REVIEW

The ecological and evolutionary significance of frost in the context of climate change

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Abstract

The effects that below-freezing temperature (frost) can have at times of year when it is unusual are an interesting ecological phenomenon that has received little attention. The physiological consequence of formation of ice crystals in plant tissue is often death of the plants, or at least of sensitive parts that can include flower buds, ovaries, and leaves. The loss of potential for sexual reproduction can have long-lasting effects on the demography of annuals and long-lived perennials, because the short-term negative effects of frosts can result in longer-term benefits through lowered populations of seed predators. The loss of host plants can have dramatic consequences for herbivores, even causing local extinctions, and the loss of just flowers can also affect populations of seed predators and their parasitoids. Frosts can cause local extinctions and influence the geographical distribution of some species. The potential for global climate change to influence the frequency and distribution of frost events is uncertain, but it seems likely that they may become more frequent in some areas and less frequent in others.

Keywords

Climate change, frost, hoarfrost, killing frost, long-term study, second-order effects.

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INTRODUCTION

The meteorological phenomenon known as frost is not as oppressive as drought, as violent as wind storms, as long-lasting as winter, or as striking as lightning, yet it can have significant, pervasive and long-term ecological effects. At a geographical scale, frost can determine plant and animal distributions and on a seasonal scale it can limit plant growth and reproduction. Ecological consequences are primarily mediated through its effects on sensitive plants (or parts of plants), which in turn cascade through plant–animal interactions, insect parasitoids and pathogenic taxa. These effects and interactions will probably change, geographically and temporally, as a consequence of global climate change. I suggest that ecologists and evolutionary biologists have not recognized the potential for interesting and significant studies of the effects of frost, and that they will find this, particularly in the context of climate change, to be a fertile field of investigation.

WHAT IS FROST?

The word "frost" has three meanings: (1) the ice crystals (hoarfrost) that can coat plants, the ground and other inanimate objects if the temperature is cold enough; (2) the effects that below-freezing temperatures can have on both living and inanimate objects (e.g. "killing frost"), and (3) the attainment of temperatures below freezing (especially in soil, as in "permafrost"). In this paper I address primarily issues related to the second definition, especially frosts at the beginning of the growing season, which have quite different contexts and evolutionary implications from freezing temperatures during the winter.

Hoarfrost is formed directly from water vapor without a transition through the liquid phase. The formation of hoarfrost and the size of crystals produced is dependent on temperature, the duration of subfreezing temperature and the amount of moisture in the air. Under some conditions, the effects of frost (i.e. subfreezing temperature) on living organisms can occur without the formation of the visible signal of hoarfrost (a condition sometimes called "black frost") (Bagdonas *et al.* 1978). Frost can even affect plants when air temperatures above the ground are substantially above freezing, as the leaf temperatures can drop substantially below air temperature if there is sufficient longwave radiative cooling (loss of heat to the cold night sky) under calm, clear and dry atmospheric conditions (Leuning & Cremer 1988).

EFFECTS ON PLANTS

The biological significance of frost has been well studied from some perspectives, such as its timing, effects on agriculture, and mechanical action on soil, but is mentioned in few ecological field studies. At the cellular level, subfreezing temperatures that signal frost conditions can cause formation of ice crystals within or between cells, which can cause physical damage and trigger physiological problems through loss of solute. The role of ice nucleation bacteria in this process adds an interesting symbiotic twist; these epiphytic bacteria catalyse the formation of ice crystals (Lindow *et al.* 1982), and thus can result in frost damage at temperatures when supercooling might otherwise protect plant tissues from freezing. Some strains are especially effective in the temperature range from −2°C to −5°C, while others are not effective until much lower temperatures (e.g. −19°C; Maki *et al.* 1974). The ecological and economic effects of this cellular death induced by low temperature are best known for crop plants, because of the economic damage wrought by a single night with unusually low temperatures. Thus, there has been an economic incentive for studies of mechanisms of frost resistance in plants, selection for adaptation to cold temperatures, and agricultural methods for minimizing frost damage (Bagdonas *et al.* 1978).

The most conspicuous effect of frost on plants is mortality from a "killing frost". The damage can be tissue-specific within a plant or specific to certain life stages. Buds, new leaves, and other rapidly differentiating tissues of woody plants are usually more susceptible than older tissues (e.g. stems, mature leaves), and although older leaves may be more susceptible than young ones in herbaceous dicotyledons, reproductive organs of all plants are usually most sensitive to frost (Sakai *et al.* 1981). At my high-altitude field site in Colorado, flowers and ovaries are often killed when older leaves are not affected. One interesting morphological consequence of bud mortality as a result of frost is removal of apical dominance by killing an apical meristem (Paige 1992), which could have consequent effects on plant architecture.

Frost can also have significant influence on plants through its effects on soil. It can be an important process in creation of soil (by breaking rocks), on creation of patterned ground, and in less organized soil disturbance. The primary consequence for plants of congeliturbation, the mechanical effects of frost on soil, is the instability of the matrix in which they are growing. The disruptive effects of needle ice in surface layers of soil, including both vertical (frost heaving) and lateral (frost thrusting) components, can generate significant mortality of seedlings (Regehr & Bazzaz 1979) and create patches of bare soil that are referred to as "frost deserts". The size sorting of mineral soil can generate patterned ground with polygons, nets, and strips (Washburn 1969), and consequent effects on plant distributions; such frost action is regarded as a primary physical factor in tundra plant communities (Sigafoos 1952).

Some effects of frost can be sublethal, and thus more subtle. Frost damage can become a site for infection of roots, petioles, buds or flower stalks (Haworth & Spiers 1992; Lederer & Seemuller 1992), and infection by one pathogen might then facilitate infection by another (Paul 1993).

EFFECTS ON ANIMALS

Direct effects of short-term frosts on animals are less well known than for plants. The endothermy of mammals and birds, and the ability of many animals to seek shelter from radiative heat loss, cold air drainage or cold air temperature in general probably explain this difference. However, frosts can still have significant effects for animal populations that depend on plants that have suffered frost damage. A few examples of this are recorded in the literature (e.g. examples described below), but I suspect that such secondary (and higher order) effects are more common than we realize.

Frost can result in widespread loss of food supplies for an animal species, either through killing the leaves that folivores need, or through loss of fruits or seeds. For example, frosts have been blamed for precipitous population crashes in voles (*Microtus montanus*) (Murray 1965). Insects may be especially vulnerable. Ehrlich *et al.* (1972) describe the catastrophic effects of a summer snowfall accompanied by hard frosts on a lycaenid butterfly species (at a high-altitude field site). The loss of lupine host plants and direct effects on the butterfly (*Glycopsyche lygdamus*) resulted in local extinction of the butterfly (which only recolonized after about 10 years). Thomas *et al.* (1996) reported a severe summer frost that killed host plants of another butterfly species (*Euphydryas editha*), causing the extinction of a source population in a butterfly metapopulation. In this case, the butterfly eggs and larvae were not directly affected by the cold but the larvae starved to death in the absence of the host plant (*Collinsia torreyi*). The frost killed 97% of host plants in one habitat and less than 1% of butterfly larval groups survived the loss (Singer & Thomas 1996). A year later, only a single egg cluster was found on the host plant at that site and it did not survive, and the butterfly population has still not recovered after 3 years (M.C. Singer, personal communication). Beck (1953) described an analogous situation in which host leaves of a psyllid (*Pachypsylla venusta*) were killed by frost, resulting in near extinction of the gall-forming species (at least locally in Georgia), and Lawson (1958) found that declines in aphid (*Myzus persicae*) populations could be attributed to low temperatures killing not the aphids but their host plants. An unusual frost event affected white oak trees in southern Missouri (U.S.A.) in the spring of 1997, and 200 species of herbivores that usually eat their leaves were almost absent after the trees put out new leaves (R. Marquis, personal communication).

Effects of frost on vertebrate animals via loss of food resources could also be relatively common, despite the paucity of reports in the literature. The ideal situation to study these effects would be to have a long-term database of population numbers, data on diet and availability of food items in the diet to examine the population before, during and after a frost event. The study by Nixon & McClain (1969) of a squirrel (*Sciurus carolinensis* and *S. niger*) population included most of these elements for 5 years before a frost that totally eliminated the seed crops of two oak (*Quercus*) species and beech (*Fagus*), most acorns of three other oak species, and seeds of 10 other species consumed by squirrels. The year of the frost the largest squirrel population in 5 years was recorded, but the next year estimated squirrel densities dropped to 17% of the previous year, and young of the year dropped to two from the previous year's 155 (breeding virtually ceased for a 15-month period). This study only reported data for 1 year following the frost, but it seems likely that it would have taken a few years for squirrel populations to recover fully. Other North American vertebrates, such as deer, bears and turkeys, which also consume many of the same seeds, would suffer the consequences of such frosts, as would insect consumers of acorns such as weevils. Sork (1993) found that late spring frosts were important in the temporal pattern of mast production of acorns, which suggests that the effect of frost on acorn consumers could be a relatively common phenomenon.

COMMUNITY-LEVEL EFFECTS

A hard frost will probably affect multiple species when it occurs, but not many community-wide studies have been conducted of frost effects. Nixon & McClain (1969) reported that following above-average temperatures in March and April, a frost on 10 May resulted in severe frost damage to 16 species of trees and shrubs in their study site in Ohio, many of which produce seeds eaten by mammals. In a long-term study of flowering in 14 permanent 2 m × 2 m plots near the Rocky Mountain Biological Laboratory in Colorado (2900 m altitude), U.S.A., I have documented frost effects on the community of herbaceous perennials in at least 7 of the past 26 years, with frost killing or damaging flower buds and open flowers (but causing minimal damage to leaves and stems). In 1985, more than 20 species of plants had already started to flower when a hard frost occurred on 27 June (Fig. 1). During the rest of that summer a peak of 25 species was in bloom on any one day, compared with 36 the next year (without a frost). On average only 13.6 species per plot flowered in 1985, *versus* 17.6 in 1986, and the peak number of flowers (totaling all species on each census date) per plot averaged 199 in 1985 and 311 in 1986. A similar pattern is seen for four other pairs of years in which there was a late frost in June in one of the pair (Inouye, unpublished data).

Regeneration of forests can also be affected by frost. For an oak species (*Quercus rubra*), the positive effects on seedlings of removing potential competitors was in some cases compromised by the increased negative effects of direct frost damage (increased radiative frost from removing the canopy) and browsing (Buckley *et al.* 1998). The increase in frost severity associated with land clearing in Australia is also impeding eucalypt regeneration (King & Ball 1998). The effect of frost may be subtle: sublethal frost effects can influence competition between tree seedlings and grass (Ball *et al.* 1997) and determine the spatial pattern of the regeneration niche (Ball *et al.* 1991) (Fig. 2).

LONG-TERM CONSEQUENCES

The consequences of frosts may extend over a period of years after the event; e.g. the declines in butterfly and squirrel populations described above. Since 1974 I have studied *Helianthella quinquenervis*, the aspen sunflower, and some of the consequences of frosts that kill its buds. The plant is a long-lived perennial endemic to the Rocky Mountains, has a mutualistic interaction with ants, and is preyed upon by four species of insect seed predators (Inouye & Taylor 1979). At intervals of 3–5 years since

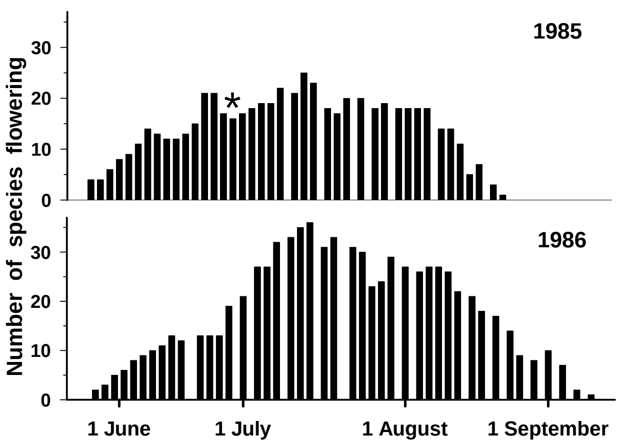

Figure 1 The number of species of plants flowering in (a) 1985 and (b) 1986 in 14 2 × 2-m plots at 2890 m near the Rocky Mountain Biological Laboratory, CO, U.S.A. There was a hard frost on 27 June (asterisk) in 1985, and no significant frost in 1986.

1974 the plants at mid-elevations (2900 m, at about the middle of the altitudinal distribution of this species) have suffered the consequences of late spring frosts (e.g. –7°C on 19 June 1985) that can kill some or all of the developing buds (Fig. 3). The seed predators then must seek other host plants to lay their eggs, and whereas flowering typically rebounds the next year, populations of the insects (tephritid and agromyzid flies, a moth, and their parasitoids) take a few years to recover. An unusually large number of seedlings may thus be established beginning 2 years after the frost. A similar effect of frost on insect communities has been reported for another composite, *Bidens pilosa* (Needham 1948). The interactions between the Dipteran seed predators and their parasitoids are also likely to be affected over multiyear intervals by these frost events. The potential for frost-induced damage or mortality of plants or flowers to provide a benefit in the long term, by reducing populations of seed predators or herbivores, does not seem to have been widely recognized. One reason might be the need for long-term studies to place the year of a frost into a context, as well as to follow events during the years following the frost.

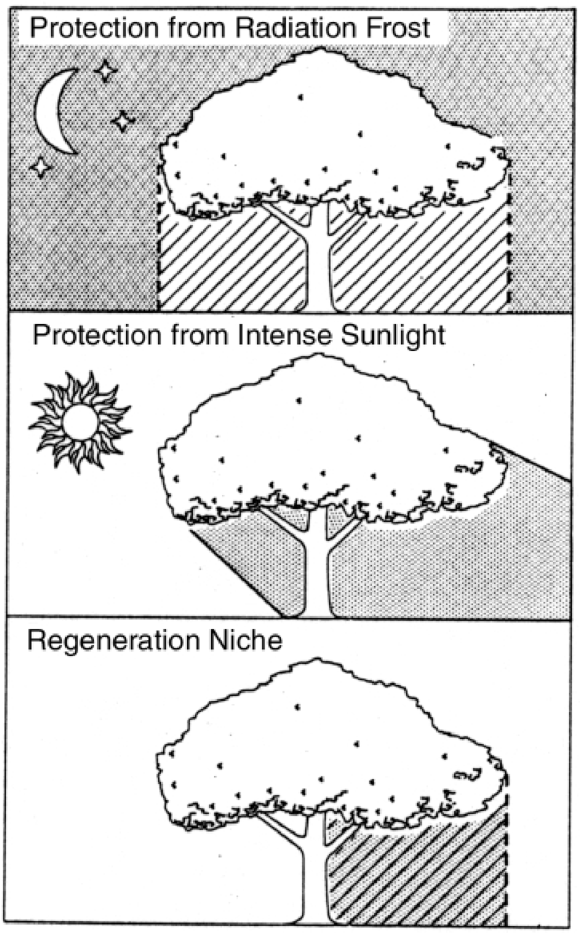

Figure 2 The additive effects of protection from radiation frost and from intense winter sunlight are consistent with observed asymmetry in the regeneration niche of the snow gum (*Eucalyptus pauciflora*) at tree-line in Australia. Reproduced from Ball *et al.* (1991), with permission.

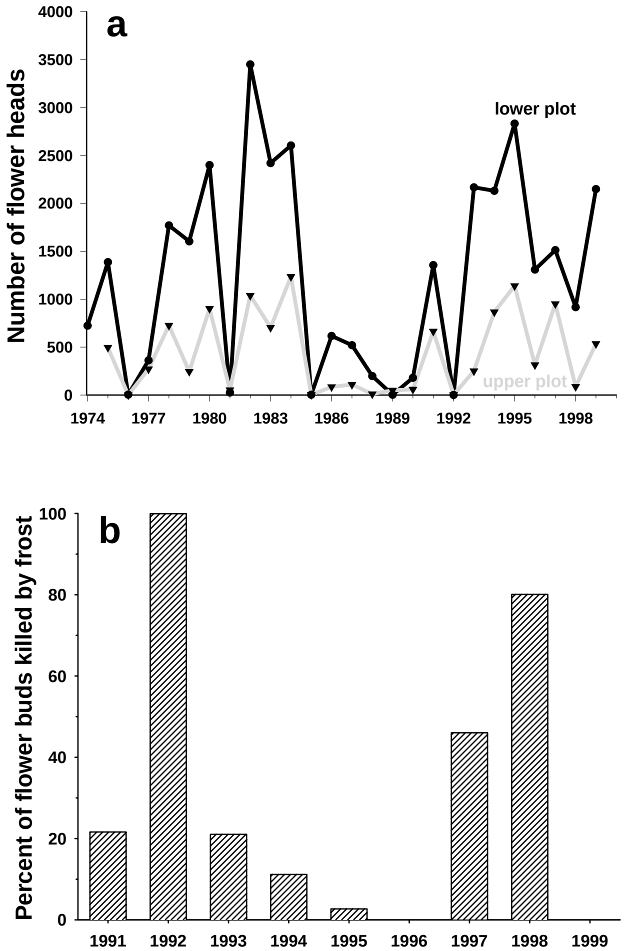

Figure 3 (a) The number of aspen sunflower (*Helianthella quinquenervis*) flower heads blooming in two plots (upper 10 × 36.5 m, lower 10 × 40 m; the upper plot is about 10 m above the lower) at the Rocky Mountain Biological Laboratory, CO, U.S.A. (b) The percentage of aspen sunflower (*Helianthella quinquenervis*) flower buds initiated that were killed by frost in the same plots shown in (a). Data from the lower plot only.

EVOLUTIONARY EFFECTS

Species that occur in habitats where frosts occur can migrate to other areas to avoid them, enter a dormant stage in order minimize damage, or adopt phenological, morphological or physiological traits that confer protection. Seasonality of growth, with a dormant state, is one method of avoiding frost damage, but delaying flowering in a temperate environment might increase the risk of frost damage at the other end of the growing season (Kudo 1993). A morphological trait as simple as flower orientation can generate differences in ovary survival of frost by up to 38% (Lu *et al.* 1992). Leaf area and shape can also evolve in response to exposure to radiation frost (Jordan & Smith 1995). A rosette growth form might allow plants to benefit from the microclimate close to the ground, and at high elevations in the tropics *Senecio* and *Lobelia* plants protect meristematic tissues from frost damage by the formation of "night buds" with outer leaves that fold inward by a nyctinastic movement (Beck *et al.* 1982).

The agricultural literature also points to inherited differences in frost resistance. Nybom (1992) studied damage to 129 apple cultivars following a spring frost in Sweden, and found almost no within-cultivar variation but highly significant among-cultivar variation in the percentage of frost-killed buds; late-flowering cultivars were least affected. In terms of phenology, plants that emerge or flower too early or too late in the season run the risk of frost damage if they have not evolved the ability to tolerate it but, in natural systems, selection for intraspecific variability of blooming dates could be important to ensure that some (late-flowering) individuals manage to reproduce even if frost kills most flowers.

The frequency of exposure to frosts will also play a role in the evolutionary responses species make to it. An unusual one-night exposure during the growing season will not generate the same responses as daily exposure during the winter. This kind of difference is probably responsible for geographical variation in response to frost seen in common gardens (Campbell & Sorensen 1973). Frost can also have quite different implications for selection depending on when it occurs during the year. For example, whereas spring frosts can affect growth and development, fall frosts might determine the success of fruit and seed production (Lee & Bazzaz 1982).

CLIMATE CHANGE AND FROSTS

Among the many potential effects of global climate change is the likelihood that the frequency and distribution of frost events will change. This is a complex issue because of the interacting effects of changes in temperature, precipitation, and CO_2 concentration, but the recently documented increase in the length of the growing season in Europe is one indication of a change that may result in more frequent spring frost damage to plants (Menzel & Fabian 1999). A change in climate accompanied by an increase in the frequency of late spring frosts has been recorded previously in Virginia, U.S.A., by Thomas Jefferson (Jefferson 1787 (reprinted 1982)) (Box 1).

Box 1. Thomas Jefferson was not only a politician but an astute observer of natural history in Virginia; his 1787 book *Notes on the State of Virginia* may be the first documentation of climate change and the frequency of frosts and points out the importance of both snow and fluctuation in temperature as factors interacting with the potential for frost damage.

"A change in our climate however, is taking place very sensibly. Both heats and colds are become much more moderate within the memory even of the middle-aged. Snows are less frequent and less deep. They do not lie, below the mountains, more than one, two or three days, and very rarely a week. They are remembered to have been formerly frequent, deep, and of long continuance. The elderly inform me the earth used to be covered with snow about three months in every year. The rivers, which then seldom failed to freeze over in the course of the winter, scarcely ever do so now. This change has produced an unfortunate fluctuation between heat and cold, in the spring of the year, which is very fatal to fruits. From the year 1741–1769, an interval of 28 years, there was no instance of fruit killed by the frost in the neighbourhood of Monticello. An intense cold, produced by constant snows, kept the buds locked up till the sun could obtain, in the spring of the year, so fixed an ascendency as to dissolve those snows, and protect the buds, during their development, from every danger of returning cold."

A few studies address how climate change might influence late spring frosts. For example, an experimental study of effects of elevated temperature and CO_2 concentration on a temperate tree species (*Betula alleghaniensis*) showed that the survivorship of buds following a simulated freeze was influenced by both CO_2 and temperature levels; plants grown at lower temperatures were not as freeze resistant as those grown at higher temperatures, but there was a significant interaction between CO_2 and temperature (Wayne *et al.* 1998). Effects on phenology will also be important. If global warming results in earlier flowering in temperate species, flowers might become more susceptible to frost damage. In an experimental study, warming *Papaver radicatum* plants in Greenland, Molgaard & Christensen (1997) found that plants protected by south-facing plexiglas screens started growth earlier in the season, flowered earlier and had more flowers, but they also had a higher risk of frost damage. Williams *et al.* found that peach trees induced to flower 2 weeks earlier suffered greater frost damage (Williams *et al.* 1992).

A complicating factor in making predictions about the effects of climate change on frost is the interaction between acid precipitation and other pollutants, such as ozone and frost hardiness (Jones 1992; Eamus 1993). Reflecting all this uncertainty, there have been predictions that the frequency of frost damage in the spring could increase in some temperate regions (Kimmins & Lavender 1992) or perhaps decrease in temperate and boreal zones

(Long & Hutchin 1991). It seems likely that altitudinal shifts in the occurrence of frost will also become important in mountainous areas, and that there may be latitudinal shifts as well. No matter what the future brings with regard to the frequency of frosts, given the potentially widespread, long-term and community-wide effects that they can have on plants and the animals and pathogens that interact with them, this will be an area worthy of additional scrutiny and experimental study by ecologists and evolutionary biologists.

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BIOSKETCH

David Inouye conducts long-term studies of flowering abundance and phenology, plant demography, insect abundance, and hummingbirds at a high-altitude field station (RMBL) in the Colorado Rocky Mountains; he is particularly interested in the effects of climate change in his studies.

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