

A Review of Major Factors Influencing Plant Responses to Recreation Impacts

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ABSTRACT / This article reviews some of the more important factors found to influence the susceptibility of plants to trampling impacts associated with recreational use of natural areas. A three-way interaction mediates plant responses to impacts: plant \times environment \times stress level(s). Plant responses vary in part according to the genetic constitution of the plant, life and growth form, the adaptive flexibility of the plant, and anatomical differences inherent to growth habit and morphology. Other factors that influence plant sensitivities to impacts are the habitat environments in which plants

grow, since a number of conditions such as moisture excesses or deficiencies, nitrogen or oxygen starvation, late frosts, etc., cause physiological injury and may increase plant sensitivity to impacts. Among the environmental factors that may increase or lessen plant sensitivities to impacts are soil moisture levels, canopy density, elevation, aspect, microclimate, soil drainage, texture, fertility and productivity. Seasonal influences also bear consideration since environmental changes and phenological and physiological events are mediated by time of year. Stresses are caused by both direct and indirect forms of impact and vary according to season of use, frequency and amount of use, and the type of activity. These interactions are further complicated by evidence that inter- and intraspecific competition, antagonism, and commensalism may influence differences in the sensitivity of plant communities to impacts.

Recreational use of natural areas causes ecological change. Very little is known about the long-term biological effects of such change; however, in a comparison of the ecological consequence of fire, grazing, and recreation, Cole (1981) has characterized recreation impacts as localized but severe. The magnitude of change is related to the amount of use, the areal extent of use, the length of time use has occurred, and the type of ecosystem. The importance of these changes is difficult to predict since this branch of impact ecology has dealt with this matter for only a comparatively short period of time. According to some investigators, severely impacted areas in alpine, subalpine, arid and semiarid ecosystems may require fifty to hundreds of years to recover (Stohlgren 1982, Reid 1979, Willard and Marr 1970). The importance of these changes also depends upon point of view since it relates to management objectives set by those responsible for the management of natural areas and the preservation and amenity values attached to these areas.

The weight of evidence suggests that factors which give balance to ecosystem organization are highly sensitive to minimal disturbance and stress levels. Among the more damaging effects of trampling reported to date is the destruction of endangered, rare, and critically rare plant species (Hamilton 1983), loss of both biological and physical integrity of the impacted

system as evidenced by soil barren of vegetative cover (Cole and Ranz 1981, Manning 1979, Frissell and Duncan 1975), surfaces eroded to bedrock (Bryan 1977, Goetz 1975), and modification of ecological niches reflected by changes in species composition, diversity, and abundance (Speight 1973).

A three-way interaction appears to mediate plant responses to impacts: plant \times environment \times stress factor(s). Plant responses in turn vary according to the genetic constitution of the plant as reflected by life and growth form, community interactions and diversity, stage of succession, the adaptive flexibility of the plant, and anatomical differences inherent to growth habit and morphology. This article synthesizes what is currently known about intrinsic and extrinsic factors that influence the susceptibility or resistance of plants to trampling, including life and growth form and selected habitat variables.

Life and Growth Form

Responses to the mechanical effects of trampling appear to be strongly associated with the morphological characteristics of plants. Some British researchers use the life form concept introduced by Raunkiaer (1934) to describe the distribution frequencies of plants within a community structure and their responses to trampling. The theory supporting the life form relationship to impact is that position of the perennating buds relative to the soil surface governs in

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large measure the survival of plants in stressed environments (Table 1). The hemicryptophytic life form which has its buds located at or just below the soil surface has been shown to be most resistant to trampling stresses in pasture plants (Bates 1935), in sand dune vegetation (Slatter 1978, Liddle and Greig-Smith 1975), in woodland and forest and chalk grassland systems (Burden and Randerson 1972), and in subalpine plant communities (Schreiner 1974). These relationships could not be demonstrated, however, in alpine systems by Willard and Marr (1970), nor in Scottish Lochshore wetlands by Rees and Tivy (1978). Most American investigators favor using the growth form concept to describe characteristics of plants tested for tolerance to trampling. These descriptions include such features as position in community stratification, type of branching, growth habit, periodicity, and leaf type. Still other investigators prefer to combine these concepts in assessments of the relative tolerance of plants and plant communities to impact (Del Moral 1979).

The work of Naito (1969) sheds some light on the relationships between life form and growth form to intensity of use. In a study of impacted plant communities on the summit of Mt. Hakkado, Japan (1585 m above sea level), Naito reported the results shown in Table 2. Distribution of plant communities was presumed to be influenced by decreasing gradients of use from barren ground to lesser used zones. Areas contiguous to bare ground (Zone 1) supported a *Poa annua*-herbaceous weed community where hemicryptophytic and therophytic life forms dominated 98% of the community; 83% of the species of this community belonged to either the tufted (69%) or rosette growth forms (14.5%), which are considered well adapted to trampling. In Zone 2, a *Deschampsia flexuosa* community was characterized by plants having the hemicryptophytic life form (66%), the disappearance of therophytes, and an increase in chamaephytes. Dominance of the tufted life form was reduced 36% and replaced by species having prostrate, branching, and erect prostrate growth forms. In Zone 3, several meters distant from the heavily impacted area, a *Vaccinium vitis-idaea* community contained mostly chamaephytes (41%) and nanophanerophytes (31%). Two-thirds of the species composition of this community was represented by erect and erect-prostrate growth forms. These findings are similar to those reported by Liddle and Greig-Smith (1975) in a phytosociological study of areas impacted by car tracks, picnic areas, and paths in a sand dune ecosystem.

Figure 1 depicts these relationships in a setting in New Hampshire and shows the impact of limited

Table 1. Characterization of life form classes recognized by Raunkiaer (1934) and Cain (1950).

Class	Characterization
I	<i>Phanerophytes</i> (Ph): upright growing woody trees and shrubs having their bud-bearing shoots in the air. These are subdivided into height classes of tall, median, and low trees and shrubs. Those with which this article is primarily concerned represent the subclass <i>nanophanerophytes</i> (N), which reach heights less than 2 m but greater than 25 cm.
II	<i>Chamaephytes</i> (Ch): plants having perennating buds above soil surface but at heights less than 25 cm. This class includes semishrubby forms, those lying on the ground but having an ascending bud apex, actively creeping forms, and cushion plants.
III	<i>Hemicryptophytes</i> (H): plants having their renewal buds at the ground surface. This class of plants are reported to make up half or more of the total species found in deciduous forests and include nonrosette, subrosette, and rosette growth forms.
IV	<i>Cryptophytes</i> (Cr): plants having perennating buds beneath the soil. <i>Geophytes</i> , a subclass, have subterranean reproductive organs such as bulbs, rhizomes, stem and root tubers filled with stored food. These plants are common as vernal flora where they develop rapidly before full leaf canopy develops. Monocotyledenous plants make up a high percentage of these forms.
V	<i>Therophytes</i> (Th): plants whose perennating bud is that of the embryo contained in the seed. These are plants that reproduce annually by seed.

camping on a highly sensitive system. The central barren core shows some recolonization by grasses (hemicryptophytes on therophytes, and a second defined zone composed of black huckleberry (*Gaylussacia baccata*) and low bush blueberry (*Vaccinium angustifolium*) that originally occupied the barren area (chamaephytes); an outer zone composed of phanerophytes such as scrub oak (*Quercus ilicifolia*), white pine (*Pinus strobus*), and greybirch (*Betula populifolia*) is visible in the background. The original stand included phanerophyte reproduction.

Holmes and Dobson (1976) also reported that subalpine grasses that were most resistant to impacts had a tufted growth form, tough, wiry, and densely bunched leaf blades, and a basal rosette of tough pliable leaves. Recovery of impacted plants was found to be closely associated with position of perennating buds, pointing to survival advantages of the hemicryptophytic life



Figure 1. The relationship of life form to gradients of recreational use. Photo by F. R. Kuss.

form. Plants most vulnerable to trampling were tall, entirely herbaceous plants with caulescent shoots and those having brittle woody stems, with thin, tender, and erect leaves on the main stem supported by weak petioles.

Differences between the British and American choices of the life or growth form concepts may possibly be explained by the fact that much of the British work deals with open, nonforested systems whereas most of the American and Canadian research has focused on woody and herbaceous flora of wooded and high elevation systems. In Britain, the most resistant plant species are confined to lower elevations and nonwooded areas (Huxley 1970).

All organisms possess adaptive characteristics to cope with their immediate environment. These adaptations may be morphological, anatomical, physiological, or behavioral. Since all species or organisms exhibit variability, those having short generation times that produce large numbers of offspring or seeds are best adapted to meeting changing environmental conditions. For example, Frenkel (1970) characterized vegetation that persisted along disturbed roadsides in California as having the following characteristics: diminutiveness, spreading habit or rosette formation, small leaves, hemicryptophytic or therophytic life form, attenuated life span under unfavorable conditions, strong and thick cell walls, flexible vegetative parts, ability to spread and reproduce vegetatively, small hard seeds, small flowers, short root to flower distance, short period to reach seed maturity, large seed production per plant, and seed dispersal by external attachment.

Species that appear to be most resistant to impact in forested systems combine these characteristics: they are woody, prostrate in growth habit, have an under-

Table 2. Percentage distribution of life and growth forms of alpine flora associated with zones of decreasing impact (Naito 1969).

Item	Percent of community		
	Zone 1	Zone 2	Zone 3
Life form			
Geophytes	0	8	1
Hemicryptophytes	52	66	27
Chamaephytes	3	18	41
Therophytes	46	1	0
Nanophanerophytes	0	6	31
Growth form			
Tufted	69	44	21
Prostrate	14	22	5
Erect prostrate	2	10	40
Erect	0	8	26
Branched	14	5	1
Rosette	0	10	8

ground perennating organ, regenerate by layering, possess sclerophyllous leaves, and have the ability to grow in dry, droughty, or stressed environments where competition is reduced. Highly sensitive plants have soft, delicate leaves, a single exposed perennating organ, are active most of the use season, and are adapted to wet or moist habitats where soils are easily compacted and competition severe (Del Moral 1979).

As a subclass of herbs, graminoid species have been found to be much more resistant to impact than other growth forms (Lesko and Robson 1975, Landals and Scotter 1974; Nagy and Scotter 1974, Willard and Marr 1970, Laing 1961). Species that have basal meristems, small protected flowers, tough and flexible vegetative parts, basal leaves, underground stems, large root mass, and the ability to reproduce vegetatively appear to be highly resistant to recreational use (Cole 1979).

Factors that appear to influence the vulnerability of vegetation to trampling other than growth or life form are plant turgor and succulence, soil moisture, habitat preferences, length of seasonal activity, height, and phenology. Morphological resistance appears to be dependent on habitat condition as well as species interactions, since interactions of plants with high soil moisture levels and competitive influences greatly increase the susceptibility of plants to trampling damage (Liddle and Greig-Smith 1975). Moreover, there may be ecotypic and morphological variation within species as reported by Leney (1974) and Pearcy and Ward (1972) for *Poa annua* and *Deschampsia caespitosa*.

Responses of different species to trampling are in part dependent upon associated vegetation (Liddle and Greig-Smith 1975, Leney 1974). For example,



Figure 2. Trails in various stages of degradation due to compaction, loss of vegetation cover, and erosion. Photos: (a) From the National Park Service, Glacier National Park, (b) by F. R. Kuss, and (c) from the National Park Service, Sequoia National Park.

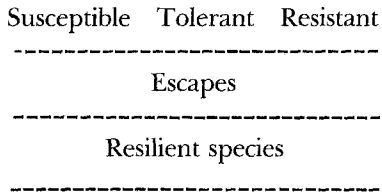
survival rates of the same species (subalpine) were found to be three times greater in mixed communities than in pure stands (Holmes and Dobson 1976). At the species level, responses to laboratory trampling experiments were markedly different than those observed in field tests where competitive conditions prevailed (Leney 1974).

Lists of plant species reported to be resistant to trampling have been compiled by Speight (1973) and reported by several other investigators (Cole and Schreiner 1981). Some caution should be exercised in the interpretation of such data since these are relative comparisons rather than absolute relationships to impacts and may confuse resiliency with resistance. The terms *sensitive*, *tolerant*, and *resistant* should be clarified.

In the context of this article the term *sensitive* refers to plants that are highly susceptible to damage by trampling. Plants that are able to withstand much greater amounts of disturbance than susceptible plants before being irreparably damaged are classed as *resistant*. Plants having morphological, phenological, or reproductive advantages that enable them to tolerate more use than susceptible plants but less than those classed as resistant are categorized as *tolerant*. An example of this class would be those plants found on light to moderately used zones along the margins of heavily impacted areas (Liddle 1975). A fourth category classed as *escapes* include plants which survive in impacted areas because of protected growing locations. In this context, resiliency refers to the ability of plants to re-

cover from disturbance after the impacting force is removed (Cole 1984, del Moral 1979). The diagram below portrays these relationships:

Relative response to trampling impacts



Habitat Influences

In addition to plant morphological and anatomical characteristics, the effect of a given intensity of recreation pressure on plants of natural environments shares a dependency with the habitats in which plants grow. Physical factors of the habitat environment mediate in great measure the extent and rate of change induced by recreational use. For example, wet habitats are more quickly denuded by trampling than dry areas; however, they may recover more rapidly (Cole 1984). Plants under stress from other factors such as nutrient and moisture excesses or deficiencies may respond differently to impacts due to these factors rather than because of genetic advantages or disadvantages. Plant sensitivity to impacts varies not only between locations but also within locations due to variations in stand density, extent of plant cover, community interactions, soil productivity, and microclimate. Habitat variables considered most important by del Moral (1979) include soils, moisture, canopy densities, elevation and aspect, and microclimate.

Soils

The type of substrate on which a plant species or community grows (that is, organic, gravel, or mineral soils) will determine moisture and drainage properties, amount of aeration, and the nutrient levels available to plants of the habitat (Parish 1971). These in turn will influence how a plant may respond to trampling. According to some investigators the most important site factor influencing the amount of and degree of impact is the fragility of the soil substrate (Leeson 1979, Strand 1972).

Trampling on mineral soils causes compaction, which in turn causes increased bulk density, decreased macropore space, and increased soil penetration resistance. According to Parish (1971), the net effect of compaction is to increase soil moisture at the expense of soil air. Consequently, factors most commonly in-

fluenced by change in soil density are: (a) drainage properties and moisture relationships in the root zone, (b) soil porosity and aeration, and (c) availability of soil nutrients (Liddle 1975, Parish 1971, Whisler and others, 1965).

Soil Compaction

The compaction process involves three sequential steps: (a) impact of the external compacting force, (b) the resistance the soil offers to the force, and finally (c) soil compression which results in a reduction of soil volume, increased density, and in some soils, long-term deformation (Lull 1959). Resistance to compaction varies according to soil texture, porosity, and moisture content. Consequently, for soils of a given texture and density, resistance or susceptibility to compaction will vary according to moisture content. Soils having the least resistance to compaction with increasing moisture content are coarse-grained, highly porous soils, sandy loams, sandy clay loams, and loamy sands. Those that resist compaction are silty clays, clays, and fine sands.

Maximum compaction of soils of different texture occurs at rather defined moisture optima. For example, maximum densities of clays are reached at moisture contents ranging from 20% to 30%, silty clays at 15% to 25%, and sandy clays at 8% to 15%. For sandy soils with no appreciable fine grains, there is no significant change in density with increasing moisture content (Marshall and Holmes 1979). Increases in moisture content beyond these optima result in both a decline in density and load-bearing capacity of the soil. Consequently, change in these properties caused by trampling depends largely on soil conditions that exist at the time trampling occurs. According to Lull (1959), soft or wet clay supports a load of 6.3 kg/6.45 cm² bearing surface, while semidry clay supports 12.6 kg and dry clay 25.65 kg/6.45 cm², indicating a twofold increase in each of the two stages of decreasing moisture content. Sands behave just the opposite since wet sands have a higher support capacity than do dry. Under wet conditions, silt loams have much lower load-bearing capacities than either clay or sandy loams.

Since the degree to which soils are compacted is dependent upon texture, porosity, moisture content, and the duration and intensity of use, a wide range of responses to the effects of trampling may be expected. Moreover, these effects will vary greatly according to the original density (degree of natural porosity or compaction) of coarse soils, and the consistency of fine-grained soils. Soil consistency in the natural state corresponds in some measure to the degree of compaction of coarse soils and is influenced by moisture

content. Variations in soil consistency are commonly referred to as hard, friable, plastic, and liquid, which correspond to hard, medium soft, soft, and very soft consistencies. Information contained in Table 3 illustrates the effect of water content on the behavior of fine-grained, cohesive soils. As moisture content increases, soil consistency changes from firm to plastic, and resistance to compaction declines as does the ability of soil to carry traffic. The potential for soil adhesion to boots also increases with moisture content until very wet conditions prevail.

When equal stresses are applied to soils, the lower the density, the greater the compression. When attempting to compact soils, however, greater kg/cm² of bearing surface are required for fine-textured soils than coarse. Consequently, some soils are much more difficult to compact than others. For example, silts, silty clays, and clays resist compaction more than do sandy or gravelly soils (Asphalt Institute 1969). Under both laboratory and field studies dealing with responses of soils to compaction, it has been shown that maximum densities decrease systematically in the order of decreasing grain size from gravels to clay (Krynine 1941). Consequently, it has been reported that maximal bulk densities decrease with increasing clay content and increase with increasing sand content (Mausbach and Gamble 1984).

The relative differences in reported resistance to compaction suggest that the order of resistance may be reversed when compared to the magnitude of potential density change. This generalization is supported by the findings that the coarser the soil and lower its density, the greater its susceptibility to compaction at higher moisture contents (Lull 1959). On coarse soils, rapid decreases in macropore volume were reported to occur under comparatively light use loads (68 to 128 passes) by Jones (1978). This was accentuated by increased moisture content. It follows that soils having large volumes of pore space and less density per unit volume are more prone to compaction hazards than are finer-grained soils. However, these same kinds of soils and soils that are gravelly or cobbly, or very shallow soils that have good gravel or a cobbly base are less susceptible to erosion than deep, gravel-free soils (Sparrow and others 1978).

Some generalizations that may be made dealing with soil resistance and susceptibility to changes caused by trampling are listed below:

- Compaction increases soil density by reducing total pore space causing varying degrees of soil deformation (Marshall and Holmes 1979).
- Soil resistance to compaction depends upon tram-

Table 3. Effect of water content of a cohesive soil on its behavior (Marshall and Holmes 1979).

Moisture status	Dry	Moist	Wet	Very wet
Consistency	Hard	Friable	Plastic	Liquid
Ability to carry traffic	High	High	Low	Very low
Adhesion	Very low	Low	High	Low
Resistance to compaction	High	Moderate	Low	High

pling intensity and duration, moisture content, texture, structure, density, and organic matter content (Jones 1978, Lull 1959).

- The coarser the soil, the lower its density, and the higher its moisture content, the greater its susceptibility to compaction (Lull 1959).
- The greater the initial porosity of the soil, the greater the depth of compaction (Lull 1959).
- Compaction increases the resistance of soils to further deformation. Loss of pore space reduces infiltration capacity and water movement through the soil thus making the soil more erosion prone (Lutz 1945, Baver 1933).
- Maximum densities that may result from compaction decrease systematically with decreasing grain size (that is, from gravel to clay soils) (Lull 1959).
- Maximum densities attained by various soils show strong relationships with rather definite optimal moisture levels. With the exception of coarse gravels and sandy soils with no appreciable fine-grain content, the less dense the soil, the greater moisture content required to reach maximum density. After optimum moisture content is reached, further increases in water content will result in lowered resistance to compaction and a reduction in density (Marshall and Holmes 1979).
- Poorly graded soils and soils that have the greatest range of particle sizes compact to greater densities than those having uniform grain size (Marshall and Holmes 1979).
- Subsurface hard pans produced by trampling are most commonly found in medium-textured soils such as loams, sandy loams, and silty loams (Malin and Parker 1979, Lull 1959). Long-term effects of compaction have greater effects on clay than sandy or silty clays and may extend deeper into the soil column than in other soil types (Orr 1960).
- Frost action may loosen compacted soils or compact loose soils (Thorud and Frissell 1969 and 1976).
- Duration of time that soils remain compacted depends in great measure upon frost action and the

shrink–swell potential of soils (Marshall and Holmes 1979).

Drainage

Owing to differences in sources of parent materials, texture, structure, composition of the substrata, depth to hard pan or bedrock, and depth to water table, soils vary in terms of their drainage properties. Consequently, soils may be grouped into several different classes ranging from excessively well-drained soils which are often drought-prone to those that are very poorly drained which remain water-saturated most of the year. Drainage properties influence moisture imbalances (excesses or deficiencies), aeration, gas exchange, and nutrient availability (Kemper and others 1971, Parish 1971). Problems associated with drainage may exert sufficient physiological stress to predispose part or all of the plant cover to severe limitations in tolerance to other stress factors (Boyce 1938). According to Leonard and Plumley (1979), moderately well-drained mineral soils are more favorable habitat soils than either rapidly drained or poorly drained soils.

While good drainage and water transmission properties are generally associated with coarse soils, the same soils may have low water-holding and cation exchange capacities which adversely affect their capabilities to support plant growth. Thus favorable drainage properties may be countered by lower productivity potentials and consequently less biomass and species diversity on these soils (Del Moral 1979).

Drainage properties influence susceptibility or resistance to trampling. As indicated earlier, soils that remain wet will be subject to greater compaction stress, while very wet soils are disrupted and displaced by the compacting force (Marshall and Holmes 1979). For the most part, well-drained soils that remain dry possess higher load-bearing capacities and more resistance to change. Exceptions are loose, dry sandy soils, soils that tend to pulverize readily, and dry porous dune soils.

Gravelly and sandy soils have high rates of infiltration while fine- to medium-textured soils are infiltrated more slowly. Clays generally have slow water transmission properties. Information taken from soil engineering data indicate that drainage characteristics of compacted soils are highly variable. Coarse-grained soils having little or no fines are least affected. This is an important feature of soil differences which suggests that under pressures of recreational use, coarse-grained gravelly and sandy soils are more resistant to adverse changes in drainage properties than are compacted silt and clay soils, which may become semi-im-

pervious to impervious to the downward movement of water.

Effects on Soil Moisture Relationships

Soil moisture relationships are highly complex but are related to the number of trampling passes a foot-path may receive. Depending upon soil texture and structure, trampling pressures may either decrease or increase moisture content of the impacted soil. In grassland soils, moisture content was reported to be reduced by low to moderate trampling. As use densities increased to high levels, the moisture content of these same soils increased above levels found in the undisturbed areas (Crawford and Liddle 1977).

Increases in moisture content may result in transforming certain soils from a firm consistency to plastic or liquid consistency. This is particularly true to soils having a high percentage of fine particles such as fine sandy, silt, and clay soils. Under firm-moist conditions, moisture provides lubrication for soil particle realignment. Since the effects of compaction are to decrease total pore space and air-filled pores, the proportion of water-filled pores is increased and the soil becomes proportionately wetter (Burden and Randerson 1972). In dry soils, particle resistance to rearrangement is greater because limited water films provide little lubrication. Additional moisture improves lubrication, reducing the force of surface tension so that compaction occurs more readily. In spongy moist soils, trampling pressures may expel water out of the soil column, and the water is then subject to evaporation. Consequently, compaction of paths in wet areas may result in lower moisture content when compared to unused areas. As pore space is reduced, the absorptive capacity (infiltration and percolation) of the soils may be greatly reduced and surface runoff and the potential for erosion enhanced (Arndt 1961). Results of hiking and compaction on soil stability of three different systems are shown in Figure 2. In these three cases, slope effects were minimal indicating that trail wear and erosion were due primarily to soil characteristics and other site variables.

Effects on Nutrient Availability

When soil is compacted, increased soil density brings about changes in both air space and moisture relationships in the root zone. These changes may have pronounced effects on plant growth due to: (a) lowered oxygen tension, (b) increased moisture content, (c) reduction in nutrient availability, and (d) physical restrictions to root elongation (Whisler and others 1965).

The effect of compaction on essential mineral avail-

able to plants is highly complex since the mobility of ions is dependent upon three major modes of transport which are influenced by soil density-moisture content interactions. This discussion will focus primarily on phosphorus and nitrogen mineralization.

The availability of minerals to root uptake is mediated by three major routes: (a) mass flow in the soil solution, (b) diffusion across concentration gradients, and (c) physical contact by the root(s) with the source of ion (Kemper and others 1971). Nitrate is completely mobile throughout the soil profile and its movement closely follows the movement of soil water (mass flow). The dominant route of phosphate is by diffusion. Most sources of phosphate exist in insoluble form and require solubilization by organic acids produced by anaerobic metabolism. Anaerobic conditions found at microsites throughout the soil column and in the center of soil crumbs facilitate the solubilization of inorganic phosphate sources. On the other hand, transformation of ammonia (NH_4) to nitrate (NO_3) is oxygen dependent, since these transformations are primarily mediated by aerobes.

Conditions which favor release of organic phosphate favor ammonification of nitrogen. In reducing environments (low oxygen tensions), the valency state of Fe and Mn may change and become toxic to plants. Moreover, reduction of sulfur compounds leads to the production of H_2S , which is very toxic to plants (Kemper and others 1971, Parish 1971). Since the effect of compaction is to reduce macropore space, mass flow may be inhibited by pore changes. As a consequence water held in micropores is less available to the plant than water contained in large pores. In many light soils, the movement of NO_3 is controlled almost entirely by wetting and evapotranspiration. As is common to many soils, infiltration and water conductivity are reduced by compaction, thereby inhibiting the flow of water through the soil column.

Almost all nitrogen found in the surface soil horizons occurs in organic combination (Alexander 1961). Transformation of NH_4 to NO_3 occurs only in well-aerated habitats. Consequently, nitrogen mineralization from soil organic matter has been found to be reduced by even slight increases in bulk density (Whisler and others 1965).

Pores and interstices of the soil profile are never entirely oxygenated even in microsites of well-drained soils (Alexander 1961). Compaction reduces pore size, thus creating more potential for anaerobic microenvironments. When biological oxygen demand exceeds the supply of carbon sources, which occurs during periods of intensive soil microbial activity, anaerobic conditions will increase. In the absence of oxygen or

during periods of oxygen shortages in the soil column, denitrifying bacteria actively convert nitrate to ammonia and free nitrogen (Alexander 1961). Consequently, when soil is very wet or highly compacted, mineralization of organic matter to nitrate nitrogen may be limited. Fresh sources of carbon produced when plant residues and humus are mixed with mineral soil, as might be expected to occur in campsites, are also important to the process (Alexander 1961).

Since bacteria which convert NH_4 to NO_3 are obligate aerobes, changes in soil structure and aeration such as occur under heavy soil compaction will adversely affect the availability of nitrate to plants. Between these two influences (denitrification and nitrification inhibition) it is quite possible that nitrogen shortages will appear in stressed environments such as campsites, picnic areas, and so on, where traffic is moderate to heavy (Stohlgren 1982, Rutherford and Scott 1979).

Soil Fertility and Productivity

The effect of soil fertility on the rate and magnitude of change has not been dealt with to any degree in the literature. Kellomaki and Saastamoinen (1975) indicate that plants growing in moderately fertile sites in coniferous forests were more tolerant to trampling than those growing in highly fertile sites, while plants growing in sites of low fertility were less tolerant to impacts than those on the highly fertile areas. In another study Kellomaki (1977) suggests that vegetation on fertile sites and meadows is more tolerant to trampling than comparable infertile sites, contradicting the inferences of del Moral's work.

Fertility of soils is based primarily on the availability of nutrients. The nutrient regime in turn is influenced by two key considerations: the amount of potential nutrient sources in the soil and the rate by which these nutrients are recycled by soil-inhabiting microflora. According to Leonard and Plumley (1979) soils that have high nutrient availability are those that are non-acidic, medium textured, have high organic content in the mineral soil, and are moderately well drained. Plant growth is enhanced by soils having good but not excessive water-holding capacity, such as sandy loams, loams, and sandy clay loams, by those that are well aggregated having a granular structure, and by those that are deep to bedrock or pan layer. Soils located in areas that receive an overabundance of precipitation may be less fertile because of nutrient leaching.

While only a few references have dealt with the effects of soil fertility on plant responses to recreation impact, the suggestion that infertile sites are more sensitive to impacts may be due to differences in the orig-

inal density of plant cover and total biomass of the plant stand rather than actual sensitivities. Many infertile soils are coarse, droughty soils which in part compensate for the sensitivity of moist or wet habitats to impact. Consequently, plants adapted to these habitats may, as Del Moral (1979) suggests, possess certain anatomical and structural features that confer greater resistance to trampling than shade-tolerant, moisture-requiring plants growing in more fertile forest habitats as reported by Cole (1979).

Moisture

In general, research findings indicate that plants growing in wet areas are most sensitive to recreational impacts. These observations range from studies of bog, marshland, meadows, and forested sites to areas of high moisture in alpine and tundra plant communities. For example, wet meadows in Yosemite National Park and Kings Canyon National Park were much more susceptible to damage than dry meadows (Malin and Parker 1976, Strand 1972). Strand (1972) considered moisture to be the most important site factor influencing the sensitivity of the system to impact. In Scotland, wet areas were reported to be denuded at lower trampling intensities than dry areas. Moreover, the trampling tolerance of the same plant species may decrease when growing on moist compared to dry sites (Leney 1974). In a study of the Sunshine Area Alpine Meadows in Banff National Park, Price (1983) concluded that plant susceptibility to hiking impacts followed moisture gradients influenced by elevation, soil depth and drainage properties, snow depth and lateness of snow melt. The effects of hiking on organic surfaces having a high moisture level and a modest slope gradient are shown in Figure 3 where erosion has exposed the root system of the overstory trees.

Canopy Densities

The effect of the overstory canopy is to retain moisture in the lower strata, resulting in higher relative humidities, cooler temperatures, and reduction or radiation reaching the ground cover. Filtered radiation reaching the ground level requires that plants growing under the overstory be shade-tolerant and adapted to higher humidities and lower diurnal temperature fluctuations. These conditions may result in more succulent growth and growth forms more sensitive to trampling. For example, vegetation under a forest canopy has been found to be 20 times more sensitive to trampling than prairie grassland (Nagy



Figure 3. Severely eroded trail surface showing root exposure of overstory trees. Photo by Robert Kaufman, Shepherd College, West Virginia.

and Scotter 1974), and timberline meadows are much less sensitive than vegetation growing under forested canopies on valley bottoms. More vegetation change is reported to occur under dense forested sites in the northern Rockies than in open forest or meadow sites where summers are wet, regardless of elevation (Cole 1979). Under these conditions, shade-tolerant plants have more supportive and conductive tissue and greater leaf area, and thinner cuticles, cell walls, and stems than plants growing in full sun (Cole 1979). These findings are in accord with those reported by Daubenmire (1974). A few major differences in the morphologic and physiologic characteristics of sun plants compared to shade-tolerant plants are shown in Table 4.

These sensitivities are reflected in the findings of Schreiner and Moorhead (1979), who found a positive correlation between the percentage of canopy cover and tree height, and the area of vegetation loss in impacted areas of Olympic National Park. Where bare ground was greatest, canopy cover was most dense. Similar observations have been made by Ripley (1962). With similar canopy densities, surfaces under coniferous overstories appear to be less sensitive than those under deciduous trees. This difference is thought to be due to a high level of unincorporated organic litter usually found in coniferous or boreal forests (Legg 1973). In communities having no canopy cover or limited vertical development such as alpine areas, wetlands and marshes, krummholz, meadows and heaths, the primary determinants of vegetative vulnerability to impact appear to be growth form, morphology of constituent species, and whether the habitat is wet or dry (Leney 1974, Palmer 1972, Strand 1972, Laing 1961).

The importance of canopy development and encl-

Table 4. Differences in morphologic and physiologic characteristics of sun plants compared to shade plants (after Daubenmire 1974).

Morphologic characteristics	Physiologic characteristics
1) Thicker stems with well-developed supporting tissue	1) Higher respiration rate
2) Less leaf area per plant	2) More rapid transpiration
3) Shorter internodes	3) Higher salt and sugar content
4) More branching	4) Lower K, CA, P content
5) Thicker leaf blades of hard texture	5) Higher C/N ratio
6) More numerous roots	6) Greater vigor of flowering fruiting
7) Greater dry and fresh weights	7) Greater resistance to temperature and drought injury
8) Thicker cuticles and cell walls	

sure in dictating site-specific reactions is documented by Schreiner and Moorhead (1976), Ripley (1962), Scoles (1977), and Dawson and others (1978). In eastern mesic environments crown closures of less than 40%–50% generally permit the development of continuous sod (Dawson and others 1978, Scoles 1977), whereas herbaceous groundcover plants under closed canopies are more sensitive to impact than those growing in more open sites (Cole 1982). These differences were further elaborated upon by Logan (1979) who reported that level of use could be shown to be strongly related to percentage of herbaceous cover, but not to percentage of grass cover. Parameters considered most important by Lesko (1973) in evaluating site capability potentials for recreational use are: (1) percentage of grass cover, (2) depth of rooting, (3) thickness of the Ah soil horizon, (4) thickness of the forest floor (LFH layers), (5) soil texture and drainage, (6) slope, and (7) length of growing season. In Figure 4, the impacts of backcountry camping in undesignated areas are shown. Both the spruce–fir Northern hardwood overstory and understory reproduction were destroyed and standing trees mutilated. Note the open, barren area has been partially recolonized by grasses and annuals (hemicryptophytes and therophytes) and the fire scar on large rock.

Elevation and Aspect

Due to its climatic influence, elevation is an important variable affecting responses to both plants and soils to impact. Precipitation generally increases with



Figure 4. The effects of changes in canopy density on ground flora and recolonization of impacted areas. Photo by F. R. Kuss.

elevation while temperature decreases roughly 1°F with each 91.4 m rise in elevation (Knight 1965). At higher elevations there are fewer frost-free days and much shorter growing seasons than at lower elevations. Two important variables which determine length of growing season are: (a) the number of degree days above 42°F, which is heat- or temperature-dependent, and (b) mean annual water deficit, which is temperature- and therefore elevation-independent (Lesko 1973).

The effect of elevation is pronounced in terms of the length of plant dormancy, the phenological development of plants, bloom period, height, soil depth, and rate of soil microbial activity (Hartley 1976, Percy and Ward 1972). Due to these factors, responses of vegetative cover to the same use intensity or responses of the same plant species to variations in use intensities may differ in different altitude zones during the same use season, as suggested by Percy and Ward (1972) and Dykema (1971). Moreover, elevation change leading to moisture gradients represent differentials in potential soils sensitivities to impact as well as plant community tolerance or intolerance to use (Price 1983). It may be generalized that plants in the rapid stage of growth and during bloom periods are most susceptible to physiological stress and injury (Hartley 1976, Parish, 1971, Donard and Cooke 1970).

Other variables influenced by elevation are stand density, type of canopy cover, canopy development and enclosure, type of ground cover, soil development, and hydrology. Thus differences may occur between and within general classes of plant communities and habitats indicating the importance of site-specific characteristics in dealing with the problem of impact evaluations. Consequently, the question of morpholog-

ical, physiological, and phenological resistance to impact must be resolved with localized environmental conditions and points to the importance of the concept of habitat resistance espoused by Liddle (1975) and del Moral (1979).

Microclimate

The effect of aspect and elevation may be localized in one area (Price 1983). For example, snowmelt is usually found to be much slower on north-facing slopes or pockets in the land. Consequently, soils under the snowpack remain cold and wet longer than those found on southerly exposed slopes. Moreover, within-area variations in microclimate may occur. Unfortunately, little documentation of the effect of trampling on microclimatic differences appears in the literature. A few notable exceptions include the work of Liddle and Moore (1974), who report a net temperature increase of 7°C in diurnal soil temperatures as a result of track damage to sand dune vegetation. Microclimate changes in beach and dune ecosystems of Padres Island National Seashore were reported by McAtee and Drawe (1981) to vary both above and below ground as much as 9.5°–10°C between areas receiving low use when compared to heavily used areas. In a study of meadow paths in Yosemite National Park, Hecht (1976) found that both ground and vegetation temperatures were higher and relative humidity lower on paths when compared to areas adjacent to the paths. These changes were more pronounced in mesic than xeric habitats. In wet meadow environments, trampling caused ground temperatures to increase an average of 3.2°C while relative humidity declined as much as 40%. In the more open xeric environments, these changes were not as pronounced. Hecht (1976) further observed that changes in ground and leaf temperatures and relative humidity appear long before other evidences of deterioration. Thus, in impacted areas, changes in the soil medium may be accompanied by microclimatic changes that impose further selection pressures on existing plant communities.

Impacted sites located on north-facing slopes have been found to support more ground cover than sites located on floodplains or south-facing slopes (Dawson and others 1974). Plants most durable to impact were found on steep northeast-facing slopes in northern Utah by Cieslinski and Wagar (1970), while shaded sites in Michigan were reported most durable by Wagar (1961). However, Helgath (1975) concluded that trail wear in the Selway-Bitterroot Wilderness was more strongly associated with vegetation type, landform, and slope than aspect or elevation.

Some caution should be noted in terms of interpretations given to the influence of aspect. While higher and prolonged moisture levels are associated with north-to-northeastern-facing slopes, which would tend to reduce the rate of desiccation of injured plants, it is also recognized that plants grown in full sun appear to harden off more quickly and thus be less succulent. Moreover, moist or wet soil and organic matter may be more rapidly disrupted by the shear stresses of foot traffic.

Summary

The effect of trampling on plant growth, survival, and regeneration cannot be separated from habitat influences. While there is persistent evidence that morphological characteristics play an important part of the susceptibility–resistance equation, the effect of unmodified or modified habitats on the growth of plants—their succulence, stunting, hardening off, phenology, amount of supportive tissue and other anatomical differences—may confer differences in responses of the same species growing in different habitats (Cole 1984). The effect of trampling is to cause two major types of stress: (a) mechanical injury to foliage, shoots, stems, and surface roots resulting in impaired photosynthetic activity, water loss, and new energy demands for regrowth and reparation; and (b) altered soil habitats which create, for the most part, adverse conditions for plant survival and regeneration by impairing vital root-associated processes such as nutrient uptake and translocation. Other environmental influences center on the effects of physical factors such as elevation, aspect, length of frost-free season, moisture and temperature on plant habitat and growth as well as biological interactions such as intra- and interspecific competition, antagonism, or commensalism and species composition of the plant community. Habitats may be classed as resistant or highly sensitive to impacts.

Changes in the soil medium brought about by trampling and compaction which reduce organic matter levels, changes in drainage–moisture relationships, and reduced oxygen levels may have a pronounced effect on the susceptibility or resistance of plants to debilitating injury. In coarse soils, compaction may actually benefit plants by increasing available moisture (Blom 1976, Lutz 1945) and by reducing the physical-spatial distances between roots and sources of nutrients (Kemper and others 1971, Parish 1971). In fine-grained soils such as very fine sandy, silt, or clay soils, compaction may cause these soils to become im-

permeable or nearly so to the downward movement of water and lead to depressed moisture and oxygen levels. Since active nutrient uptake by roots is both water and oxygen dependent, these conditions may result in serious nutritional disorders which add to the stress levels of plants injured by trampling. Because of the behavior of clay under compaction loads, both del Moral (1979) and Leeson (1979) consider soils having high percentages of clay as important factors which increase habitat sensitivities to impacts.

Comparisons of the relative resistance of forest communities to trampling impacts have shown that communities growing on gravelly or sandy soils having little organic matter and clay content and a sunny exposure appear to be most resistant. Community resistance has been attributed to the presence of a relatively sparse ground cover made up of plants with sclerophyllous leaves, dry-well drained soils which do not compact easily, and the presence of a number of surface rocks. On the other hand, highly sensitive communities were found in habitats located on relatively steep north-facing slopes, having soils that remained wet. Habitats supporting high groundcover densities, wet soils, and understories dominated by woody species with brittle stems and lush forbs were most sensitive to trampling impacts. The most resistant communities were dominated by an understory made up of xerophytic herbs (Del Moral 1979).

Soil depth is considered a more important factor in mediating change than is slope, vegetative cover, or duration of use. Shallow soils are perhaps more sensitive to change since soil depth affects the rooting depth of plant cover. It is generally reported that the first six inches of soil is that which is most impacted by trampling. This is also the zone of greatest biologic and chemical activity and where a high concentration of feeder roots are found. This zone is also where organic matter is incorporated into mineral soils and the focus of much of the soil and litter inhabiting fauna. Depth of rooting is a measure of effective soil depth, since root penetration may be limited because of shallow to bedrock soils or restricted because of the presence of pan layers that impede further root growth.

Problems associated with textural-drainage-compaction relationships may exert sufficient physiological stress to predispose a part or all of the plant cover to increased sensitivities in their tolerance to other stress factors. Thus, the limiting factor mediating plant tolerance to mechanical damage may shift from genetic governance of above-ground morphology to physiological stress associated with changes in the soil environment.

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