CHAPTER - 2

REVIEW OF LITERATURE
Physiological tolerance and relative abundance

Permissive environmental temperatures and humidity are fundamental requirements for the survival of all ectothermic species. Species are experiencing changes in temperatures as well as local water availability due to recent global climate warming such changes are expected to accelerate with time (IPCC, 2007). Species can change their distribution and abundance pattern in response to climatic thermal and drought stresses (Robinson et al., 1997; Erasmus et al., 2002). In Britain, the distributions of many butterfly species have fluctuated over the past two centuries (Asher et al., 2001). Several studies have documented range expansion in insects to their high-latitude and high-elevation cool range margins (Warren et al., 2001; Hickling et al., 2006. Parmesan and Yohe, 2003 Parmesan et al., 1999) and retracting at their low-latitude and low-elevation warm margins (Anderson et al., 2008; Franco et al., 2006; Parmesan, 1996; Wilson et al., 2005). However, most species have evolved their ability to tolerate these adverse conditions which determines the fundamental niche of species (Addo- Bediako et al., 2000; Bradshaw and Holzapfel, 2008; Chown and Terblanche, 2007).

Physiological limits to climatic stresses determine susceptibility to environmental changes and can be assessed at individual, population or species level (Hoffmann, 2010). There is strong relationship between individual thermal physiology and latitudinal range in fourteen ecologically similar congeneres of European diving beetles (Calosi et al., 2010). Further, a significant correlation between heat resistance and average temperature have found across the range of distribution of different Drosophila species; and between heat resistance and humidity conditions in D. melanogaster (Bubily et al., 2012) but several other studies did not evidence such an association (Hoffmann et al., 2003; Sgro et al., 2010). In contrast, a combined role of temperature and precipitation has explained variation in the heat resistance of 94 Drosophila species (Kellermann et al., 2012a); and desiccation and cold resistance in 95 Drosophila species (Kellermann et al., 2012b). Evolutionary potential at population level is most directly measured by estimating the quantitative genetic variation for stress related traits (Roff, 1997). However,
most of the studies have focused on generalist widespread species but not on the distribution and abundance of endemic species.

**Water conservation in context of global climate change**

Water constitutes a large proportion of insect tissues and survival depends on the ability to maintain water balance in the body. Maintenance of water balance is a great challenge for insects and they have developed divergent strategies to cope with drought stress. In the context of global climate change, there is much focus on the effects of changing temperatures on organisms (Bale et al., 2002; Harvell et al., 2002; Parmesan, 2006; Helmuth et al., 2010. However, changing patterns of rainfall, humidity and water availability deserves similar attention for several reasons. Because variation in precipitation has profound effects on animals (Jetz and Rubsenstein, 2011) as well as insects (Andrewartha and Birch, 1954; Wolda, 1988) and it determines the range position of many species (Robinson et al., 1997; Erasmus et al., 2002; Lobo et al., 2006; Steiner et al., 2008; Vieites et al., 2009; Roura- Pascual et al., 2011). It is also a significant correlate of many species richness in areas (Erasmus et al., 2002; Hawkins et al., 2003; Algar et al., 2009; Chown and Klok., 2011) and thermal optimum is more strongly related to ambient precipitation than to average ambient temperatures (Clusella-Trullas et al., 2011) which also affects thermal preferences and performance (Bonebrake and Mastrandrea, 2010. Further, in the case of disease vectors with aquatic larvae, changes in water availability relate to alterations to run off and to the size and distribution of impoundments (Laffertey, 2009; Fung et al., 2011). Finally, much of the current and forecast global change includes very large direct (Fung et al., 2011) and indirect effects on both precipitation and water availability (Makarieva and Gorshkov, 2007). Thus, the physiological mechanisms underlying variation in the ability of insects to tolerate drought stress need to assessed in the context of global climate change.

**Physiological regulation and the components of water loss**

Insects show a wide range of responses to environmental variation from behavioral to physiological change. The sensing of changes in environmental conditions is the most critical step in the series of events leading to organismal responses and homeostasis (Woods, 2009). Identification of key hygrosensing sites and understanding of sensing ability of insects has typically been through antennal ablation and electrophysical studies of nerve impulse...
Hygrosensors are generally located on the antennal arista, and have been reported from numerous taxa, including caterpillars, bees, mosquitos, locusts, bugs, flies, stick insects, beetles and cockroaches (Altner and Prillinger, 1980; Tichy and Loftus, 1996; Tichy, 2003, 2007; Merivee et al., 2010). Two types of moisture receptors exist: moist receptors which increase firing rate frequency in response to higher humidity, and dry receptors that increase frequency in response to lowered humidity (Waldow, 1970; Yokahari, 1978; Tichy, 2003). Both the moist and dry receptors can be present in the same sensillum and can have markedly different sensing resolution. This dual system for moisture sensing enables insects to differentiate subtle changes in climatic humidity for microsite selection hence optimising their survival (Merivee et al., 2010).

Given the range of habitats insects occupy, interspecific variation in hygrosensing abilities is not unexpected. For example, the ground beetle *Pterostichus oblongopunctatus* is capable of discriminating relative humidity changes of as little as 2% in the dry receptor (Merivee et al., 2010), while perception of humidity change in *Periplaneta americana* is approximately half the resolution with responses to humidity in the order of 5% at the CNS (Nishino et al., 2003). However, the cellular mechanisms of humidity sensing have received far less attention than temperature sensing in insects (Chown and Terblanche, 2007), though these two senses may be strongly interlinked.

Besides the behavioral responses as physiological effects of environmental change (Huey et al., 2003), insects can respond to changes in water availability in several different ways i.e. changes in initial water content, rates of water loss (desiccation resistance) and tolerance of water loss (Hadley, 1994; Hoffmann and Harshman, 1999; Chown, 2002; Gibbs et al., 2003). Variation in these components of insect water economy among species and populations has given rise to the idea that adaptive responses will largely take place via them, although variation in desiccation tolerance is typically less pronounced than variation in the rates of water loss (Hadley, 1994; Addo-Bediako et al., 2001; Benoit and Denlinger, 2010), and in some cases among population variation may be negligible (Klok and Chown, 1998, 2000).

**Preadult stages**

The lacuna of previous comparative work on water loss is that, it has been restricted to the adult stages but preadult stages have received lesser attention. However, the immature stages,
and especially of holometabolous species, may be much more vulnerable to dry conditions than are the adults (Klok and Chown, 1998, 1999; Woods and Bernays, 2000; Woods and Harrison, 2001; Woods, 2010). Although an argument may be made that vulnerable immature stages encounter favorable conditions, extreme events can still have effects on these stages. These events may take several forms, such as anomalous high temperatures, which might increase ambient saturation deficit or reduce water availability in host plants, or biotically induced incidents, such as defoliation of an area during outbreak conditions, so limiting water available from host plants (Klok and Chown, 1999). Moreover, neonatal herbivorous insects may be exposed routinely to desiccating conditions as a consequence of host plant responses which may be geared to enhance desiccation stress to their benefit, but at a cost to the herbivores. In the context of changing water regimes forecast under global climate change, and especially increasing variation in rainfall, all of these topics, as well as the significance of the oxygen-water tradeoff in eggs and the role of microclimates and their change in affecting water loss, require further investigation (Woods, 2010; Fung et al., 2011; New et al., 2011; Sanderson et al., 2011). Thus, adaptability of the drosophila species to different climates can be estimated through assessment of physiological tolerance of preadult stages to stressful conditions.

**Role of cuticular hydrocarbons**

Several studies have demonstrated that water loss rate is the main factor accounting for variation in insect desiccation resistance, and that cuticular loss forms its main component (Chown and Nicolson, 2004; Benoit, 2010). The primary mechanisms underlying variation in cuticular permeability are the amount and composition of the water proofing components of the epicuticle lipids, mainly cuticular hydrocarbons (Edney, 1977). Increased compactness (amount), linearity and length (composition), and saturation of CHCs result in greater water retention properties. These characteristics vary both among species and within species exposed to varying drought conditions. However, in spite of these general patterns, variation in CHCs does not always conform to adaptive expectations, and may not solely serve a function for water conservation. In *D. melanogaster* and *Drosophila simulans*, although CHC length varies in a seemingly adaptive fashion, the absolute amount of cuticular lipids is generally not variable among geographical strains. In *D. melanogaster*, CHC composition varies adaptively with breeding temperature while *D. simulans* shows the opposite response (Rouault et al., 2004). The
sexes in *D. melanogaster* also show marked differences in the composition of CHCs while the genders of *D. simulans* are much more alike. Among multiple species of *Drosophila* (Gibbs et al., 2003) and among populations of *Glossina pallidipes* (Jurenka et al., 2007) the absolute amount and composition of CHCs vary inconsistently with environmental conditions. However, population level changes in CHC amount has received lesser attention in diverse *Drosophila* species.

**Plastic responses**

In response to changing environmental conditions, insects may either show the production of an alternative phenotype from a given genotype, or may show some other form of reaction to the environmental input. Such phenotypic plasticity has been widely discussed in insects (West-Eberhard, 2003; DeWitt and Scheiner, 2004; Chown et al., 2008; Whitman and Ananthakrishnan, 2009). It may promote or retard adaptation (Endler, 1986), and may itself evolve (Ghalambor et al., 2007). These are significant components of the response of organisms to change and have an influence on the extent to which plastic vs. fixed responses will evolve. (Chown and Terblanche, 2007; Whitman and Ananthakrishnan, 2009; Chevin et al., 2010; Hoffmann and Sgro, 2011). However, plastic responses are not especially well understood as far as water balance is concerned. Therefore, there is need to investigate plastic responses of the components of water loss to changing humidity and temperature regimes, and the extent to which the components of water loss might evolve in response to changing conditions.

**Desiccation acclimation (adult)**

For *Drosophila* species, responses to altered humidity levels can take place rapidly and are clearly reversible in the few instances where time-courses have been examined. A prior non-lethal period of exposure to low humidity of only a few hours markedly improves desiccation resistance (LT50 increases from <16 h to >19 h) in *D. melanogaster* (Hoffmann, 1990). These responses develop rapidly (within 2 h) and persist for more than a day after a 9 h exposure period. Moreover, genetic variation for acclimation ability to humidity also seems plausible, because desiccation-selected lines show weaker acclimation responses than unselected lines. Variation in these acclimation responses to desiccation has also been investigated in several *Drosophila*
species and populations from different environmental moisture regimes (Hoffmann, 1991). Acclimation responses to humidity are limited in a rainforest species, *Drosophila birchii*, while other, more widespread species (*D. simulans*, *Drosophila immigrans* and *Drosophila serrata*) are readily capable of acclimating to low humidity. However, *D. serrata* populations from different environments have similar acclimation responses and therefore it has been suggested limited geographic variation in acclimation ability exists in this species (Hoffmann et al., 2003). Tests of the extent to which alterations in water loss responses to changing humidity might be beneficial have recently been undertaken for tsetse pupae of species from mesic and xeric environments (Terblanche and Kleynhans, 2009). In this study, several major alternatives to the beneficial acclimation hypothesis (Leroi et al., 1994; Deere and Chown, 2006) were proposed and tested. Holding puparia of any of the species at low humidity (ca. 0%) for 10 days generally reduces water loss rates, typically by as much as 4-fold compared with saturated conditions. Nonetheless, the outcomes also showed several subtleties. For example, in the mesic *Glossina palpalis*, the deleterious acclimation hypothesis could not be rejected – the low humidity acclimation results in higher water loss rates on subsequent testing at low humidity (interpreted in this case as poorer performance). By contrast, in the xeric-adapted *Glossina morsitans* the ‘drier is better’ hypothesis could not be rejected. In the other related species, the optimal acclimation hypothesis (or possibly the beneficial acclimation hypothesis) and the drier is better hypotheses could not be rejected, suggesting that water balance responses to low humidity are adaptive across the entire genus (Bursell, 1959; Kleynhans and Terblanche, 2009).

**Rate of water loss**

Insects exposed to desiccating conditions tend to have lower water loss rates on a subsequent exposure (Appel and Rust, 1985; Hoffmann, 1990, 1991; Woods and Harrison, 2001; Terblanche and Kleynhans, 2009) and hence survive for longer under dry conditions (e.g. Hoffmann, 1990). For example, rearing *Manduca sexta* larvae on a low water content diet, reduces cuticular water loss rates, rather than altering body water content, excretion rates, faecal water content or other avenues of water balance (Woods and Harrison, 2001). A similar outcome has been found in the cockroach *Periplaneta fuliginosa* (Appel and Rust, 1985), which responded to the treatment by reducing cuticular permeability and faecal water content. In another cockroach species, *Nauphoeta cinerea*, chronic exposure (five weeks) to low humidity
conditions results in a ca. 10-fold reduction in rates of mass loss, accompanied by a reduction in duration of the discontinuous gas exchange cycle (Schimpf et al., 2009). While cuticular and respiratory water losses were not distinguished in the study, it seems likely from the data presented that water loss through both avenues is reduced. A recent study also demonstrated that rapid responses to desiccation in *D. melanogaster* are likely affected by reductions in cuticular water loss rates and not changes in respiratory water loss (Bazinet et al., 2010).

**Effect of temperatures on desiccation resistance**

In several species, water loss rates also respond to changes in temperature. For example, in *D. melanogaster*, summer-like acclimation conditions improve desiccation resistance (Hoffmann et al., 2005). Similar increases in desiccation resistance with exposure to elevated temperatures have been found in *G. pallidipes*, following acclimation of pupae or (Terblanche and Chown, 2006), and in the dung beetle *S. spretus*, with both cuticular and respiratory components contributing to the acclimation. By contrast, some studies have found little indication of acclimation responses with changing temperature. For example, in a desert-dwelling *Drosophila* species, high temperature acclimation does not alter desiccation rates although cuticular hydrocarbon chain length increases (Gibbs et al., 2003).

**Gaps in the studies on water balance**

Although much is known about insect water balance and the components thereof, the field continues to develop rapidly. These developments clearly have considerable relevance to understanding of the impacts of environmental change. The inevitability of respiratory water loss, and its likely increase given increased metabolic rates over the last several decades (Dillon et al., 2010; Woods and Smith, 2010) provide an example of the significance of recent work. Other areas also remain comparatively under explored, and particularly interactions between climate change drivers and how these might play out. Likewise, despite a call more than a decade ago for better understanding of the role of rainfall and humidity in diapause induction and termination (Tauber et al., 1998), these topics remain relatively poorly investigated, especially from a mechanistic perspective for insects from habitats that experience seasonal drought (Danks, 2000; Seymour and Jones, 2000; Pappas et al., 2008; Benoit, 2010; Benoit et al., 2010; Vinod and Sabu,
2010). Moreover, the mechanistic underpinnings of many of the responses continue to provide substantial evidence of cross tolerance or at least the similarity of responses to desiccation and other stresses (Chown and Terblanche, 2007; Denlinger and Lee, 2010). Insect responses have both costs and benefits, and understanding their interaction will continue to form an important component of understanding the significance of water balance physiology in an environmental change context.

**Starvation stress**

Individuals within many species must survive periods of starvation or exposure to suboptimal diets. Starvation resistance is an important trait related to survival in many species and often involves dramatic changes in physiology and homeostasis. As a consequence, positive selection for resistance to starvation stress is expected in localities where food is likely to be less abundant or temporally less reliable. When faced with nutritionally imbalanced diets, compensatory feeding for the limiting nutrient results in over ingestion of other nutrients, as is often seen when insects are confined to foods low in protein relative to carbohydrate (P:C) (Raubenheimer and Simpson, 1999). This may result in increased lipid storage and reduced fitness (Simpson et al., 2004; Warbrick-Smith et al., 2006). There is relationship between starvation stress, lipid proportion and survival in five recently caught *Drosophila simulans* populations.

Three mechanisms have been proposed to increase starvation resistance (Rion and Kawecki, 2007). First, greater accumulation of energy reserves, particularly lipid, may be stored (Hoffmann and Harshman, 1999; Hoffmann et al., 2005; Rion and Kawecki, 2007). Starvation-resistant insects may carry greater lipid reserves at eclosion (Aguila et al., 2007) or continue to increase their lipid reserves during early adulthood (Chippindale et al., 1996). However, Hoffmann and coworkers (2001) did not find any correlation between lipid content and starvation resistance among isofemale lines of *Drosophila melanogaster* derived from wild populations, either within or across populations (Hoffmann et al., 2001). Furthermore, Baldal et al. (2005) observed that raising *Drosophila* larvae under crowded conditions increased the adult fat content without improving starvation resistance. An alternate mechanism to increase starvation resistance may be to reduce the rate at which reserves are utilized. Evidence supporting this alternative is equivocal but may involve a reduction in energy expenditure (Rion and Kawecki, 2007). Drosophila lines selected for starvation resistance have also been reported
to show lower locomotor activity under some but not all conditions (Hoffmann and Parsons, 1993; Williams et al., 2004). A final mechanism that may, at least in theory, increase starvation resistance is the lowering of the minimal resources required for survival (Rion and Kawecki, 2007). Evolutionarily this may be expected to be disadvantageous, except under extreme conditions, because fecundity is likely to be reduced.

There is evidence for a positive relationship between stress resistance and longevity in D. melanogaster. Long-lived selection lines of D. melanogaster are often relatively more resistant to starvation and desiccation stress (Rose and Archer, 1996). In addition, long-lived mutants tend to be stress resistant (Lin et al., 1998) and selection for stress resistance can increase longevity (Rose et al., 1992; Hoffmann and Parsons, 1993; Baldal et al., 2006). However, there are multiple exceptions to the general trend that stress resistance is positively correlated with longevity (Force et al., 1995; Zwaan et al., 1995; Harshman et al., 1999; Archer et al., 2003; Vermeulen et al., 2006). We may consider three examples that illustrate variability in the relationship between stress resistance and longevity i.e. starvation resistance was initially accompanied by an increase in lifespan, but in subsequent generations further increase in starvation resistance was associated with a decline in longevity (Archer et al., 2003). Harshman et al. (1999) observed that one set of D. melanogaster lines selected for increased resistance to starvation, and showing increased resistance to a diversity of stresses, did not show a correlated change in longevity. In another study, lines selected for long virgin lifespan showed a decrease in starvation resistance (Vermeulen et al., 2006). Thus, starvation resistance seems to be a complex trait which might involve multiple mechanisms.

**Thermal resistance**

Tolerance of stressful (deleterious) temperatures is a major adaptation to thermally variable environments. All organisms are physiologically limited to a defined temperature range (Huey and Kingsolver 1993; Hoffmann et al. 2003). Temperature variation provides a good framework for testing predictions on the evolution of phenotypic plasticity because many traits are highly sensitive to changes in thermal conditions. In ectotherms, temperature is a key environmental factor that affects a large number of morphological traits as well as fitness traits (Roff, 2002). Evidence for habitat-specific thermal reaction norms comes mostly from studies comparing populations from contrasting thermal regimes (Cohet et al., 1980; Noach et al., 1996;
Morin et al., 1999; Trotta et al., 2006; Liefting and Ellers, 2008). Only a few studies compared the strength of phenotypic plasticity along a latitudinal cline (Robinson and Partridge, 2001; Gilchrist and Huey, 2004). The general expectation is that populations from colder habitats are more cold tolerant, whereas populations from warmer habitats are more heat tolerant. This expectation is often confirmed, suggesting geographic variation in temperature-mediated selection (Castaneda et al., 2004; Sorensen et al., 2005; Winne and Keck, 2005; Collinge et al., 2006). Thermotolerance does often vary across the life cycle (Lee and Denlinger, 1985; Kostal, 1994; Kostal and Simek, 1995; Krebs, 1999; Zani et al., 2005a; Terblanche et al., 2007), and this variation is often well explained by field thermal ecology (Evans and Brust 1972; Lee and Denlinger, 1985). In studies of geographic variation in thermotolerance, however, the selective forces that drive local adaptation are often inferred from average temperatures or geographic proxies such as altitude or latitude (Krebs and Loeschcke, 1995; Gibert and Huey, 2001; Hallas et al., 2002; Hoffmann et al., 2002; David et al., 2003; Castaneda et al., 2004).

Quantitative genetic analyses have revealed genetic variation for thermoresistance under laboratory conditions, but variation under natural conditions has rarely been identified (Hoffmann and Watson, 1993; Hoffmann et al., 2002). In a few cases selection responses within laboratory populations have been linked to specific candidate genes and physiological mechanisms (Krebs et al., 2001). Population comparisons have provided evidence for clinal variation in thermoresistance traits, although many studies lack power because only a few populations have been considered (Hoffmann and Watson, 1993). Clinal responses to cold extremes can involve changes in diapause strategies and altered patterns of reproduction. Inbreeding influences thermoresistance and acclimation responses, but inbreeding effects may be environment-specific. Species differences in heat or in cold resistance commonly match the geographical (climatic) distributions of species. Interspecific differences for heat resistance are usually smaller than for cold resistance. Drosophila species from the same location can differ markedly for stress resistance, and this may allow species to occupy different niches.

Recently observed increases in global temperature have been associated with shifts in the geographical distribution of a range of terrestrial and aquatic organisms (Root et al., 2003), and although geographical variation in physiological traits has been investigated in many ectotherms (Addo-Bediako et al., 2000; Hoffmann et al., 2005; Ghalambor et al., 2006), there are few examples of direct causal links between environmental temperatures and changes in species’
biogeography. During periods of rapid climate change, taxa that are unable to shift their geographical ranges (Bradshaw and Holzapfel, 2001) are particularly at risk from extinction (Pounds et al., 2006), especially if they cannot compensate physiologically. Consequently, we need to improve our understanding of the physiological mechanisms underpinning thermal tolerance limits and the acclamatory capacity of those limits, if we are to predict the direct impact of climatic warming on biodiversity (Chown et al., 2004). Arguably, estimating population and ecosystem level effects of climate change merely on the basis of large-scale patterns, without an understanding of organismal physiological responses, can result in erroneous predictions.
Table 2.1 Approaches for predicting and describing evolutionary responses to recent climate change in natural populations (Source- Hoffmann and Sgro, 2011).

<table>
<thead>
<tr>
<th>Approach</th>
<th>Outcome</th>
<th>Limitation</th>
<th>References</th>
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<tbody>
<tr>
<td>Longitudinal studies testing for genetic changes in populations</td>
<td>Where relationships among individuals are available or genotypes can be repeatedly sampled and tested in a common environment, changes can be partitioned into genetic and environmental components.</td>
<td>Requires longitudinal and relatedness data or common environment comparisons, only possible for some populations</td>
<td>Dahlhoff et al., 2008; Ozgul et al., 2009</td>
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<td>Spatial studies across climatic gradients involving transplants or common garden experiments</td>
<td>Indicates the relative importance of plastic and genetic contributions to variation along a gradient. Can be used to identify patterns of selection</td>
<td>May not indicate the speed at which adaptation occurs, patterns of local adaptation will depend on gene flow, transplants only possible for plants/relatively sessile organisms unless these can be confined</td>
<td>Ayrinhac et al., 2004; Etterson and Shaw, 2001</td>
</tr>
<tr>
<td>Standing quantitative genetic variation estimates within populations</td>
<td>Heritable variation reflects evolutionary potential.</td>
<td>Only possible for subset of species, evolutionary costs of adaptation are not commonly measured</td>
<td>Hoffmann et al., 2005; Visser et al., 2008</td>
</tr>
<tr>
<td>Quantitative genetic variation estimated through selection experiments</td>
<td>Species/populations with genetic variation respond to selection, others do not.</td>
<td>Can be slow, requires multiple generation selection experiments, only possible for a subset of species, intense artificial selection and laboratory adaptation may mean results are not reflective of processes in natural populations.</td>
<td>Hoffmann et al., 2003; Pulido et al., 2010</td>
</tr>
<tr>
<td>Experimental evolution in simulated environments</td>
<td>Populations exposed to conditions relevant to climate change indicate potential for selection, may include biotic interactions.</td>
<td>Can be slow across multiple generations, may reflect genetic variation in direction of selection, but target of selection can be unclear.</td>
<td>Collins and Bell, 2004; Van Doorslaer et al., 2009</td>
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<td>Evidence of loss of function of candidate gene/protein</td>
<td>Where function has been lost, may indicate fundamental limits and loss of evolutionary potential.</td>
<td>Depends on understanding the biochemical molecular basis of key ecological traits.</td>
<td>Somero, 2010</td>
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<tr>
<td>Genetic variation in candidate genes for traits pointing to potential for evolution</td>
<td>Where candidate genes control a substantial amount of the phenotypic variance in traits associated with climate adaptation, these might be directly assessed to indicate evolutionary potential.</td>
<td>Requires important candidates to be identified, applicable where phenotypic variation is controlled by major genes or their expression.</td>
<td>Larsen et al., 2007; Michalski et al., 2010</td>
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</table>
Genetic clines for stress related traits there is abundant evidence for genetic adaptation to climatic conditions varying in space rather than time, particularly in cases where transplant/common garden experiments have been carried out along environmental gradients

Table 2.2 Geographical variation for resistance to desiccation and starvation stress among populations of various Drosophila species.

<table>
<thead>
<tr>
<th>Stress type / Species</th>
<th>Clinal pattern</th>
<th>References</th>
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<tbody>
<tr>
<td><strong>A. Desiccation resistance</strong></td>
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<tr>
<td><em>D. melanogaster</em></td>
<td>temperate &gt; tropical</td>
<td>Parsons, 1980; Stanley and Parsons, 1981; Hoffmann 1991; Karan et al., 1998; Parkash et al., 2010; Parkash et al., 2012.</td>
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<tr>
<td><em>D. melanogaster</em></td>
<td>temperate = tropical</td>
<td>Da Lage et al., 1990</td>
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<tr>
<td><em>D. ananassae</em></td>
<td>temperate &gt; tropical</td>
<td>Karan et al., 1998</td>
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<tr>
<td><em>D. bipectinata</em></td>
<td>temperate &gt; tropical</td>
<td>Parkash et al., 1994</td>
</tr>
<tr>
<td><em>D. kikkawai</em></td>
<td>temperate &gt; tropical</td>
<td>Karan and Parkash, 1998</td>
</tr>
<tr>
<td><em>D. malerkotliana</em></td>
<td>temperate &gt; tropical</td>
<td>Parkash et al., 1994</td>
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<tr>
<td><em>D. pseudoobscura</em></td>
<td>No pattern</td>
<td>Coyne et al., 1983</td>
</tr>
<tr>
<td><em>D. serrata</em></td>
<td>No pattern</td>
<td>Hoffmann, 1991</td>
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<td><em>D. simulans</em></td>
<td>temperate &gt; tropical</td>
<td>Parsons, 1980; Hoffmann 1991</td>
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<tr>
<td><em>Z. indianus</em></td>
<td>temperate &gt; tropical</td>
<td>Karan et al., 1998; Parkash et al., 2008</td>
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<td><strong>B. Starvation resistance</strong></td>
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<tr>
<td><em>D. melanogaster</em></td>
<td>tropical &gt; temperate</td>
<td>Da Lage et al., 1990; Karan et al., 1998</td>
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<td><em>D. ananassae</em></td>
<td>tropical &gt; temperate</td>
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<td><em>D. bipectinata</em></td>
<td>tropical &gt; temperate</td>
<td>Parkash et al., 1994</td>
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<td><em>D. kikkawai</em></td>
<td>tropical &gt; temperate</td>
<td>Karan and Parkash, 1998</td>
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<td><em>D. malerkotliana</em></td>
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<td>No pattern</td>
<td>Hallas et al, 2002</td>
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<tr>
<td><em>Z. indianus</em></td>
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<td>Karan et al, 1998; Parkash and Munjal, 1999</td>
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<tr>
<td><em>D. birchii</em></td>
<td>tropical &gt; temperate</td>
<td>Griffith et al., 2005</td>
</tr>
<tr>
<td><em>D. takahashii</em></td>
<td>tropical &gt; temperate</td>
<td>Parkash et al., 2005</td>
</tr>
<tr>
<td><em>D. nepalensis</em></td>
<td>tropical &gt; temperate</td>
<td>Parkash et al., 2005</td>
</tr>
</tbody>
</table>
Table 2.3 Geographical variation for resistance to thermal stresses among populations of various *Drosophila* species.

<table>
<thead>
<tr>
<th>Stress type / Species</th>
<th>Clinal pattern</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. Heat resistance</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. melanogaster</em></td>
<td>tropical &gt; temperate</td>
<td>Hoffmann and Watson, 1993; Hoffmann et al., 2002</td>
</tr>
<tr>
<td><em>D. buzzatti</em></td>
<td>tropical &gt; temperate</td>
<td>Dahlgaard et al., 2001; Sorensen et al., 2001; Sarup et al., 2009</td>
</tr>
<tr>
<td><em>D. simulans</em></td>
<td>tropical &gt; temperate</td>
<td>Hoffmann and Watson, 1993</td>
</tr>
<tr>
<td><strong>B. Cold resistance</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. melanogaster</em></td>
<td>temperate &gt; tropical</td>
<td>Parsons, 1977; Guerra et al., 1997; Davidson, 1988; Hoffmann and Watson, 1993; Hoffmann et al., 2001; Bubily et al., 2002; Hoffmann et al., 2002.</td>
</tr>
<tr>
<td><em>D. melanogaster</em></td>
<td>No difference</td>
<td>Davidson, 1990; Mitrovski and Hoffmann, 2001.</td>
</tr>
<tr>
<td><em>D. simulans</em></td>
<td>temperate &gt; tropical</td>
<td>Parsons, 1977; Hoffman and Watson, 1993;</td>
</tr>
<tr>
<td><em>D. serrata</em></td>
<td>temperate &gt; tropical</td>
<td>Hallas et al., 2002</td>
</tr>
<tr>
<td><em>D. takahashii</em></td>
<td>No pattern</td>
<td>Kimura et al., 1994</td>
</tr>
<tr>
<td><em>D. lutescens</em></td>
<td>temperate &gt; tropical</td>
<td>Kimura et al., 1994</td>
</tr>
</tbody>
</table>
Plastic responses to environmental stress

Plastic responses to temperature variation can offer quick and effective means to cope with thermal stress, including, amongst others, rapid hardening and acclimation. Phenotypic plasticity, the ability of one genotype to express different phenotypes in different environments (Bradshaw, 1965); can be measured as the slope of a reaction norm (de Jong, 1990). Plasticity can be adaptive if it increases an organism’s fitness under a particular circumstance compared to organisms that are not plastic. Plasticity can also be nonadaptive if it results from a passive response to environmental conditions. Understanding how environmental variation may shape plasticity of a trait is not straightforward because the adaptive value of plasticity is different for fitness traits and nonfitness traits (Richards et al., 2006). For many traits that are not directly related to fitness, such as morphological or physiological traits, predictable environmental variation is known to select for increased phenotypic plasticity (Bradshaw, 1965; de Jong, 1995; Roff, 2002). On the other hand, fitness traits such as reproduction and survival should be stable despite environmental change because this will enable organisms to maintain high fitness levels across environments.

Seasonal adaptation in insects

Ectothermic insects encounter significant seasonal variations in the subtropical and Mediterranean regions; and are expected to cope with climatic stresses (Tauber and Tauber, 1981; Tauber et. al., 1998; Danks, 2007). Selection responses due to thermal conditions across seasons have evidenced changes in population genetic structure e. g. cyclic seasonal variations have been reported for chromosomal inversions in *D. pseudoobscura* and *D. persimilis* (Dobzhansky, 1948) and in *D. subobscura* (Rodriguez- Trelles and Rodriguez, 1998); for body size traits in *D. robusta, D. melanogaster* and *D. simulans* (Stalker and Carson, 1949; Tantawy, 1964); for body color in *D. putrida* (Sabath et. al., 1973); changes in the frequencies of melanic morphs in *Harmonia axyridis* (Tan, 1946); and associations between reproductive diapause and seasonal color changes in diverse insect taxa (Danks, 1987). The adaptive role of seasonal polyphenism due to plasticity has been shown in several species of butterflies (Brakefield, 1987; Brakefield and Reitsma, 1991; Kemp and Jones, 2001; Stoehr and Goux, 2008). Most of the seasonal field surveys have emphasized the role of thermal selection (Ritland, 1986; Brakefield, 1987) but also
rainfall in few cases (Brakefield and Reitsma, 1991; Roskam and Brakefield, 1999). In contrast, seasonal changes of body color dimorphism in females of *D. jambulina* are under selection due to humidity changes (Parkash et al., 2009). Thus, seasonal adaptations in insects might involve different mechanisms (phenotypic plasticity and/or genetic polymorphism) to cope with climatic stresses. Seasonal responses of insects to environmental signals and adaptations to survive under changing situations require detailed simultaneous analyses of natural environments that drive the patterns of response. Studies on long term analysis of habitat variability for a species are required to understand how seasonal adaptations are maintained and governed in a given species. Different species have different divergent strategies to survive changing environments in the same place. Therefore, multiple simultaneous experimental approaches are needed to identify the components of such strategies.