Appendix 10. Daily measurements of pH, conductance (ms) and nitrate during the growth period from February-March (chapter IV). Light intensity =250 μmol/m^2/s.

	Full-strength		1\5		1\10		1\50	
Date	pH	ms	pH	ms	pH	ms	pH	ms
5-Feb	5.65	1.92	5.5	1.01	5.55	0.3	5.68	0.07
	5.8	1.9	5.64	1.03	5.57	0.3	5.65	0.09
	5.62	1.85	5.6	0.9	5.63	0.29	5.81	0.1
6-Feb	5.71	1.78	5.7	1.02	5.63	0.28	5.6	0.06
	5.58	1.95	5.6	0.85	5.65	0.25	5.7	0.08
	5.5	1.81	6	0.89	5.6	0.26	5.6	0.1
7-Feb	5.8	1.93	5.65	0.2	5.76	0.17	5.45	0.04
	5.7	1.93	5.5	0.9	5.58	0.18	5.4	0.001
	5.5	1.89	5.64	0.89	5.64	0.22	5.45	0.002
8-Feb	6.01	1.8	5.65	0.88	5.77	0.24	5.8	0.05
	5.6	1.93	5.5	0.91	5.5	0.29	5.6	0.1
	5.5	1.92	5.4	0.65	5.7	0.15	5.5	0.06
9-Feb	5.7	1.86	5.5	1.02	5.43	0.1	5.51	0.08
	5.5	1.89	5.8	0.99	5.64	0.2	5.6	0.09
	5.6	1.95	5.5	1.03	5.63	0.23	5.6	0.07
12-Feb	5.65	1.9	5.6	0.86	5.65	0.2	5.46	0.09
	5.6	1.86	5.5	0.8	5.7	0.25	5.5	0.1
	5.61	1.82	5.5	0.64	5.69	0.26	5.6	0.1
13-Feb	5.54	1.8	5.4	0.81	5.6	0.24	5.7	0.09
	5.6	2.6	5.49	0.82	5.62	0.26	5.5	0.1
	5.64	1.82	5.5	0.75	5.7	0.28	5.4	0.05
14-Feb	5.75	1.92	5.59	0.75	5.68	0.26	5.49	0.05
	5.5	2.2	5.5	0.81	5.7	0.24	5.5	0.06
	5.6	2.3	5.6	0.69	5.65	0.23	5.59	0.07
15-Feb	5.9	1.81	5.5	0.74	5.5	0.21	5.8	0.08
	5.7	1.91	5.5	0.82	5.66	0.29	5.7	0.1
	5.6	2.2	5.5	0.84	5.6	0.25	5.6	0.04
16-Feb	5.7	1.88	5.6	0.74	5.65	0.24	5.5	0.001
	5.6	1.88	5.4	0.68	5.62	0.27	5.6	0.002
	5.8	2.55	5.71	0.9	5.6	0.23	5.7	0.002
19-Feb	5.6	1.88	5.75	0.9	5.6	0.26	5.7	0.003
	5.62	1.88	5.77	0.91	5.65	0.29	6.05	0.01
	5.6	1.82	5.72	0.78	5.7	0.28	5.7	0.01
20-Feb	5.55	1.82	5.6	0.68	5.58	0.26	5.46	0.06
	5.65	1.89	5.58	0.77	5.6	0.25	5.59	0.05
	5.48	1.81	5.55	0.74	5.55	0.26	5.56	0.01
21-Feb	5.6	1.92	5.62	0.73	5.5	0.28	5.6	0.08
	5.6	2.3	5.6	0.73	5.67	0.25	5.75	0.1
	5.68	1.6	5.53	0.75	5.61	0.21	5.78	0.09
22-Feb	5.65	1.76	5.66	0.7	5.65	0.23	5.7	0.1

	Full-strength		1\5		1\10		1\50	
Date	pH	ms	pH	ms	pH	ms	pH	ms
	5.65	1.92	5.54	0.7	5.5	0.25	5.6	0.09
	5.6	1.89	5.57	0.73	5.65	0.21	5.61	0.1
23-Feb	5.55	1.8	5.59	0.75	5.6	0.22	5.62	0.05
	5.62	1.9	5.45	0.76	5.56	0.21	5.5	0.05
	5.55	1.93	5.5	0.8	5.58	0.16	5.45	0.06
26-Feb	5.6	1.9	5.44	0.74	5.58	0.18	5.52	0.07
	5.63	1.92	5.78	0.88	5.6	0.16	5.75	0.08
	5.6	1.8	5.64	0.83	5.63	0.2	5.62	0.1
27-Feb	5.5	1.81	5.6	0.72	5.5	0.2	5.5	0.04
	5.61	2.2	5.51	0.65	5.6	0.16	5.5	0.001
	5.61	1.75	5.44	0.55	5.5	0.13	5.46	0.002
28-Feb	5.72	1.92	5.57	0.56	5.66	0.19	5.35	0.002
	5.6	1.93	5.79	0.54	5.6	0.14	5.71	0.003
	5.6	1.88	5.5	0.72	5.6	0.16	5.61	0.01
29-Feb	5.63	1.76	5.78	0.72	5.65	0.18	5.5	0.01
	5.65	1.92	5.64	0.73	5.55	0.16	5.46	0.06
	5.6	1.91	5.71	0.74	5.63	0.17	5.5	0.05
1-Mar	5.5	1.86	5.54	0.79	5.7	0.19	5.52	0.01
	5.62	1.9	6	0.8	5.45	0.25	5.34	0.08
	5.58	1.95	5.8	0.79	5.48	0.24	5.46	0.1
4-Mar	5.61	1.9	5.55	0.77	5.56	0.22	5.53	0.09
	5.8	1.89	5.91	0.91	5.55	0.11	5.8	0.06
	5.6	1.8	5.69	0.65	5.8	0.16	5.59	0.07
5-Mar	5.61	1.81	5.29	0.8	5.6	0.19	5.35	0.08
	5.55	1.95	5.4	0.87	5.5	0.22	5.6	0.1
	5.55	1.9	5.6	0.94	5.77	0.21	5.41	0.04
6-Mar	5.61	1.92	5.5	0.88	5.67	0.13	5.62	0.001
	5.62	1.93	5.82	0.75	5.75	0.26	5.82	0.002
	5.5	1.88	5.8	0.84	5.5	0.21	5.5	0.002
7-Mar	5.62	1.76	5.54	0.83	5.8	0.1	5.44	0.003
	5.65	1.92	5.5	0.54	5.5	0.18	5.48	0.01
	5.8	1.91	5.4	0.55	5.51	0.16	5.43	0.01
8-Mar	5.6	1.86	5.6	0.45	5.6	0.17	5.6	0.06
	5.62	1.9	5.43	0.35	5.6	0.19	5.4	0.05
	5.5	1.95	5.78	0.29	5.71	0.16	5.63	0.01
11-Mar	5.8	1.9	5.5	0.35	5.49	0.16	5.6	0.08
	5.6	1.89	5.8	0.5	5.7	0.19	5.72	0.1
	5.6	1.8	5.7	0.31	5.5	0.18	5.5	0.09
13-Mar	5.5	1.81	5.45	0.89	5.51	0.17	5.6	0.1
	5.6	1.92	5.4	0.8	5.5	0.13	5.6	0.08
	5.63	1.75	5.5	0.6	5.48	0.2	5.4	0.05
14-Mar	5.6	1.92	5.6	0.7	5.87	0.28	5.5	0.7
	5.62	1.93	5.85	0.8	5.76	0.25	5.4	0.002
	5.6	1.88	5.5	0.79	5.7	0.26	5.7	0.003
15-Mar	5.8	1.76	5.6	0.65	5.6	0.24	5.5	0.01
	5.55	1.92	5.4	0.64	5.5	0.16	5.5	0.01
	5.6	1.91	5.6	0.63	5.45	0.19	5.49	0.06

Appendix 11. Daily measurements of pH, conductance (ms) and nitrate during the growth period from April-May (chapter IV). Light intensity = 125 μmol/m^2/s.

	Full-strength		1\5		1\10		1\50	
Date	pH	ms	pH	ms	pH	ms	pH	ms
8-Apr	5.61	1.75	5.5	1.01	5.55	0.3	5.68	0.1
	5.62	1.95	5.64	1.03	5.57	0.3	5.65	0.09
	5.62	1.85	5.73	0.82	5.63	0.29	5.81	0.1
9-Apr	5.71	1.78	5.6	0.79	5.63	0.28	5.6	0.08
	5.58	1.95	5.62	0.68	5.65	0.25	5.7	0.05
	5.5	1.81	5.7	0.76	5.6	0.26	5.6	0.7
10-Apr	5.8	1.93	5.7	0.74	5.5	0.24	5.55	0.002
	5.6	1.89	5.78	0.29	5.71	0.16	5.63	0.003
	5.55	1.8	5.65	0.2	5.76	0.17	5.45	0.01
11-Apr	5.48	1.81	5.5	0.9	5.58	0.18	5.4	0.01
	5.63	1.92	5.64	0.89	5.64	0.22	5.45	0.06
	5.61	1.75	5.65	0.88	5.77	0.24	5.8	0.05
12-Apr	5.7	1.86	5.66	0.72	5.43	0.1	5.51	0.01
	5.5	1.89	5.64	0.76	5.64	0.2	5.6	0.08
	5.6	1.95	5.57	0.77	5.63	0.23	5.6	0.1
15-Apr	5.65	1.9	5.64	0.76	5.65	0.2	5.46	0.09
	5.6	1.86	5.5	0.54	5.5	0.18	5.48	0.06
	5.55	1.9	5.4	0.55	5.51	0.16	5.43	0.07
16-Apr	5.55	1.95	5.6	0.45	5.6	0.17	5.6	0.08
	5.55	1.9	5.43	0.35	5.6	0.19	5.4	0.1
	5.52	1.89	5.46	1.92	5.7	0.28	5.4	0.04
17-Apr	5.5	1.96	5.59	0.75	5.68	0.26	5.49	0.001
	5.6	1.94	5.5	0.81	5.7	0.24	5.5	0.002
	5.63	1.92	5.6	0.69	5.65	0.23	5.59	0.002
18-Apr	5.9	1.81	5.5	0.74	5.5	0.21	5.8	0.003
	5.7	1.91	5.5	0.82	5.66	0.29	5.7	0.01
	5.62	1.95	5.5	0.91	5.5	0.29	5.6	0.01
19-Apr	5.55	1.93	5.6	0.94	5.77	0.21	5.41	0.06
	5.55	1.92	5.5	0.88	5.67	0.13	5.62	0.05
	5.52	1.95	5.73	0.82	5.65	0.15	5.66	0.01
22-Apr	5.7	1.89	5.6	0.79	5.67	0.13	5.73	0.08
	5.62	1.88	5.77	0.91	5.65	0.29	6.05	0.1
	5.6	1.82	5.72	0.78	5.7	0.28	5.7	0.09
23-Apr	5.55	1.82	5.6	0.68	5.58	0.26	5.46	0.1
	5.65	1.89	5.58	0.77	5.6	0.25	5.59	0.08
	5.7	1.8	5.55	0.74	5.55	0.26	5.56	0.05
24-Apr	5.6	1.92	5.62	0.73	5.5	0.28	5.6	0.7
	5.6	2.3	5.6	0.73	5.67	0.25	5.75	0.002
	5.68	1.6	5.53	0.75	5.61	0.21	5.78	0.003
25-Apr	5.65	1.76	5.66	0.7	5.65	0.23	5.7	0.01

	Full-strength		1\5		1\10		1\50	
Date	pH	ms	pH	ms	pH	ms	pH	ms
	5.65	1.92	5.54	0.7	5.5	0.25	5.6	0.01
	5.6	1.91	5.57	0.73	5.65	0.21	5.61	0.06
26-Apr	5.61	1.86	5.59	0.75	5.6	0.22	5.62	0.002
	5.62	1.9	5.45	0.76	5.56	0.21	5.5	0.003
	5.58	1.95	5.5	0.8	5.58	0.16	5.45	0.01
28-Apr	5.6	1.9	5.44	0.74	5.58	0.18	5.52	0.01
	5.6	1.88	5.5	0.79	5.7	0.26	5.7	0.06
	5.8	1.76	5.6	0.65	5.6	0.24	5.5	0.05
29-Apr	5.55	1.92	5.4	0.64	5.5	0.16	5.5	0.01
	5.6	1.91	5.6	0.63	5.45	0.19	5.49	0.08
	6	1.94	5.62	0.68	5.71	0.12	5.74	0.1
30-Apr	5.8	1.92	5.7	0.76	5.68	0.15	5.5	0.09
	5.54	1.93	5.7	0.74	5.61	0.16	5.4	0.06
	5.6	1.9	5.5	0.72	5.57	0.19	5.59	0.07
1- May	5.63	1.76	5.62	0.78	5.65	0.18	5.5	0.08
	5.65	1.92	5.46	0.79	5.55	0.16	5.46	0.1
	5.6	1.91	5.53	0.77	5.63	0.17	5.5	0.04
2- May	5.5	1.86	5.54	0.79	5.7	0.19	5.52	0.001
	5.62	1.9	6	0.8	5.45	0.25	5.34	0.002
	5.58	1.95	5.8	0.79	5.48	0.24	5.46	0.002
3- May	5.61	1.9	5.55	0.77	5.56	0.22	5.53	0.003
	5.8	1.89	5.91	0.91	5.55	0.11	5.8	0.01
	5.6	1.8	5.69	0.65	5.8	0.16	5.59	0.01
6- May	5.61	1.81	5.29	0.8	5.6	0.19	5.35	0.06
	5.65	1.92	5.4	0.87	5.5	0.22	5.6	0.05
	5.63	1.75	5.6	0.82	5.5	0.28	5.5	0.01
7- May	5.61	1.92	5.49	0.79	5.55	0.24	5.49	0.08
	5.55	1.92	5.7	0.31	5.5	0.18	5.5	0.1
	5.6	1.94	5.64	0.76	5.65	0.13	5.5	0.09
8- May	5.63	1.92	5.57	0.77	5.68	0.18	5.57	0.1
	5.5	1.93	5.64	0.76	5.69	0.17	5.6	0.08
	5.65	1.88	5.64	0.75	5.56	0.18	5.62	0.05
9- May	5.48	1.76	5.53	0.76	5.55	0.16	5.6	0.7
	5.62	1.9	5.4	0.48	5.4	0.16	5.46	0.002
	5.5	1.95	5.6	0.47	5.5	0.2	5.48	0.06
10- May	5.8	1.9	5.5	0.35	5.49	0.16	5.6	0.01
	5.6	1.89	5.8	0.5	5.7	0.19	5.72	0.01
	5.75	1.88	5.7	0.43	5.65	0.19	5.66	0.01

Appendix 12. Data set of 6 species used in chapter IV. Light treatment: 500 (1), 250 (2) and 125 (3)μ mol/m^2/s. Nutrient treatment: full-strength (1), 1/5 dilute (2) and 1/10 dilute (3). Species: *Achillea millefolium* (1), *Chrysanthemum leucanthemum* (2), *Cichorium intybus* (3), *Matricaria matricarioides* (4) and *Rudbeckia hirta* (6).

Light Treat.	Species	Nutrient Treat.	Harvest day	Root:shoot	Growth rate	Weight	RGR	SLA	Phenolics total	Toxic. (LC_{50})	Toxic. ($1/LC_{50}$)	Leaf Nitrog.	Leaf Phen.
3	1	3	21	0.329	.	.	0.135	412.521	0.849	13.0	0.077	.	1.040
3	1	3	28	0.339	0.198	-5.076	0.135	400.685	0.590	12.9	0.078	.	0.731
3	1	3	35	0.201	0.097	-3.557	0.135	469.530	0.480	11.9	0.084	3.533	0.510
3	1	3	42	0.216	0.158	-3.157	0.135	223.433	0.488	3.3	0.303	.	0.559
3	1	2	21	0.235	.	.	0.143	412.909	0.521	13.5	0.074	4.209	0.905
3	1	2	28	0.148	0.148	-4.015	0.143	382.385	0.444	11.4	0.088	4.385	0.698
3	1	2	35	0.145	0.165	-3.064	0.143	364.936	0.408	11.4	0.088	2.791	0.622
3	1	2	42	0.176	0.131	-1.877	0.143	284.342	0.402	12.3	0.081	3.460	0.515
3	1	1	21	0.237	.	.	0.129	458.742	0.777	15.9	0.063	2.182	0.833
3	1	1	28	0.071	0.165	-4.111	0.129	456.302	0.408	20.8	0.048	3.650	0.622
3	1	1	35	0.122	0.116	-3.006	0.129	310.694	0.454	25.8	0.039	3.721	0.572
3	1	1	42	0.273	0.100	-2.151	0.129	244.282	0.577	10.2	0.098	3.232	0.607
3	2	3	21	0.617	.	.	0.145	324.552	1.174	100.0	0.010	2.861	0.799
3	2	3	28	0.635	0.209	-2.608	0.145	305.529	0.809	65.2	0.015	3.836	0.588
3	2	3	35	0.425	0.093	-1.143	0.145	283.535	0.627	33.2	0.030	3.761	0.462
3	2	3	42	0.516	0.153	-0.494	0.145	216.297	0.523	30.6	0.033	3.838	0.538
3	2	2	21	0.322	.	.	0.185	266.591	0.944	18.7	0.053	4.231	0.499
3	2	2	28	0.306	0.245	-3.082	0.185	323.512	0.738	67.5	0.015	4.842	0.444
3	2	2	35	0.545	0.167	-1.366	0.185	320.917	0.633	85.3	0.012	3.851	0.405
3	2	2	42	0.271	0.150	-0.194	0.185	242.149	0.501	67.9	0.015	2.250	0.424
3	2	1	21	0.326	.	.	0.116	378.814	0.880	26.7	0.037	4.362	0.756
3	2	1	28	0.253	0.196	-2.451	0.116	323.004	0.632	39.2	0.026	3.903	0.396
3	2	1	35	0.224	0.063	-1.055	0.116	266.749	0.558	68.8	0.015	3.623	0.472
3	2	1	42	0.271	0.120	-0.703	0.116	220.919	0.728	58.5	0.017	3.041	0.528

Light Treat.	Species	Nutrient Treat.	Harvest day	Root:shoot	Growth rate	Weight	RGR	SLA	Phenolics total	Toxic. (LC_{50})	Toxic. ($1/LC_{50}$)	Leaf Nitrog.	Leaf Phen.
3	3	3	21	0.391	.	.	0.143	446.663	0.244	4.3	0.233	.	0.950
3	3	3	28	0.315	0.209	-4.264	0.143	430.950	0.461	10.6	0.094	3.928	0.990
3	3	3	35	0.292	0.153	-2.970	0.143	373.412	0.382	16.6	0.060	2.920	0.814
3	3	3	42	0.198	0.080	-1.821	0.143	300.512	0.244	8.7	0.115	3.031	0.608
3	3	2	21	0.134	.	.	0.133	439.140	0.387	6.2	0.161	.	0.974
3	3	2	28	0.223	0.208	-4.296	0.133	408.108	0.376	7.8	0.128	3.853	0.877
3	3	2	35	0.151	0.097	-2.884	0.133	460.201	0.430	1.7	0.588	4.681	0.700
3	3	2	42	0.144	0.115	-2.273	0.133	385.605	0.692	4.5	0.222	4.054	0.609
3	3	1	21	0.133	.	.	0.135	496.928	0.336	4.9	0.204	.	0.947
3	3	1	28	0.276	0.227	-4.366	0.135	445.165	0.367	15.8	0.063	4.305	0.744
3	3	1	35	0.131	0.059	-2.654	0.135	437.237	0.502	10.6	0.094	4.656	0.947
3	3	1	42	0.290	0.153	-2.540	0.135	352.233	0.350	3.6	0.278	3.441	0.877
3	4	3	21	0.427	.	.	0.138	599.963	0.800	36.1	0.028	4.584	0.312
3	4	3	28	0.579	0.207	-2.610	0.138	404.837	0.767	38.1	0.026	3.436	0.556
3	4	3	35	0.277	0.054	-1.163	0.138	469.856	0.781	39.0	0.026	4.045	0.562
3	4	3	42	0.377	0.195	-0.977	0.138	381.550	0.522	32.1	0.031	2.929	0.500
3	4	2	21	0.334	.	.	0.172	540.171	0.846	71.2	0.014	4.505	0.527
3	4	2	28	0.303	0.256	-2.962	0.172	495.232	0.775	36.1	0.028	4.140	0.541
3	4	2	35	0.463	0.177	-1.168	0.172	430.238	0.617	33.3	0.030	4.366	0.619
3	4	2	42	0.251	0.079	0.070	0.172	353.977	0.555	25.3	0.040	2.743	0.469
3	4	1	21	0.343	.	.	0.137	552.831	0.827	34.3	0.029	4.506	0.573
3	4	1	28	0.174	0.216	-2.529	0.137	557.436	0.678	32.9	0.030	5.381	0.457
3	4	1	35	0.155	0.123	-1.018	0.137	414.538	0.882	35.6	0.028	3.138	0.511
3	4	1	42	0.234	0.075	-0.158	0.137	376.388	0.814	39.7	0.025	4.396	0.608
3	5	3	21	0.445	.	.	0.128	347.812	0.825	100.0	0.010	3.443	0.538
3	5	3	28	0.293	0.204	-4.395	0.128	342.857	0.592	68.6	0.015	3.983	0.459
3	5	3	35	0.211	0.082	-3.104	0.128	522.493	0.599	61.9	0.016	3.420	0.429
3	5	3	42	0.240	0.094	-2.390	0.128	348.964	0.446	78.4	0.013	4.280	0.335
3	5	2	21	0.083	.	.	0.137	362.989	0.530	55.3	0.018	5.547	0.375
3	5	2	28	0.107	0.063	-4.057	0.137	520.768	0.514	42.0	0.024	4.207	0.365
3	5	2	35	0.155	0.211	-3.916	0.137	419.495	0.579	38.5	0.026	4.572	0.474
3	5	2	42	0.145	0.115	-2.254	0.137	328.118	0.432	78.4	0.013	3.116	0.535
3	5	1	21	0.188	.	.	0.108	429.086	0.585	100.0	0.010	.	0.285

Light Treat.	Species	Nutrient Treat.	Harvest day	Root:shoot	Growth rate	Weight	RGR	SLA	Phenolics total	Toxic. (LC_{50})	Toxic. ($1/LC_{50}$)	Leaf Nitrog.	Leaf Phen.
3	5	1	28	0.146	0.156	-4.418	0.108	461.657	0.420	42.8	0.023	6.107	0.361
3	5	1	35	0.245	0.134	-3.433	0.108	426.268	0.626	26.5	0.038	3.314	0.620
3	5	1	42	0.211	0.022	-2.386	0.108	439.052	0.604	47.8	0.021	4.725	0.382
3	6	3	21	0.395	.	.	0.136	358.167	1.119	40.4	0.025	.	1.008
3	6	3	28	0.222	0.079	-4.803	0.136	561.102	0.654	.	.	.	0.619
3	6	3	35	0.256	0.133	-4.250	0.136	550.691	0.632	22.2	0.045	1.705	0.570
3	6	3	42	0.255	0.196	-3.318	0.136	353.072	0.494	.	.	3.383	0.550
3	6	2	21	0.148	.	.	0.170	548.076	0.708	21.4	0.047	.	0.711
3	6	2	28	0.150	0.079	-5.000	0.170	518.658	0.505	.	.	.	0.511
3	6	2	35	0.221	0.200	-4.445	0.170	609.882	0.386	47.2	0.021	2.125	0.380
3	6	2	42	0.193	0.115	-3.044	0.170	556.290	0.388	19.7	0.051	3.322	0.400
3	6	1	21	0.282	.	.	0.170	472.653	0.553	31.0	0.032	.	0.533
3	6	1	28	0.255	0.040	-4.763	0.170	763.895	0.487	44.2	0.023	.	0.472
3	6	1	35	0.094	0.062	-4.484	0.170	737.048	0.472	.	.	.	0.469
3	6	1	42	0.213	0.415	-4.053	0.170	348.847	0.470	71.7	0.014	3.399	0.477
2	1	3	21	0.467	.	.	0.136	273.558	0.754	16.9	0.059	3.401	0.679
2	1	3	28	0.593	0.028	-2.739	0.136	214.315	0.792	17.7	0.056	2.058	0.932
2	1	3	35	0.482	0.253	-2.544	0.136	137.282	1.033	12.7	0.079	2.875	0.946
2	1	3	42	0.538	0.079	-0.775	0.136	149.699	0.753	24.2	0.041	3.094	1.040
2	1	2	21	0.590	.	.	0.123	258.651	1.232	18.9	0.053	2.913	0.590
2	1	2	28	0.295	0.062	-2.596	0.123	217.426	0.494	49.6	0.020	3.785	0.683
2	1	2	35	0.353	0.178	-2.161	0.123	159.434	0.689	13.1	0.076	3.864	0.856
2	1	2	42	0.486	0.114	-0.913	0.123	146.834	0.501	12.8	0.078	3.139	0.966
2	1	1	21	0.427	.	.	0.146	276.465	1.032	39.8	0.025	2.425	0.493
2	1	1	28	0.219	0.094	-2.578	0.146	227.222	0.723	15.9	0.063	3.898	0.689
2	1	1	35	0.232	0.219	-1.848	0.146	158.259	0.626	26.4	0.038	4.077	0.677
2	1	1	42	0.245	0.090	-0.316	0.146	154.547	0.688	65.3	0.015	3.973	0.707
2	2	3	21	0.500	.	.	0.060	199.503	0.568	100.0	0.010	3.466	0.837
2	2	3	28	0.957	0.109	-1.267	0.060	173.159	0.950	100.0	0.010	1.632	0.717
2	2	3	35	1.046	0.054	-0.505	0.060	179.548	0.889	100.0	0.010	2.562	1.108
2	2	3	42	1.028	0.033	-0.187	0.060	153.629	0.937	100.0	0.010	2.423	0.776
2	2	2	21	0.419	.	.	0.095	233.270	0.530	43.8	0.023	5.227	1.578
2	2	2	28	0.471	0.078	-1.029	0.095	204.922	0.828	43.2	0.023	3.307	0.451

Light Treat.	Species	Nutrient Treat -	Harvest day	Root:shoot	Growth rate	Weight	RGR	SLA	Phenolics total	Toxic. (LC_{50})	Toxic. ($1/LC_{50}$)	Leaf Nitrog.	Leaf Phen -
2	2	2	35	0.615	0.083	-0.486	0.095	155.150	0.933	100.0	0.010	1.876	0.656
2	2	2	42	0.786	0.128	0.096	0.095	127.139	0.726	53.3	0.019	2.839	0.498
2	2	1	21	0.308	.	.	0.096	211.154	0.504	100.0	0.010	5.083	1.199
2	2	1	28	0.230	0.155	-0.663	0.096	145.962	0.729	100.0	0.010	4.111	0.744
2	2	1	35	0.238	0.096	0.423	0.096	128.593	0.679	46.3	0.022	.	0.634
2	2	1	42	0.443	0.036	1.096	0.096	141.465	0.679	59.4	0.017	3.456	0.713
2	3	3	21	0.607	.	.	0.082	286.933	0.634	42.8	0.023	3.338	0.861
2	3	3	28	0.484	0.072	-2.769	0.082	227.301	0.821	100.0	0.010	3.300	0.753
2	3	3	35	0.440	0.165	-2.269	0.082	213.260	0.706	37.2	0.027	3.241	1.120
2	3	3	42	0.486	-0.009	-1.112	0.082	175.014	0.617	61.7	0.016	2.394	0.615
2	3	2	21	0.352	.	.	0.123	387.247	0.666	11.9	0.084	5.890	0.723
2	3	2	28	0.371	0.133	-3.232	0.123	372.191	0.685	32.8	0.030	4.256	0.711
2	3	2	35	0.271	0.153	-2.298	0.123	209.237	0.620	43.1	0.023	3.866	0.362
2	3	2	42	0.291	0.083	-1.230	0.123	168.114	0.650	50.7	0.020	3.650	0.495
2	3	1	21	0.216	.	.	0.123	399.314	0.543	28.1	0.036	5.230	0.758
2	3	1	28	0.249	0.268	-3.372	0.123	312.670	0.598	28.3	0.035	4.209	0.687
2	3	1	35	0.174	0.006	-1.498	0.123	259.066	0.450	100.0	0.010	3.968	1.046
2	3	1	42	0.274	0.142	-1.453	0.123	217.058	0.303	72.2	0.014	3.483	0.702
2	4	3	21	0.485	.	.	0.102	364.776	0.700	53.1	0.019	3.870	0.683
2	4	3	28	0.772	0.176	-1.494	0.102	267.841	0.628	35.9	0.028	2.272	0.837
2	4	3	35	0.783	0.061	-0.262	0.102	260.118	0.813	35.4	0.028	2.913	0.717
2	4	3	42	1.197	0.084	0.165	0.102	213.854	0.520	52.4	0.019	1.892	0.589
2	4	2	21	0.440	.	.	0.095	354.144	0.612	22.2	0.045	4.463	0.800
2	4	2	28	0.571	0.176	-1.022	0.095	317.997	0.651	57.5	0.017	3.631	0.636
2	4	2	35	0.551	0.061	-0.401	0.095	229.132	0.408	43.8	0.023	3.004	0.605
2	4	2	42	0.817	0.084	0.382	0.095	199.839	0.380	34.2	0.029	2.451	0.668
2	4	1	21	0.304	.	.	0.133	357.918	0.672	30.1	0.033	5.592	0.553
2	4	1	28	0.259	0.092	-1.008	0.133	265.508	0.634	29.3	0.034	4.201	0.612
2	4	1	35	0.326	0.168	-0.365	0.133	227.628	0.896	10.2	0.098	2.334	0.434
2	4	1	42	0.520	0.127	0.813	0.133	193.434	0.616	4.8	0.208	3.637	0.288
2	5	3	21	0.434	.	.	0.065	288.235	0.443	92.4	0.011	4.071	0.488
2	5	3	28	0.387	0.073	-2.259	0.065	236.771	0.671	73.8	0.014	2.221	0.716
2	5	3	35	0.569	0.052	-1.745	0.065	292.606	0.572	100.0	0.010	2.532	0.695

Light Treat.	Species	Nutrient Treat.	Harvest day	Root:shoot	Growth rate	Weight	RGR	SLA	Phenolics total	Toxic. (LC_{50})	Toxic. ($1/LC_{50}$)	Leaf Nitrog.	Leaf Phen.
2	5	3	42	0.708	0.073	-1.383	0.065	231.153	0.443	70.9	0.014	3.042	0.552
2	5	2	21	0.302	.	.	0.112	312.720	0.465	36.5	0.027	5.366	0.516
2	5	2	28	0.254	0.162	-2.746	0.112	266.027	0.549	37.4	0.027	3.814	0.548
2	5	2	35	0.265	0.122	-1.614	0.112	208.626	0.315	76.6	0.013	3.710	0.283
2	5	2	42	0.428	0.039	-0.759	0.112	334.266	0.616	48.2	0.021	3.554	0.799
2	5	1	21	0.244	.	.	0.128	286.280	0.464	29.8	0.034	4.779	0.502
2	5	1	28	0.231	0.251	-3.191	0.128	258.151	0.381	26.1	0.038	5.471	0.363
2	5	1	35	0.361	0.076	-1.436	0.128	280.788	0.410	20.5	0.049	3.981	0.466
2	5	1	42	0.293	0.068	-0.905	0.128	191.914	0.364	33.9	0.029	4.706	0.402
2	6	3	21	0.629	.	.	0.121	392.744	0.460	68.8	0.015	.	0.556
2	6	3	28	0.518	0.145	-3.922	0.121	254.753	1.092	60.7	0.016	1.948	1.154
2	6	3	35	0.393	0.047	-2.910	0.121	303.808	0.997	66.4	0.015	2.667	0.988
2	6	3	42	0.535	0.190	-2.583	0.121	224.174	1.046	57.4	0.017	2.355	1.143
2	6	2	21	0.326	.	.	0.128	480.673	0.576	46.7	0.021	3.112	0.646
2	6	2	28	0.326	0.125	-4.143	0.128	399.862	0.660	74.8	0.013	.	0.703
2	6	2	35	0.302	0.154	-3.266	0.128	253.144	0.978	41.9	0.024	2.891	0.961
2	6	2	42	0.395	0.055	-2.187	0.128	232.110	1.219	39.5	0.025	.	1.286
2	6	1	21	0.330	.	.	0.250	468.230	0.503	.	.	2.108	0.670
2	6	1	28	0.286	0.160	-4.609	0.250	355.572	0.657	27.2	0.037	3.135	0.595
2	6	1	35	0.394	0.354	-3.490	0.250	217.477	0.976	59.6	0.017	3.079	0.918
2	6	1	42	0.243	0.189	-1.012	0.250	161.053	0.771	54.5	0.018	3.927	0.766
1	1	3	21	0.622	.	.	0.067	136.770	1.179	25.6	0.039	3.741	1.423
1	1	3	28	0.519	0.059	-2.801	0.067	175.228	1.423	20.6	0.049	2.873	1.773
1	1	3	35	0.665	-0.010	-2.388	0.067	154.471	1.090	24.6	0.041	2.875	1.226
1	1	3	42	0.853	0.162	-2.446	0.067	182.137	0.844	17.2	0.058	2.064	1.563
1	1	2	21	0.466	.	.	0.140	191.844	0.791	11.1	0.090	3.372	0.877
1	1	2	28	0.308	0.212	-3.588	0.140	201.254	1.117	32.9	0.030	3.379	1.233
1	1	2	35	0.464	0.138	-2.105	0.140	157.806	1.151	10.0	0.100	2.371	1.360
1	1	2	42	0.557	0.083	-1.137	0.140	151.260	1.535	15.5	0.065	2.236	1.814
1	1	1	21	0.198	.	.	0.091	149.990	0.777	19.8	0.051	4.422	0.816
1	1	1	28	0.339	0.080	-2.170	0.091	175.260	0.591	17.5	0.057	3.490	0.572
1	1	1	35	0.212	0.152	-1.608	0.091	155.868	0.971	13.1	0.076	3.446	1.030
1	1	1	42	0.272	0.030	-0.545	0.091	108.894	0.700	5.3	0.189	3.527	0.695

Light Treat.	Species	Nutrient Treat.	Harvest day	Root:shoot	Growth rate	Weight	RGR	SLA	Phenolics total	Toxic. (LC_{50})	Toxic. ($1/LC_{50}$)	Leaf Nitrog.	Leaf Phen.
1	2	3	21	0.745	.	.	0.093	185.166	1.675	29.2	0.034	2.416	1.182
1	2	3	28	0.719	0.091	-1.031	0.093	152.512	1.282	92.2	0.011	1.960	1.435
1	2	3	35	0.774	0.078	-0.394	0.093	133.102	1.328	48.9	0.020	1.574	1.484
1	2	3	42	0.951	0.067	0.154	0.093	113.056	1.190	84.0	0.012	1.245	1.304
1	2	2	21	0.482	.	.	0.085	186.672	1.315	100.0	0.010	3.195	1.083
1	2	2	28	0.449	0.138	-0.879	0.085	135.058	1.471	100.0	0.010	3.098	1.423
1	2	2	35	0.514	0.046	0.085	0.085	137.338	1.380	100.0	0.010	2.781	1.487
1	2	2	42	0.718	0.081	0.407	0.085	119.641	1.562	100.0	0.010	1.761	1.760
1	2	1	21	0.307	.	.	0.086	188.590	0.987	30.8	0.032	4.970	1.065
1	2	1	28	0.266	0.142	-0.262	0.086	143.625	0.859	35.9	0.028	5.095	0.850
1	2	1	35	0.265	0.072	0.735	0.086	138.737	0.888	100.0	0.010	3.713	0.874
1	2	1	42	0.396	0.051	1.236	0.086	141.164	0.840	35.7	0.028	3.436	0.905
1	3	3	21	0.660	.	.	0.077	152.799	0.955	45.6	0.022	3.329	1.229
1	3	3	28	0.640	0.126	-2.992	0.077	208.529	0.954	27.3	0.037	2.303	1.533
1	3	3	35	0.573	0.123	-2.107	0.077	160.835	1.107	17.9	0.056	2.583	1.242
1	3	3	42	0.680	0.012	-1.249	0.077	177.223	1.104	39.3	0.025	2.307	1.468
1	3	2	21	0.363	.	.	0.090	282.940	0.820	29.9	0.033	6.072	1.218
1	3	2	28	0.273	0.193	-3.420	0.090	251.095	0.750	30.0	0.033	3.810	1.201
1	3	2	35	0.350	0.062	-2.071	0.090	203.029	0.762	42.2	0.024	3.804	1.014
1	3	2	42	0.371	0.041	-1.639	0.090	162.680	0.709	100.0	0.010	3.511	0.990
1	3	1	21	0.327	.	.	0.087	270.406	0.576	.	.	5.549	0.925
1	3	1	28	0.349	0.122	-3.039	0.087	251.278	0.519	44.800	0.022	5.243	0.821
1	3	1	35	0.159	0.035	-2.188	0.087	235.025	0.464	44.100	0.023	4.976	1.242
1	3	1	42	0.239	0.122	-1.942	0.087	179.786	0.405	21.800	0.046	4.785	0.163
1	4	3	21	0.825	.	.	0.092	336.315	0.959	35.000	0.029	3.538	1.143
1	4	3	28	0.818	0.101	-1.002	0.092	264.225	1.082	54.700	0.018	2.407	1.156
1	4	3	35	1.094	0.085	-0.294	0.092	233.131	0.945	23.700	0.042	2.774	1.240
1	4	3	42	1.284	0.092	0.298	0.092	195.176	0.970	36.800	0.027	3.029	1.280
1	4	2	21	0.558	.	.	0.084	314.065	0.973	14.900	0.067	3.972	0.937
1	4	2	28	0.558	0.125	-0.872	0.084	262.222	0.963	48.500	0.021	3.588	0.793
1	4	2	35	0.738	0.045	-0.001	0.084	245.752	0.837	34.000	0.029	2.263	0.805
1	4	2	42	1.099	0.096	0.314	0.084	215.377	0.771	23.200	0.043	2.925	0.691
1	4	1	21	0.364	.	.	0.095	233.781	0.809	34.600	0.029	5.356	0.710
1	4	1	28	0.338	0.145	-0.562	0.095	208.149	0.694	9.800	0.102	5.883	0.575

Light Treat.	Species	Nutrient Treat.	Harvest day	Root:shoot	Growth rate	Weight	RGR	SLA	Phenolics total	Toxic. (LC_{50})	Toxic. ($1/LC_{50}$)	Leaf Nitrog.	Leaf Phen.
1	4	1	35	0.405	0.050	0.452	0.095	229.192	0.868	28.400	0.035	4.013	0.482
1	4	1	42	0.765	0.109	0.799	0.095	221.835		.	.	3.681	0.427
1	5	3	21	0.686	.	.	0.077	170.554	0.663	16.4	0.061	3.619	0.678
1	5	3	28	0.515	0.031	-2.964	0.077	204.744	0.758	31.8	0.031	3.579	0.787
1	5	3	35	0.384	0.109	-2.749	0.077	228.911	0.818	66.0	0.015	2.657	0.917
1	5	3	42	0.503	0.076	-1.985	0.077	237.508	0.564	32.6	0.031	1.575	0.671
1	5	2	21	0.621	.	.	0.071	216.719	0.550	20.0	0.050	3.557	0.611
1	5	2	28	0.245	0.033	-2.733	0.071	259.253	0.687	30.8	0.032	2.428	0.722
1	5	2	35	0.183	0.069	-2.502	0.071	278.797	0.643	49.9	0.020	4.179	0.745
1	5	2	42	0.384	0.110	-2.020	0.071	251.891	0.911	30.4	0.033	3.281	1.060
1	5	1	21	0.275	.	.	0.059	258.326	0.564	51.1	0.020	4.836	0.655
1	5	1	28	0.398	0.034	-2.853	0.059	285.377	0.441	18.4	0.054	4.225	0.515
1	5	1	35	0.153	0.100	-2.615	0.059	280.835	0.320	42.0	0.024	3.956	.
1	5	1	42	0.186	0.034	-1.918	0.059	336.567	0.551	47.7	0.021	4.480	0.678
1	6	3	21	0.572	.	.	0.067	184.746	2.266	56.2	0.018	2.639	2.850
1	6	3	28	0.609	0.061	-3.432	0.067	228.237	1.162	49.4	0.020	1.558	1.323
1	6	3	35	0.657	0.093	-3.002	0.067	213.165	1.407	47.1	0.021	1.452	1.705
1	6	3	42	0.588	0.044	-2.353	0.067	226.775	1.549	49.9	0.020	1.623	1.490
1	6	2	21	.	.	.	0.100	.	.	52.2	0.019	.	.
1	6	2	28	0.318	0.075	-2.682	0.100	293.461	1.108	43.9	0.023	2.349	1.184
1	6	2	35	0.385	0.053	-2.159	0.100	279.204	39.4	0.025	2.113	1.015	0.015
1	6	2	42	0.408	0.136	-1.905	0.100	171.436	1.513	93.7	0.011	1.595	1.664
1	6	1	21	0.277	.	.	0.095	269.908	1.111	48.2	0.021	.	1.356
1	6	1	28	0.345	0.117	-3.407	0.095	385.964	0.912	24.9	0.040	3.321	1.080
1	6	1	35	.	0.071	-2.587	0.095	.	.	36.1	0.028	.	.
1	6	1	42	0.385	0.193	-2.091	0.095	273.179	0.509	67.8	0.015	3.807	0.531

Appendix 13. Data set of 6 species used in chapter IV. Light treatment: 250 (2), 125 (3) μ mol/m^2/s. Nutrient treatment: full-strength (1), 1/5 dilute (2), 1/10 dilute (3), 1/50 dilute (4). Species: *Achillea millefolium* (1), *Chrysanthemum leucanthemum* (2), *Cichorium intybus* (3), *Matricaria matricarioides* (4) and *Rudbeckia hirta* (6).

Light Treat.	Species	Nutrient Treat.	Harvest day	Root:shoot	Growth rate	Weight	RGR	SLA	Phen. total	Toxic. (LC_{50})	Toxic. ($1/LC_{50}$)	Leaf Nitrog.	Leaf Phen.
3	1	4	21	0.213	.	.	0.149	443.828	0.699	14.25	0.07	4.869	0.924
3	1	4	28	0.1	0.231	-4.839	0.149	282.495	0.53	11.1	0.09	3.131	0.822
3	1	4	35	0.319	0.017	-3.224	0.149	338.827	0.58	9.8	0.102	2.447	0.863
3	1	4	42	0.594	0.234	-3.105	0.149	208.116	0.997	10.7	0.093	1.896	0.882
3	1	3	21	0.329	.	.	0.135	412.521	0.849	13	0.077	.	1.04
3	1	3	28	0.339	0.198	-5.076	0.135	400.685	0.59	12.9	0.078		0.731
3	1	3	35	0.201	0.097	-3.557	0.135	469.53	0.48	11.9	0.084	3.533	0.51
3	1	3	42	0.216	0.158	-3.157	0.135	223.433	0.488	3.3	0.303	.	0.559
3	1	2	21	0.235	.	.	0.143	412.909	0.521	13.5	0.074	4.209	0.905
3	1	2	28	0.148	0.148	-4.015	0.143	382.385	0.444	11.4	0.088	4.385	0.698
3	1	2	35	0.145	0.165	-3.064	0.143	364.936	0.408	11.4	0.088	2.791	0.622
3	1	2	42	0.176	0.131	-1.877	0.143	284.342	0.402	12.3	0.081	3.46	0.515
3	1	1	21	0.237	.	.	0.129	458.742	0.777	15.9	0.063	2.182	0.833
3	1	1	28	0.071	0.165	-4.111	0.129	456.302	0.408	20.8	0.048	3.65	0.622
3	1	1	35	0.122	0.116	-3.006	0.129	310.694	0.454	25.8	0.039	3.721	0.572
3	1	1	42	0.273	0.1	-2.151	0.129	244.282	0.577	10.2	0.098	3.232	0.607
3	2	4	21	0.485	.	.	0.135	309.488	0.974	100	0.01	4.897	0.634
3	2	4	28	0.782	0.162	-3.006	0.135	308.102	0.959	57.2	0.017	2.18	0.499
3	2	4	35	1.016	0.145	-1.871	0.135	293.93	0.808	100	0.01	1.48	0.496
3	2	4	42	1.15	0.097	-0.853	0.135	232.72	0.695	100	0.01	1.434	1.137
3	2	3	21	0.617	.	.	0.145	324.552	1.174	100	0.01	2.861	0.799
3	2	3	28	0.635	0.209	-2.608	0.145	305.529	0.809	65.2	0.015	3.836	0.588
3	2	3	35	0.425	0.093	-1.143	0.145	283.535	0.627	33.2	0.03	3.761	0.462
3	2	3	42	0.516	0.153	-0.494	0.145	216.297	0.523	30.6	0.033	3.838	0.538
3	2	2	21	0.322	.	.	0.185	266.591	0.944	18.7	0.053	4.231	0.499

Light Treat.	Species	Nutrient Treat	Harvest day	Root:shoot	Growth rate	weight	RGR	SLA	Phen. total	Toxic. (LC_{50})	Toxic. ($1/LC_{50}$)	Leaf Nitrog.	Leaf Phen.
3	2	2	28	0.306	0.245	-3.082	0.185	323.512	0.738	67.5	0.015	4.842	0.444
3	2	2	35	0.545	0.167	-1.366	0.185	320.917	0.633	85.3	0.012	3.851	0.405
3	2	2	42	0.271	0.15	-0.194	0.185	242.149	0.501	67.9	0.015	2.25	0.424
3	2	1	21	0.326	.	.	0.116	378.814	0.88	26.7	0.037	4.362	0.756
3	2	1	28	0.253	0.199	-2.451	0.116	323.004	0.632	39.2	0.026	3.903	0.396
3	2	1	35	0.224	0.05	-1.055	0.116	266.749	0.558	68.8	0.015	3.623	0.472
3	2	1	42	0.271	0.12	-0.703	0.116	220.919	0.728	58.5	0.017	3.041	0.528
3	3	4	21	0.346	.	.	0.14	346.965	0.56	0.6	1.667	.	0.836
3	3	4	28	0.494	0.216	-4.416	0.14	394.893	0.662	29.6	0.034	3.66	1.012
3	3	4	35	0.548	0.133	-2.903	0.14	335.04	0.53	26.3	0.038	2.857	1.09
3	3	4	42	0.419	0.089	-2.009	0.14	281.649	0.568	21.6	0.046	2.666	1.025
3	3	3	21	0.391	.	.	0.143	446.663	0.244	4.3	0.233	.	0.95
3	3	3	28	0.315	0.209	-4.264	0.143	430.95	0.461	10.6	0.094	3.928	0.99
3	3	3	35	0.292	0.153	-2.97	0.143	373.412	0.382	16.6	0.06	2.92	0.814
3	3	3	42	0.198	0.08	-1.821	0.143	300.512	0.244	8.7	0.115	3.031	0.608
3	3	2	21	0.134	.	.	0.133	439.14	0.387	6.2	0.161	.	0.974
3	3	2	28	0.223	0.208	-4.296	0.133	408.108	0.376	7.8	0.128	3.853	0.877
3	3	2	35	0.151	0.097	-2.884	0.133	460.201	0.43	1.7	0.588	4.681	0.7
3	3	2	42	0.144	0.115	-2.273	0.133	385.605	0.692	4.5	0.222	4.054	0.609
3	3	1	21	0.133	.	.	0.135	496.928	0.336	4.9	0.204	.	0.947
3	3	1	28	0.276	0.227	-4.366	0.135	445.165	0.367	15.8	0.063	4.305	0.744
3	3	1	35	0.131	0.059	-2.654	0.135	437.237	0.502	10.6	0.094	4.656	0.947
3	3	1	42	0.29	0.153	-2.54	0.135	352.233	0.35	3.6	0.278	3.441	0.877
3	4	4	21	0.432	.	.	0.162	588.454	0.802	69.5	0.014	4.698	0.712
3	4	4	28	0.741	0.25	-3.374	0.162	476.022	0.814	100	0.01	3.002	0.507
3	4	4	35	0.641	0.043	-1.624	0.162	492.281	0.902	65.4	0.015	1.898	0.795
3	4	4	42	1.022	0.234	-1.324	0.162	334.274	0.736	93.7	0.011	2.595	0.742
3	4	3	21	0.427	.	.	0.138	599.963	0.8	36.1	0.028	4.584	0.312
3	4	3	28	0.579	0.207	-2.61	0.138	404.837	0.767	38.1	0.026	3.436	0.556
3	4	3	35	0.277	0.054	-1.163	0.138	469.856	0.781	39	0.026	4.045	0.562
3	4	3	42	0.377	0.195	-0.977	0.138	381.55	0.522	32.1	0.031	2.929	0.5
3	4	2	21	0.334	.	.	0.172	540.171	0.846	71.2	0.014	4.505	0.527
3	4	2	28	0.303	0.256	-2.962	0.172	495.232	0.775	36.1	0.028	4.14	0.541
3	4	2	35	0.463	0.177	-1.168	0.172	430.238	0.617	33.3	0.03	4.366	0.619

Light Treat.	Species	Nutrient Treat.	Harvest day	Root:shoot	Growth rate	Weight	RGR	SLA	Phen. total	Toxic. (LC_{50})	Toxic. ($1/LC_{50}$)	Leaf Nitrog.	Leaf Phen.
3	4	2	42	0.251	0.079	0.07	0.172	353.977	0.555	25.3	0.04	2.743	0.469
3	4	1	21	0.343	.	.	0.137	552.831	0.827	34.3	0.029	4.506	0.573
3	4	1	28	0.174	0.216	-2.529	0.137	557.436	0.678	32.9	0.03	5.381	0.457
3	4	1	35	0.155	0.123	-1.018	0.137	414.538	0.882	35.6	0.028	3.138	0.511
3	4	1	42	0.234	0.075	-0.158	0.137	376.388	0.814	39.7	0.025	4.396	0.608
3	5	4	21	0.275	.	.	0.128	377.696	0.659	100	0.01	4.995	0.534
3	5	4	28	0.359	0.164	-4.166	0.128	364.897	0.517	100	0.01	3.405	0.654
3	5	4	35	0.294	0.091	-3.018	0.128	394.155	0.721	100	0.01	3.462	0.587
3	5	4	42	0.63	0.135	-2.383	0.128	330.787	0.697	100	0.01	2.935	0.734
3	5	3	21	0.445	.	.	0.128	347.812	0.825	100	0.01	3.443	0.538
3	5	3	28	0.293	0.204	-4.395	0.128	342.857	0.592	68.6	0.015	3.983	0.459
3	5	3	35	0.211	0.082	-3.104	0.128	522.493	0.599	61.9	0.016	3.42	0.429
3	5	3	42	0.24	0.094	-2.39	0.128	348.964	0.446	78.4	0.013	4.28	0.335
3	5	2	21	0.083	.	.	0.137	362.989	0.53	55.3	0.018	5.547	0.375
3	5	2	28	0.107	0.063	-4.057	0.137	520.768	0.514	42	0.024	4.207	0.365
3	5	2	35	0.155	0.211	-3.916	0.137	419.495	0.579	38.5	0.026	4.572	0.474
3	5	2	42	0.145	0.115	-2.254	0.137	328.118	0.432	78.4	0.013	3.116	0.535
3	5	1	21	0.188	.	.	0.108	429.086	0.585	100	0.01	.	0.285
3	5	1	28	0.146	0.156	-4.418	0.108	461.657	0.42	42.8	0.023	6.107	0.361
3	5	1	35	0.245	0.134	-3.433	0.108	426.268	0.626	26.5	0.038	3.314	0.62
3	5	1	42	0.211	0.022	-2.386	0.108	439.052	0.604	47.8	0.021	4.725	0.382
3	6	4	21	0.314	.	.	0.146	405.569	0.848	63.2	0.016	.	0.767
3	6	4	28	0.481	0.019	-5.146	0.146	473.968	0.892	.	.	.	0.829
3	6	4	35	0.499	0.244	-5.013	0.146	331.504	0.949	.	.	1.671	0.722
3	6	4	42	0.494	0.146	-3.305	0.146	280.4	0.94	13.8	0.072	1.997	1.027
3	6	3	21	0.395	.	.	0.136	358.167	1.119	40.4	0.025	.	1.008
3	6	3	28	0.222	0.079	-4.803	0.136	561.102	0.654	.	.	.	0.619
3	6	3	35	0.256	0.133	-4.25	0.136	550.691	0.632	22.2	0.045	1.705	0.57
3	6	3	42	0.255	0.196	-3.318	0.136	353.072	0.494	.	.	3.383	0.55
3	6	2	21	0.148	.	.	0.17	548.076	0.708	21.4	0.047	.	0.711
3	6	2	28	0.15	0.079	-5	0.17	518.658	0.505	.	.	.	0.511
3	6	2	35	0.221	0.2	-4.445	0.17	609.882	0.386	47.2	0.021	2.125	0.38
3	6	2	42	0.193	0.115	-3.044	0.17	556.29	0.388	19.7	0.051	3.322	0.4
3	6	1	21	0.282	.	.	0.17	472.653	0.553	31	0.032	.	0.533

Light Treat.	Species	Nutrient Treat	Harvest day	Root:shoot	Growth rate	Weight	RGR	SLA	Phen. total	Toxic. (LC_{50})	Toxic. ($1/LC_{50}$)	Leaf Nitrog.	Leaf Phen.
3	6	1	28	0.255	0.04	-4.763	0.17	763.895	0.487	44.2	0.023		0.472
3	6	1	35	0.094	0.062	-4.484	0.17	737.048	0.472	.	.	.	0.469
3	6	1	42	0.213	0.415	-4.053	0.17	348.847	0.47	71.7	0.014	3.399	0.477
2	1	4	21	0.882	.	.	0.124	190.143	0.877	22.5	0.044	1.942	1.005
2	1	4	28	2.007	0.136	-3.739	0.124	174.023	1.027	21.6	0.046	1.372	1.018
2	1	4	35	1.11	0.113	-2.785	0.124	146.945	1.208	22	0.045	2.1	1.343
2	1	4	42	0.826	0.127	-1.997	0.124	156.596	0.948	12.9	0.078	3.057	1.529
2	1	3	21	0.467	.	.	0.136	273.558	0.754	16.9	0.059	3.401	0.679
2	1	3	28	0.593	0.028	-2.739	0.136	214.315	0.792	17.7	0.056	2.058	0.932
2	1	3	35	0.482	0.253	-2.544	0.136	137.282	1.033	12.7	0.079	2.875	0.946
2	1	3	42	0.538	0.079	-0.775	0.136	149.699	0.753	24.2	0.041	3.094	1.04
2	1	2	21	0.59	.	.	0.123	258.651	1.232	18.9	0.053	2.913	0.59
2	1	2	28	0.295	0.062	-2.596	0.123	217.426	0.494	49.6	0.02	3.785	0.683
2	1	2	35	0.353	0.178	-2.161	0.123	159.434	0.689	13.1	0.076	3.864	0.856
2	1	2	42	0.486	0.114	-0.913	0.123	146.834	0.501	12.8	0.078	3.139	0.966
2	1	1	21	0.427	.	.	0.146	276.465	1.032	39.8	0.025	2.425	0.493
2	1	1	28	0.219	0.094	-2.578	0.146	227.222	0.723	15.9	0.063	3.898	0.689
2	1	1	35	0.232	0.219	-1.848	0.146	158.259	0.626	26.4	0.038	4.077	0.677
2	1	1	42	0.245	0.09	-0.316	0.146	154.547	0.688	65.3	0.015	3.973	0.707
2	2	4	21	0.889	.	.	0.031	153.925	0.871	100	0.01	1.094	0.644
2	2	4	28	1.111	0.087	-1.92	0.031	154.955	0.844	49.4	0.02	2.247	1.359
2	2	4	35	1.607	0.068	-1.312	0.031	154.675	0.957	100	0.01	1.809	1.379
2	2	4	42	1.585	-0.077	-0.835	0.031	162.748	1.199	100	0.01	1.897	1.24
2	2	3	21	0.5	.	.	0.06	199.503	0.568	100	0.01	3.466	0.837
2	2	3	28	0.957	0.109	-1.267	0.06	173.159	0.95	100	0.01	1.632	0.717
2	2	3	35	1.046	0.054	-0.505	0.06	179.548	0.889	100	0.01	2.562	1.108
2	2	3	42	1.028	0.033	-0.187	0.06	153.629	0.937	100	0.01	2.423	0.776
2	2	2	21	0.419	.	.	0.095	233.27	0.53	43.8	0.023	5.227	1.578
2	2	2	28	0.471	0.078	-1.029	0.095	204.922	0.828	43.2	0.023	3.307	0.451
2	2	2	35	0.615	0.083	-0.486	0.095	155.15	0.933	100	0.01	1.876	0.656
2	2	2	42	0.786	0.128	0.096	0.095	127.139	0.726	53.3	0.019	2.839	0.498
2	2	1	21	0.308	.	.	0.096	211.154	0.504	100	0.01	5.083	1.199
2	2	1	28	0.23	0.155	-0.663	0.096	145.962	0.729	100	0.01	4.111	0.744

Light Treat.	Species	Nutrient Treat	Harvest day	Root:shoot	Growth rate	Weight	RGR	SLA	Phen. total	Toxic. (LC_{50})	Toxic. ($1/LC_{50}$)	Leaf Nitrog.	Leaf Phen.
2	2	1	35	0.238	0.096	0.423	0.096	128.593	0.679	46.3	0.022	.	0.634
2	2	1	42	0.443	0.036	1.096	0.096	141.465	0.679	59.4	0.017	3.456	0.713
2	3	4	21	0.742	.	.	0.129	174.574	0.653	.	.	.	0.915
2	3	4	28	1.067	0.074	-3.724	0.129	150.724	0.878	22.5	0.044	.	1.001
2	3	4	35	1.394	0.239	-3.205	0.129	147.447	1.241	67.7	0.015	1.775	1.268
2	3	4	42	0.775	0.05	-1.532	0.129	183.93	0.762	51.5	0.019	3.124	0.987
2	3	3	21	0.607	.	.	0.082	286.933	0.634	42.8	0.023	3.338	0.861
2	3	3	28	0.484	0.072	-2.769	0.082	227.301	0.821	100	0.01	3.3	0.753
2	3	3	35	0.44	0.165	-2.269	0.082	213.26	0.706	37.2	0.027	3.241	1.12
2	3	3	42	0.486	-0.009	-1.112	0.082	175.014	0.617	61.7	0.016	2.394	0.615
2	3	2	21	0.352	.	.	0.123	387.247	0.666	11.9	0.084	5.89	0.723
2	3	2	28	0.371	0.133	-3.232	0.123	372.191	0.685	32.8	0.03	4.256	0.711
2	3	2	35	0.271	0.153	-2.298	0.123	209.237	0.62	43.1	0.023	3.866	0.362
2	3	2	42	0.291	0.083	-1.23	0.123	168.114	0.65	50.7	0.02	3.65	0.495
2	3	1	21	0.216	.	.	0.123	399.314	0.543	28.1	0.036	5.23	0.758
2	3	1	28	0.249	0.268	-3.372	0.123	312.67	0.598	28.3	0.035	4.209	0.687
2	3	1	35	0.174	0.006	-1.498	0.123	259.066	0.45	100	0.01	3.968	1.046
2	3	1	42	0.274	0.142	-1.453	0.123	217.058	0.303	72.2	0.014	3.483	0.702
2	4	4	21	1.275	.	.	0.081	309.135	0.677	100	0.01	2.394	0.632
2	4	4	28	1.406	0.192	-2.12	0.081	272.496	0.648	100	0.01	1.864	0.799
2	4	4	35	1.498	0	-0.775	0.081	244.359	0.792	100	0.01	2.487	1.215
2	4	4	42	1.449	0.076	-0.777	0.081	240.04	0.654	81.9	0.012	2.575	0.969
2	4	3	21	0.485	.	.	0.102	364.776	0.7	53.1	0.019	3.87	0.683
2	4	3	28	0.772	0.176	-1.494	0.102	267.841	0.628	35.9	0.028	2.272	0.837
2	4	3	35	0.783	0.061	-0.262	0.102	260.118	0.813	35.4	0.028	2.913	0.717
2	4	3	42	1.197	0.084	0.165	0.102	213.854	0.52	52.4	0.019	1.892	0.589
2	4	2	21	0.44	.	.	0.095	354.144	0.612	22.2	0.045	4.463	0.8
2	4	2	28	0.571	0.176	-1.022	0.095	317.997	0.651	57.5	0.017	3.631	0.636
2	4	2	35	0.551	0.061	-0.401	0.095	229.132	0.408	43.8	0.023	3.004	0.605
2	4	2	42	0.817	0.084	0.382	0.095	199.839	0.38	34.2	0.029	2.451	0.668
2	4	1	21	0.304	.	.	0.133	357.918	0.672	30.1	0.033	5.592	0.553
2	4	1	28	0.259	0.092	-1.008	0.133	265.508	0.634	29.3	0.034	4.201	0.612
2	4	1	35	0.326	0.168	-0.365	0.133	227.628	0.896	10.2	0.098	2.334	0.434

Light Treat.	Species	Nutrient Treat	Harvest day	Root:shoot	Growth rate	Weight	RGR	SLA	Phen. total	Toxic. (LC_{50})	Toxic. ($1/LC_{50}$)	Leaf Nitrog.	Leaf Phen.
2	4	1	42	0.52	0.127	0.813	0.133	193.434	0.616	4.8	0.208	3.637	0.288
2	5	4	21	0.926	.	.	0.077	188.372	0.68	77.4	0.013	2.796	0.577
2	5	4	28	1.072	0.093	-3.595	0.077	204.89	0.727	100	0.01	2.927	0.601
2	5	4	35	1.213	0.052	-2.942	0.077	184.666	0.834	62.2	0.016	1.748	0.84
2	5	4	42	0.686	0.097	-2.582	0.077	207.235	0.565	55.3	0.018	2.892	0.697
2	5	3	21	0.434	.	.	0.065	288.235	0.443	92.4	0.011	4.071	0.488
2	5	3	28	0.387	0.073	-2.259	0.065	236.771	0.671	73.8	0.014	2.221	0.716
2	5	3	35	0.569	0.052	-1.745	0.065	292.606	0.572	100	0.01	2.532	0.695
2	5	3	42	0.708	0.073	-1.383	0.065	231.153	0.443	70.9	0.014	3.042	0.552
2	5	2	21	0.302	.	.	0.112	312.72	0.465	36.5	0.027	5.366	0.516
2	5	2	28	0.254	0.162	-2.746	0.112	266.027	0.549	37.4	0.027	3.814	0.548
2	5	2	35	0.265	0.122	-1.614	0.112	208.626	0.315	76.6	0.013	3.71	0.283
2	5	2	42	0.428	0.039	-0.759	0.112	334.266	0.616	48.2	0.021	3.554	0.799
2	5	1	21	0.244	.	.	0.128	286.28	0.464	29.8	0.034	4.779	0.502
2	5	1	28	0.231	0.251	-3.191	0.128	258.151	0.381	26.1	0.038	5.471	0.363
2	5	1	35	0.361	0.076	-1.436	0.128	280.788	0.41	20.5	0.049	3.981	0.466
2	5	1	42	0.293	0.068	-0.905	0.128	191.914	0.364	33.9	0.029	4.706	0.402
2	6	4	21	0.965	.	.	0.093	213.916	1.278	.	.	.	1.162
2	6	4	28	0.636	0.045	-4.026	0.093	227.772	1.154	.	.	.	1.147
2	6	4	35	0.909	0.052	-3.712	0.093	194.269	1.423	.	.	.	1.253
2	6	4	42	0.658	0.187	-3.347	0.093	281.296	0.838	.	.	2.402	1.046
2	6	3	21	0.629	.	.	0.121	392.744	0.46	68.8	0.015	.	0.556
2	6	3	28	0.518	0.145	-3.922	0.121	254.753	1.092	60.7	0.016	1.948	1.154
2	6	3	35	0.393	0.047	-2.91	0.121	303.808	0.997	66.4	0.015	2.667	0.988
2	6	3	42	0.535	0.19	-2.583	0.121	224.174	1.046	57.4	0.017	2.355	1.143
2	6	2	21	0.326	.	.	0.128	480.673	0.576	46.7	0.021	3.112	0.646
2	6	2	28	0.326	0.125	-4.143	0.128	399.862	0.66	74.8	0.013	.	0.703
2	6	2	35	0.302	0.154	-3.266	0.128	253.144	0.978	41.9	0.024	2.891	0.961
2	6	2	42	0.395	0.055	-2.187	0.128	232.11	1.219	39.5	0.025	.	1.286
2	6	1	21	0.33	.	.	0.25	468.23	0.503	.	.	2.108	0.67
2	6	1	28	0.286	0.16	-4.609	0.25	355.572	0.657	27.2	0.037	3.135	0.595
2	6	1	35	0.394	0.354	-3.49	0.25	217.477	0.976	59.6	0.017	3.079	0.918
2	6	1	42	0.243	0.189	-1.012	0.25	161.053	0.771	54.5	0.018	3.927	0.766

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